Beyond true navigation: Auxiliary navigational processes in the Manx shearwater



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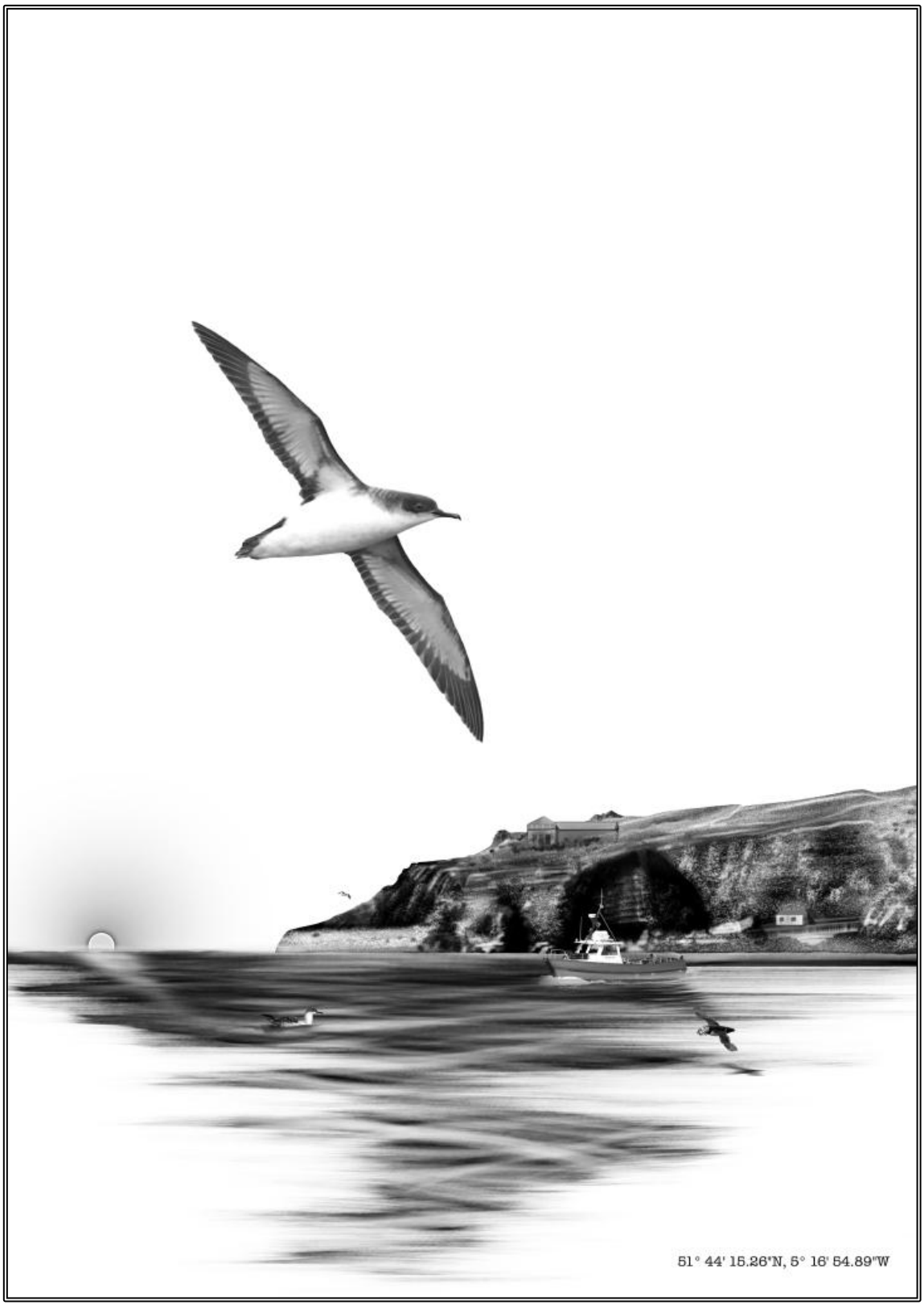


*Illustration by **Sam Beeston**, artist and friend.*

Abstract

The feat of animal navigation is particularly highlighted in avian taxa, who display well-orientated movements across all spatial scales. The processes underlying this orientation have been extensively studied in the central model of avian navigation, the homing pigeon. However, whilst this model, and the displacement paradigm established within it, have significantly advanced our understandings of these navigational processes, such findings cannot necessarily be generalised to wild navigators. Therefore, in this thesis I explore the navigational processes of the Manx shearwater (*Puffinus puffinus*), a Procellariform seabird renowned for its long-distance oceanic movements, using a long-term tracking dataset of free-ranging foraging trips to study navigation in an ecologically relevant context. I investigate the ability of Manx shearwaters to make efficient route decisions when faced with at-sea obstacles, at both vast and very fine spatial scales, and demonstrate that this appears to be achieved through learning. Additionally, I investigate the role of outward journey information in their free-ranging movements, which is actively denied in displacement procedures, finding evidence that aspects of these outward movements inform both their route decisions at sea and ultimate homeward orientation. Finally, I examine the role of topographical landmarks in their navigation, finding evidence that such landmarks may appear useful close to home, but that at larger spatial scales the likely hierarchical organisation of their navigational strategies makes such cues redundant. This thesis serves as an example for the insights that are to be gained from recontextualising navigation in the natural behaviour of avian species, moving beyond the experimental paradigms that have long dominated the field into exploration of such behaviours in free-ranging movements.

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The work presented in this thesis is primarily my own effort. However, this thesis makes use of a long-term tracking dataset which has been collected by a range of authors who deserve recognition for their efforts in the field. Furthermore, it is important to acknowledge the authors who assisted in the development of this thesis, whose contributions are detailed below:

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Chapter 1

General Introduction



Thank you to Ceris Aston, Freya Blockley, and Mari Elin Jones for the wonderful linocut shearwaters that open each chapter of this thesis.

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There are few phenomena in biology that capture the imagination quite like the ability of animals to navigate through our world. From an ant's successful relocation of its pin-sized nest entrance across a barren desert, to a seabird's capacity to cross entire ocean basins with extreme precision, this ability to accurately find one's way through vast and complex environments remains one of the most remarkable achievements of animal behaviour.

Navigation, in its broadest sense, refers to the processes by which an animal charts a course to a goal and directs its movements accordingly (Able, 2001; Etienne & Jeffery, 2004; Griffin, 1952; Schöne, 1984). It encompasses a range of processes and mechanisms, spanning from simplistic orientation responses guided by immediate sensory cues, to complex strategies that integrate the learning and memory of environmental features to locate oneself in space and direct an onward course (Wiener et al., 2011). Across taxa, these processes are expressed to enable animals to locate resources, return to breeding grounds, and migrate to distant wintering sites, often with extraordinary accuracy (Able, 2001; Gagliardo, 2013; Healy, 1998).

Of all animals, it is perhaps birds who best exemplify this feat of navigation, displaying well-orientated movements spanning across all spatial scales. From routine transhemispheric migrations (Alerstam, 1993), down to fine-scale foraging decisions (Healy & Hurly, 1998), birds demonstrate impressive navigational capabilities throughout a suite of ecological scenarios. This thesis, whilst drawing upon examples across the field of animal navigation, continues this investigation into the navigational processes of birds. Specifically, I aim to capitalise on the development of a new free-ranging, wild avian navigation model, expanding beyond the experimental displacement paradigm that has directed the field for decades (Gagliardo, 2013; Guilford & Biro, 2014; Papi et al., 1971; Wiltschko & Wiltschko, 2017).

A brief history of avian navigation

The processes that underpin animal navigation have been long questioned by natural historians, but until the mid-20th century these processes remained largely speculative. It was broadly accepted that animals were capable of orientation behaviour, this being the ability to respond to immediate stimuli and direct movements in relation to these: a caterpillar being attracted to the odours of its food plant, for example (Verschaffelt, 1910). 'True' navigation however (not to be confused with the contemporary phenomenon of True Navigation), involving higher-order processes such as map-like representations and route planning, was thought to be reserved only for human cognition, leaving the processes underpinning large-scale animal movements largely a mystery (Griffin, 1943; Putman, 2021; Tolman, 1948).

"Even if we grant to animals a sense of the points of the compass, of which there is no evidence, how can we account, for instance, for the turtles ... on the shores of the Isle of Ascension, finding their way to that speck of land in the midst of the great Atlantic Ocean?" – ***Charles Darwin, 1873, p.360***

Tolman (1948) argued that rats, in fact, were capable of learning map-like representations of their environments, rather than the array of stimuli-response connections previously attributed to their ability to solve maze tasks, which marked the introduction of cognitive processes into the study of animal navigation (O'Keefe & Nadel, 1978). During the same period, Griffin (1952) began to question the mechanisms by which long distance navigation was being achieved in wild animals, defining three types of orientation mechanisms – Type I: the reliance on visual landmarks within a familiar area; Type II: the ability to chart a course in a given compass direction independent of such landmarks; Type III: the ability to orientate towards a goal, irrespective of its direction, without the use of landmarks. Whilst inherently descriptive, as at this time little was known about the underlying mechanisms (Able, 2001), Griffin's type III navigation has

matured into what is now known as True Navigation and endures as one of the great mysteries in animal behaviour (Able, 2001; Bingman & Cheng, 2005).

While Griffin (1952) provided a conceptual framework for the categorisation of navigational abilities, Kramer evidenced the mechanistic foundations of these processes, structuring what has now become a central pillar in the modern study of animal navigation, the map-and-compass model (Kramer, 1953). Kramer supposed that an animal could only exhibit accurate homing orientation if it both knew where it was *and* which direction it needed to go, coining this as a two-part "map and compass" process (Able, 2001; Kramer, 1953, 1957; Putman, 2021). In this first 'map' step, using information available at their current locale, an animal is able to estimate its position in space relative to home (Kramer, 1953). In the second step, the animal uses a compass mechanism (a global indicator of direction; Guilford & Taylor, 2014) to determine the allocentric direction of this homeward bearing in space (Kramer, 1953). Although somewhat metaphorical, the separation of these two components of navigation is the most central paradigm in the study of avian navigation, evidenced by many studies showing manipulations that target each component independently of the other (Able, 2001; Gagliardo, 2013; Wiltschko & Wiltschko, 2023a).

The historic exploration of this map-and-compass model through such manipulations therefore required a subject tolerant to these, and it is within this paradigm that the homing pigeon, *Columba livia domestica*, emerged as a central model in the field of avian navigation (Wallraff, 2005a; Wiltschko & Wiltschko, 2003). Their well-developed homing instinct, coupled with their trainability and capacity for repeated experimental release made them uniquely suited to the experimental manipulations needed to further investigate the processes underlying avian navigation (Gagliardo, 2013; Holland, 2003; Wallraff, 2005a). Procedures which precluded a pigeon's ability to detect specific environmental cues (such as the denial of the olfactory sense through anosmia treatments), coupled with displacements that took them beyond their familiar area, became integral to the study of map-and-compass senses (Benvenuti & Wallraff, 1985; Gagliardo, 2013; Keeton, 1974; Wiltschko & Wiltschko, 2003).

The map-step

The map sense of mobile animals has been the subject of a huge number of research papers and much controversy (Gagliardo, 2013; Phillips, 2006; Wiltschko & Wiltschko, 2023b). To facilitate effective homing from a novel site, the prevailing view is that a candidate map cue must vary consistently over global (by globally, here I mean at least over the distance being navigated) scales such that an animal can learn (or inherit) how the gradient operates within its familiar area so that it can then extrapolate this when exposed to unfamiliar values following release (Wallraff, 1974, 2005b; Wiltschko & Wiltschko, 2023a). Despite agreement on the properties a cue must presumably have to be useful in this map-step, the structure of such a map is often informed by the author's view on the most likely cue candidate (Phillips, 2006; Wallraff, 2005a; Wiltschko & Wiltschko, 2023a). Gradients of intersecting cues that span global scales, such as those proposed in magnetic maps, could plausibly constitute to a global gradient map (Boström et al., 2012; Lohmann et al., 2022), whilst cues with more patchy local distributions, such as olfactants, may constitute a mosaic map of local cue ratios (Gagliardo, 2013; Papi et al., 1972). However, it is proposed that such cues could also form large scale gradient maps where specific environmental olfactants vary monotonically across vast scales (dependent on the regional distribution of atmospheric olfactants; Wallraff, 2005b; Wallraff & Andreae, 2000).

Research has thus far demonstrated limited evidence for the role of magnetic cues in the map-sense of birds, with findings constrained to sea turtles (Lohmann et al., 2012), salamanders (Fischer et al., 2001), spiny lobsters (Boles & Lohmann, 2003), and reed warblers (Chernetsov et al., 2017; Kishkinev et al., 2015). Olfactory navigation, conversely, has been widely demonstrated in the successful homing of pigeons (Gagliardo, 2013; Papi et al., 1971) and seabirds (Gagliardo et al., 2013; Padget et al., 2017; Pollonara et al., 2015), whilst also seeming to underpin migration in adult Gray Catbirds (Holland et al., 2009). Additional candidates for the environmental cues in these large-scale maps have been proposed, such as global variation in infrasound (Hagstrum, 2000) and the Earth's gravitational field (Blaser et al., 2014), but these have failed to gain substantial

evidence in avian models in comparison to olfactory and magnetic cues. Nevertheless, substantial disagreement remains between those who propose the use of magnetic and olfactory cues within this map process (Jorge et al., 2009; Phillips, 2006; Phillips & Jorge, 2014; Walcott et al., 2018).

At present, evidence suggests that the most plausible candidate for this map-sense in avian models (particularly in seabirds, the focus of this thesis) remains olfactory cues. First reported by Papi et al. (1971), it has been repeatedly demonstrated that anosmic individuals (those with their olfactory sense inhibited) display impeded homing compared to controls (Gagliardo, 2013; Gagliardo et al., 2013; Padget et al., 2017; Pollonara et al., 2015). Furthermore, in 'false release site' experiments, pigeons allowed to sample local air at one site, but who are then released from another orientate as though they are still at the air-exposure site (Benvenuti & Wallraff, 1985). These results suggest that olfactory cues can be used to inform a pigeon of its position in space, through the extrapolation of learnt olfactory gradients within a familiar area (Gagliardo, 2013; Wallraff, 1970). It has indeed been demonstrated that the learning of this olfactory landscape occurs whilst pigeons are in their loft and during localised flights (Gagliardo, 1997; Papi, 1991; Papi et al., 1973, 1989). Moreover, by deflecting the direction of winds entering the loft, follow up investigations showed predictable errors in the homing orientation of birds reared there, indicating a rotation in their learned olfactory maps (Baldaccini et al., 1975; Ioalé et al., 1978; Ioalè, 1980). Finally, it has been demonstrated that pigeons can incorporate artificial odours into these learnt olfactory maps, providing they are introduced through specific directions (Ioalè et al., 1990; Papi et al., 1974), highlighting that these birds readily associate environmental olfactants with directional information.

The compass-step

To be useful as a compass a cue needs to provide directional information globally (again, in the context of the distances covered by the animal). An example of such can be found in the night sky, where the stars, and their apparent rotation around the poles, provides a near global cue for both human and avian compasses (Mouritsen & Larsen, 2001). During the day, use of the sun is also possible but

only if an animal can account for the sun's horizontal movement clockwise around the sky as earth rotates, requiring an endogenous clock to maintain an expectation of the sun's position in the sky relative to the time of day (Guilford & Taylor, 2014). When Kramer proposed the map-and-compass model, he hypothesised that it was the sun that provided the directional information used in the compass step of the homing pigeon, and this was later shown to be the case (Hoffmann, 1960; Schmidt-Koenig, 1960). The sun compass is now marked as one of the primary orientation mechanisms used by homing pigeons (Guilford & Taylor, 2014; Matthews, 1953b; Wiltschko & Wiltschko, 2003), and other diurnal animals, allowing them to infer a compass bearing by judging the azimuthal position of the sun against their endogenous circadian clock (Kramer, 1953). Experimental manipulations to this compass, where birds are 'clock-shifted' using artificial light regimes to shift their internal clock, have confirmed the role of the sun in this 'compass' step (Guilford & Taylor, 2014; Padget et al., 2018; Schmidt-Koenig, 1960, 1990). Upon release at novel sites, birds deduce the correct homeward direction from their map but misjudge the position of the sun with regards to their altered clock and adopt an incorrect, but predictably deflected, homeward orientation (Schiffner et al., 2014; Schmidt-Koenig, 1960). These results demonstrate that the map-stage is unaffected by such treatments, reinforcing the idea that these 'map' and 'compass' steps operate independently (whilst also providing evidence against a mechanism proposed for 'complete sun navigation' by Matthews, 1955). In passerines, Emlen funnels, which were classically used to measure directional preferences in migratory birds (Emlen & Emlen, 1966), were adapted to allow for the investigation of various proposed compass hypotheses through the manipulation of suspected senses. This resulted in the discovery of avian compasses that employed both celestial (stars) and magnetic cues to derive directional information (Emlen, 1975; Wiltschko & Wiltschko, 1976). Indeed, later works have since demonstrated the presence of such alternative compasses that are also employed in pigeon navigation. Under cloudy skies, where the sun's position cannot be derived, it was proposed that pigeons appear to rely on a magnetic compass to act as an orientation reference (Keeton, 1971; Wallraff, 2005a; Wiltschko & Wiltschko, 2003, 2023b).

True navigation

Whilst Kramer was not explicit in what information may constitute to the map step, it is strongly suggested that this only refers to information obtained at the point at which homing begins (Able, 2001; Kramer, 1961). This suggests that, using only environmental information perceived at a far-off site, an animal could plausibly both deduce its position in space (the *map-step*) and direct its movements from here to a goal (the *compass-step*). In this, Kramer's map-and-compass navigation, and indeed Griffin's Type III orientation, are synonymous with the contemporary phenomenon of True Navigation, in which an animal can determine its position relative to a goal and chart a course to such from novel sites, without access to familiar or goal-associated cues, and without knowledge of the outbound route (Holland, 2014; Keeton, 1974; Phillips, 2006).

This ability has been widely reported in avian taxa, from passerines (Chernetsov et al., 2017; Holland, 2014; Kishkinev et al., 2015; Perdeck, 1958), to homing pigeons (Gagliardo, 2013; Matthews, 1951), and more recently, in Procellariform seabirds (Gagliardo et al., 2013; Matthews, 1953a; Padget et al., 2019; Pollonara et al., 2015). This ability also extends beyond birds, with evidence in bats (Holland, 2007), snakes (Pittman et al., 2014), eels (Naisbett-Jones et al., 2017), and lobsters (Boles & Lohmann, 2003).

It is important here though to distinguish the phenomenological definition of true navigation, as described above, from the mechanistic definition that defines true navigation as: **An adaptive mechanism for homing without outward journey information and goal emanating cues, that probably makes use of large-scale gradients with which an animal can compare currently perceived values to those learnt close to home, allowing them to chart a course between the two**. This definition is what this thesis will refer to when discussing true navigation, as it is the cognitive and mechanistic processes underlying this phenomenon which we are concerned with when investigating the navigation of free-ranging animals (Guilford & Burt de Perera, 2017; Padget et al., 2019, 2022).

Investigations of true navigation have largely focussed on the sensory basis of these large-scale maps, and how the learning of such gradients at a proximal scale could facilitate this homing ability from far-off sites (Boström et al., 2012; Gagliardo, 2013; Morford et al., 2025; Wallraff & Andreae, 2000). True navigation is likely to be underpinned through 'grid maps', which exploit the continuous and predictable gradients of salient environmental cues through space (Morford et al., 2025), such as the olfactants widely reported in pigeon navigation (Gagliardo, 2013). Central to this ability to then orientate from an entirely novel location, is the capacity to extrapolate the structure of these gradients from beyond the area within which they were learnt (Gagliardo, 2013; Wallraff, 2000, 2005b). It is in this extrapolation that the olfactory and magnetic map hypotheses endure over alternative strategies, as both are theorised to vary predictably through space and time (Boström et al., 2012; Gagliardo, 2013; Lohmann et al., 2007; Papi, 1991; Wallraff & Andreae, 2000). Therefore, even with variation in their resolution or source, such maps would allow for the extrapolation of spatial gradients acquired within an animal's familiar area to novel sites (Putman, 2021).

While an extrapolated map provides a plausible mechanism for an animal to home from a novel site, large scale gradients are unlikely to be able to provide sufficiently precise positional information for fine-scale navigation (see **Chapter 3**; Phillips, 1996; Wallraff, 2005a). Unlike human coordinate systems, which can theoretically achieve infinite precision, at fine spatial scales, adjacent positions within environmental maps may converge in their perceived gradient value, rendering them indistinguishable in composition within this grid map (Hagstrum, 2025; Komolkin et al., 2017; Mouritsen, 2018; Phillips, 2006; Wallraff, 2004, 2005a). Furthermore, shifts in gradients caused by winds or secular variation would make directional information increasingly unreliable at such fine scales (Komolkin et al., 2017; Wallraff, 2004). Therefore, we cannot expect that the position-fixing (map) process which underpins true navigation is generalisable to all navigational contexts. Indeed, there is evidence to suggest that a range of alternative processes operate in tandem with, and in absence of, these large-scale maps.

True navigation in a natural context?

When studying navigation in the wild, an emphasis on true navigation (typically investigated through displacement experiments) can obscure the fact that animals rarely move without access to information from their outward journey and usually explore only areas with which they are already familiar. Despite its power in revealing an array of mechanisms within avian navigation, the displacement paradigm invoked to investigate this true navigation ability has limited our inferences of how navigation operates in nature. The displacement of an animal to a site with which it has no experience through a procedure which explicitly denies the animal outward journey information, does, whilst providing insight into the mechanisms underpinning true navigation, make many other processes of navigation impossible. In the wild, it is implausible that an animal would ever arrive in such a situation as those induced during this displacement procedure, and so how navigational processes may be organised in natural avian navigation remains largely unknown (Demšar et al., 2025; Wynn & Liedvogel, 2023). When an animal displaces itself during free-ranging behaviours, it has access to information about the outward movements it made to facilitate that displacement (Padget et al., 2022). Furthermore, once an animal has explored the area which it inhabits, it is unlikely that it would find itself at an entirely novel location, and moreover if it did venture into unfamiliar terrain, it would have the information pertaining to the outbound movements it made to get there (Alvernhe et al., 2012; O'Keefe & Nadel, 1978; Savelli & Knierim, 2019).

Outward journey information

Whilst this true navigation displacement paradigm has demonstrated the ability of pigeons to home from unfamiliar sites without outward journey information, the use of such information has been widely demonstrated in the spatial cognition of animal exploration (Wehner & Srinivasan, 2003). By tracking its own egocentrically derived movements, either through idiothetic or allothetic signals, an animal can integrate a vector of its own displacement relative to a start point, through a process termed path integration. Path integration allows an animal to

successfully return to the start point (homing) without any other learnt representations of space and is widely reported in invertebrate and mammalian models (Etienne & Jeffery, 2004; Wehner & Srinivasan, 2003).

It may be argued that, if animals possess an allocentric representation of space (a map), then path integration is no longer required (Savelli & Knierim, 2019). However, this process has been proposed to act as a scaffolding for the learning of such spatial relationships, allowing animals to explore their environment from a central location and successfully return, whilst learning the allocentric structure of salient locations and encoding this cognitively (O'Keefe & Nadel, 1978; Savelli & Knierim, 2019; Müller & Wehner, 2010; Wiener et al., 2011). Furthermore, the continued integration of self-motion cues may allow for the maintenance of allocentric maps through the continual refinement of these internal spatial relationships (Biegler, 2000; O'Keefe & Nadel, 1978; Wiener et al., 2011). It has then been proposed that these allocentric maps may then maintain the accuracy of homeward vectors inferred from such path-tracking processes, in turn making them viable processes that may aid in the steering of homing behaviour (This is further explored in **Chapter 5**; Biegler, 2000; Etienne & Jeffery, 2004; McNaughton et al., 2006; O'Keefe & Nadel, 1978).

Despite these potential mechanisms that may facilitate the involvement of path integration, the involvement of such processes in the movements of avian species has received little investigation (Saint Paul, 1982). However, whilst not through path-tracking processes, the attention to outward journey information by pigeons during displacements is shown in several ways. Detours taken on the outward journey can lead to orientation errors upon release, termed the 'detour effect' (Papi et al., 1973, 1978), whilst the denial of outward olfactants can produce poorer initial orientation compared to controls (Baldaccini et al., 1982; Ioalé et al., 1983; Wallraff & Foà, 1981; Wallraff & Sinsch, 1988). Such results imply that olfactory information perceived on the outward journey affects the subsequent homing decision, even during passive displacements.

Landmark guidance

Although poor orientation is reported in anosmic or clock-shifted pigeons following displacement, each alluding to the disruption of their corresponding steps under a map-and-compass framework, this failure to orientate seems to only persist when birds are released at unfamiliar sites (Benvenuti & Wallraff, 1985; Bingman & Ioale, 1989; Biro et al., 2007, 2007; Filannino et al., 2014; Gagliardo et al., 2001; Guilford & Biro, 2014). When released from sites with which birds have previous experience, it is shown that the disorientation effects of such treatments largely subside (Armstrong et al., 2013; Bingman & Cheng, 2005; Biro et al., 2007; Filannino et al., 2014; Gagliardo et al., 2001; Guilford & Biro, 2014; Holland, 2003). This has been widely attributed to the availability and recognition of familiar visual landmarks, which provide stable spatial information that allows the bird to infer its position relative to home independent of the map and compass steps isolated in investigations of true navigation (Biro et al., 2007; Braithwaite & Guilford, 1991; Gagliardo, 2013; Holland, 2003; Meade et al., 2006).

Landmarks represent discrete features in the environment that are fixed in their position and so can be used to guide an animal's movements (Etienne & Jeffery, 2004; Kheradmand & Nieh, 2019). It should be noted here that whilst investigations into landmark use, and especially those concerning familiar-area navigation, often make reference to visual features, landmarks could constitute any environmental feature so long as it is positionally stable over time and salient, including features such as olfactory or auditory signals (Åkesson et al., 2014; Bonadonna et al., 2003; Hasler & Scholz, 1983; Rossier et al., 2000). Such landmarks can be theoretically used in a variety of ways, ranging from goal-associated waypoints to the construction of large-scale cognitive maps built upon the learnt allocentric relationships with landmarks encountered in space (which will be discussed further in **Chapter 6**; Able, 2001; Armstrong et al., 2013; Guilford & Biro, 2014; Toledo et al., 2020; Wiltschko & Wiltschko, 2017). Furthermore, landmarks may be critical in guiding homeward movements at very proximal scales, such as those close to home, where movements are made at a

scale plausibly smaller than the resolution large-scale gradient maps (Lohmann & Lohmann, 2006; Meade et al., 2005; Phillips, 1996; Schmidt-Koenig & Walcott, 1978; Wallraff, 2005a; Wiltschko & Wiltschko, 2015).

Route learning

Landmarks, and the spatial information they relay, can be further utilised in an area of familiarity to build idiosyncratic routes, which facilitate successful homing along previously rewarding paths (Guilford & Biro, 2014; Guilford & Burt de Perera, 2017; Meade et al., 2005). These routes may be learnt associatively, where routes adopted are associated with the reward of reaching a goal, and as such are reinforced cognitively (Guilford & Burt de Perera, 2017; Pearce & Bouton, 2001); or learnt latently, where cognitively primed modules detect and associate route stimuli without direct reinforcement (Wang & Hayden, 2021). These routes may prove particularly useful in complex environments, where additional navigational tasks, such as detours and circumnavigations must be overcome (Baron et al., 2015; Bonadonna et al., 1997). If gradient map processes were the only representations of space available to a navigator, meaning they could only represent their current location and their goal, then directional guidance could only manifest as a direct goalward beeline (Padget et al., 2019). This would mean that, when faced with an obstacle, such a navigator would have no reference with how to overcome this obstruction (Padget et al., 2019, 2022). However, we find that, particularly in areas of high experience, animals are capable of adopting efficient detour routes, indicating that they are in fact learning allocentric representations of space beyond those contained within true navigation processes (explored further in **Chapter 4**; Bonadonna et al., 1997; Guilford & Biro, 2014; Meade et al., 2005; Padget et al., 2022).

Pigeons to Procellariiformes

"Homing pigeons provide a reliable model for studying navigation and there's no reason to believe that other diurnal birds won't use similar methods … We mainly use pigeons for studies like this because we can be confident that they will bring back the GPS devices with the data." – ***Tim Guilford, 2014, University of Oxford News***

Through the breadth of experimental work, employing sensory manipulations and this well-established true navigation displacement paradigm, we have gained an understanding of, not only the multitude of navigational processes that operate within the pigeon model, but also how the spatial scale and familiarity of navigational tasks mediates the performance of these processes (Bingman, 2018; Gagliardo, 2013; Guilford & Biro, 2014; Wallraff, 2005a). However, as discussed previously, there are several navigational mechanisms that are inhibited through such displacements. Moreover, whilst serving as a candidate model for the experimental basis of navigational questions, the homing pigeon does not allow us to investigate the structure and organisation of these processes in the wild (Bingman, 2018). The homing pigeon has been bred for its navigational efficiency (Brinkman et al., 2025; Shao et al., 2020), and to remain highly sedentary to its loft, without the need for self-motivated trips in search of resources. It is fundamentally an artificially selected breed of a domesticated species, and as such we should be tentative when extrapolating findings from this artificial model to natural ecological contexts within which these birds no longer operate (Bingman, 2018; Wiltschko & Wiltschko, 2017). To contextualise this navigational behaviour in the wild, there has been a growing body of research into an impressive group of free-ranging avian navigators, the Procellariiformes.

Procellariiform seabirds must surely represent the most far-ranging avian navigators. During their breeding seasons many species make routine foraging trips that span hundreds, often thousands, of kilometres, before accurately pinpointing their colony and returning across open oceans (Bolton, 2021; Guilford et al., 2008; Nevitt, 2008; Phillips et al., 2007; Weimerskirch et al., 2002). Their

long lives presumably allow for the acquisition of vast spatial knowledge throughout these foraging areas, allowing for the operation of numerous plausible processes and the formation of underlying cognitive structures to facilitate navigation across spatial scales. Once more, these processes, and their organisation within a procellariiform's navigational toolkit, have been selected for under natural pressures, making them an opportune model to investigate this behaviour in the wild. Their long-ranging abilities have drawn the attention of researchers for decades, and, whilst peripherally, they have formed a part of the wider investigation into avian navigation for almost as long as the homing pigeon (Lack & Lockley, 1938; Massa et al., 1991; Matthews, 1953a).

In 1953, dissatisfied with the evidence at the time supporting the existence of 'true' navigation in avian models, Matthews sought to provide an unequivocal example of such a faculty, capitalising on the long-distance capabilities of Procellariiformes to push the bounds of navigational investigations (Matthews, 1953a). No doubt inspired by previous displacements of this species (Lack & Lockley, 1938), Matthews displaced Manx shearwaters, *Puffinus puffinus*, from their island colony of Skokholm, Pembrokeshire, to inland sites across the British Isles which were entirely novel to these seabirds, and found that upon release they were well orientated towards Skokholm, returning home with notable efficiency (Matthews, 1953a). Even a bird displaced to Boston, Massachusetts, showed an impressive return, traversing the Atlantic Ocean in just 12 days (Keeton, 1974; Matthews, 1953a). These recordings demonstrated the navigational prowess of Procellariiformes and impressively were made with nothing more than a pair of binoculars and a compass (Matthews, 1953a). It is then of no surprise that the recent advances in miniature tracking technology have granted us the capacity to quantify far more nuanced insights into the navigational strategies operating within the highly pelagic and wide-ranging movements of these species (Bingman, 2018; Demšar et al., 2025; Guilford et al., 2011).

Procellariiform seabirds, the 'tubenose' seabirds, are well-known for their olfactory sense and enlarged olfactory bulb (Bang & Cobb, 1968). They are

sensitive to dimethyl sulphide, which they use to guide their movements towards areas of high oceanic productivity (foraging patches) through plume following (Dell'Ariccia et al., 2014; Nevitt, 2008; Nevitt et al., 1995; Nevitt & Bonadonna, 2005). This sensitivity to environmental olfactants led to the proposal that, much like the homing pigeon, olfactory cues may also provide the spatial information necessary for efficient homeward orientation within their pelagic environments (Nevitt & Bonadonna, 2005). Through the coupling of modern GPS tracking technology with pre-established olfactory deprivation displacements, Gagliardo et al. (2013) demonstrated that the successful navigation of Cory's shearwaters, *Calonectris borealis*, across large spatial scales required access to olfactory cues, supporting the existence of analogous olfactory maps in a wide-ranging pelagic species. Such displacements were then carried out on a range of shearwater species (Dell'Ariccia & Bonadonna, 2013; Padget et al., 2018, 2022; Pollonara et al., 2015; Shiomi et al., 2019), demonstrating not only their navigation abilities, but also their high tolerance to, and motivation to home following, displacement experiments. These findings established them as a candidate group for the investigation of navigational questions in natural contexts.

Despite their suitability for experimental paradigms such as displacements and sensory inhibitions (Gagliardo et al., 2013; Matthews, 1953a; Padget et al., 2017), what truly distinguishes these seabirds as candidates for the study of wild navigation is the vast scales with which they routinely navigate in free-ranging movements. GPS tracking of their natural foraging trips allows us to not only quantity previously elusive at-sea behaviours (Dean et al., 2015; Guilford et al., 2008), but also investigate their subsequent homing behaviour from these far-off sites, that spans across a range of spatial scales at which different processes may be operating (Bingman & Cheng, 2005; Demšar et al., 2025; Mouritsen, 2018; Reynolds et al., 2015).

Such a range of navigational processes, and associated route decisions, can all be found within a single foraging trip of a free-ranging Manx shearwater (see **Figure 1.1**). Therefore, through the careful analysis of a culmination of decades

worth of tracking effort, coupled with displacement experiments operating at very fine scales, this thesis aims to further investigate the range of processes that may underpin shearwater navigation throughout their natural movements, beyond those previously centred in the historic study of true navigation.

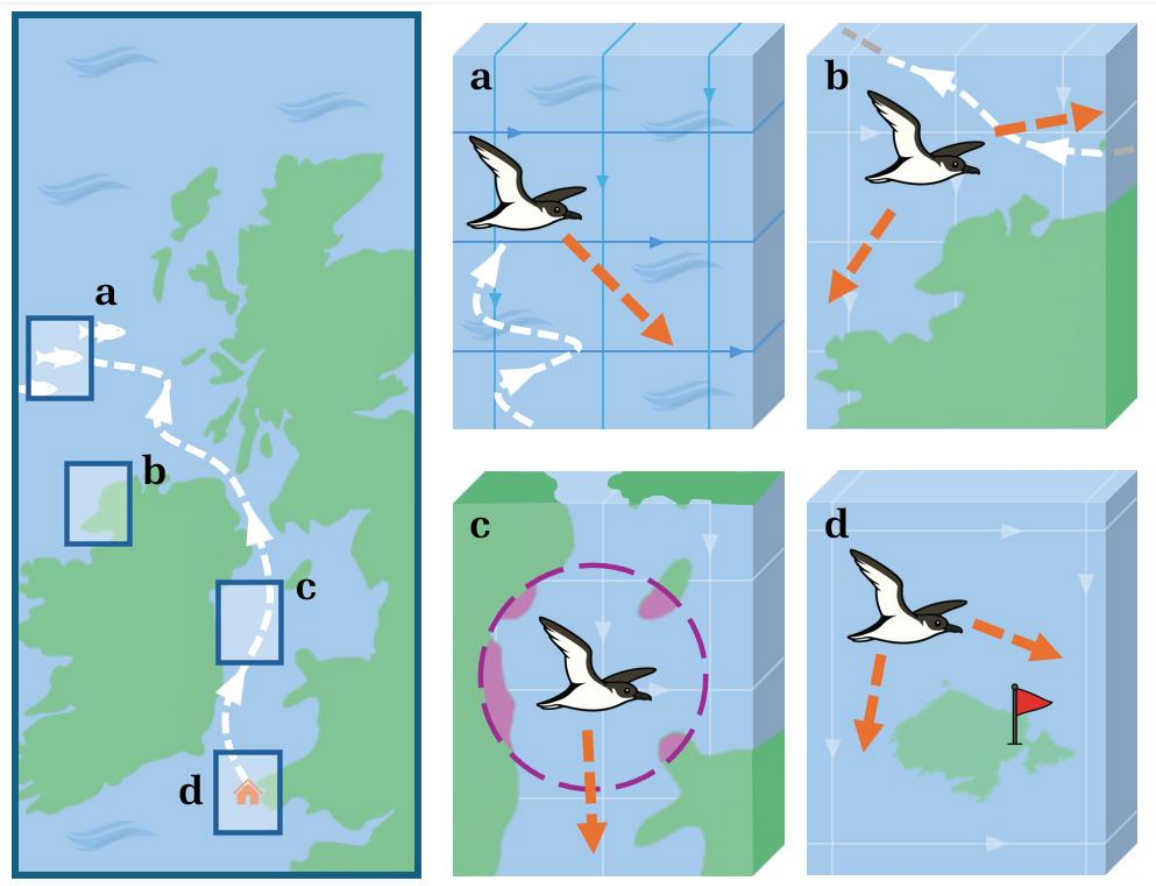


Figure 1.1. The range of navigational contexts a Manx shearwater may experience in a single free-ranging foraging trip. This shearwater embarks on a long outward journey (white track) to reach far-off foraging sites in the North Atlantic, and, once satiated, **a)** begins homing from this pelagic location without the reference of any familiar landmarks, likely using true navigation to chart a beeline course (with the potential aid of outward journey information). But this beeline is blind to obstacles (Padget et al., 2019) and **b)**, once they are encountered, the shearwater must choose a route around them, drawing upon recent and prior experience. Once past this obstacle and in the Irish Sea, **c)**, a suite of coastal topographic features becomes available to our shearwater, potentially aiding orientation. When almost home, **d)**, these movements operate at a spatial scale plausibly finer than the resolution of any available grid maps and so route guidance may switch to learnt routes and locally mediated signals.

Thesis aims and chapter summaries

This thesis aims to investigate the auxiliary mechanisms of navigation in the Manx shearwater, beyond those examined in true navigation. Through such investigations, I aim to demonstrate the utility of free-ranging, ecologically relevant, tracking data in the study of natural navigation. This thesis comprises four data chapters formatted as self-contained manuscripts for publication, each containing its own introduction, methods, results, and discussion. Each data chapter has been co-authored by collaborators but in all cases, the work presented is primarily my own. **Chapter 3** is in submission at the *Journal of Experimental Biology*. **Chapters 4**, **5**, and **6** are *in prep* for submission at peer-reviewed journals.

Since all data chapters make us of a long-term Manx shearwater GPS tracking dataset, I use **Chapter 2** as an introduction to this data, detailing the processing that occurred prior to the analyses within this thesis. In this I present the on-going tracking efforts of the Oxford Navigation Group, including the range of shearwater colonies monitored and tracked as part of this project, and the advancements in miniature tracking technology that have facilitated this data collection. This chapter will serve as a foundation to all subsequent data chapters by illustrating the filtering, interpolation, and data selection that occurred prior to the analyses carried out in this thesis.

True navigation has captivated the field of navigation for decades and is likely underpinned through large-scale map representations of predictable gradients through space. However, there is presumably a limit to the spatial resolution that such cues can provide (Wallraff, 2004, 2005a). This means that at very fine scales, movements must surely be guided by alternative mechanisms. Hence, in **Chapter 3** I use a displacement paradigm, coupled with the reluctance of Manx shearwaters to fly over land, to force a fine-scale route choice that could not be resolved with true navigation alone. I find that, even at such proximal scales, these birds are able to make optimised route choices, highlighting their navigational capabilities at an often-overlooked spatial scale. I then discuss how

different frameworks of learning could have plausibly facilitated the encoding of such fine-scale route optimisations.

A course chartered using only true navigation would be blind to any intervening obstacles (Padget et al., 2019). Yet, we see that during their natural movements, shearwaters make efficient route decisions when faced with such obstacles during homing (Padget et al., 2022). As in **Chapter 3**, this is likely to be facilitated through learning. Therefore, in **Chapter 4**, using the natural variation of obstacles encountered in the long-term database available in this thesis, I investigate the potential drivers of this learning in shearwater free-ranging movements. I find that a shearwater's likelihood of adopting the optimum circumnavigation route is greater when it has more experience with the obstacle, and when the cost of adopting the longer alternative increases. Furthermore, it seems that the circumnavigation route adopted during the outward journey could provide additional context to this route decision during homing.

True navigation, and the displacement procedures employed to study it, actively deny the use of outward journey information. Yet, wherever outward journey information has been explicitly studied, its role in the spatial cognition of exploring animals has been demonstrated (Wehner & Srinivasan, 2003). Whilst the use of path-tracking processes in long-distance movements is often disregarded, there are several theoretical mechanisms that could facilitate their use, such as the simultaneous integration of spatial information derived from landmarks (Biegler, 2000). In light of this, in **Chapter 5** I explore the potential role of outward journey information in the homing behaviour of free-ranging shearwaters. I find that, contrary to prior investigations, properties of outward movements, such as tortuosity, influence the accuracy of subsequent homing behaviour, in line with expectations of path-tracking processes. However, the ultimate successful homing of these birds, coupled with the relatively small observed deflections, suggest that this path-tracking is not the only guidance available to these birds, and from this I discuss the likely hierarchical organisation, and redundancy, of mechanisms within a shearwater's navigational toolkit.

Visual landmarks represent stable sources of allocentric positional information and are used in navigation across taxa (Guilford & Biro, 2014). Indeed, shearwater species have been shown to use topographical landmarks to guide their homewards movements, although this has only been demonstrated after the induction of anosmia (Pollonara et al., 2015). It is in **Chapter 6** that I therefore look for evidence of landmark guidance in free-ranging, unmanipulated, movements of both Manx (*Puffinus puffinus*) and Balearic (*Puffinus mauretanicus*) shearwaters. Despite the breadth of data, and investigations into several plausible cases of landmark use, I find little evidence of landmark availability mediating improvements in the accuracy of homing behaviour. I then discuss these results in light of the evidence of landmark use in anosmic shearwaters, which again suggests an underlying hierarchy to the navigational mechanisms a shearwater likely possesses.

Finally, in **Chapter 7** I summarise the findings of these data chapters, synthesising their results and integrating them within the broader literature of animal navigation. I suggest future directions for the field and highlight the insights that can be gained from investigating navigation within free-ranging movements as opposed to the true navigation displacement paradigm that been readily evoked in experimental studies.

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Chapter 2

General Methods: A data-driven approach to the study of free-ranging navigation



With thanks extended to the contributors of the long-term Manx shearwater dataset, as well as all island wardens, staff, and volunteers who continue to facilitate this work.

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Abstract

For the past two decades the OxNav research group have been deploying biologging devices on free-ranging adult Manx shearwaters in an attempt to uncover the unseen behaviours and spatial distribution of their wide-ranging pelagic movements. These devices have ranged from position-fixing loggers, such as GPS and miniature GLS, to those which quantify body position and orientation, including accelerometers and time-depth recorders, even employing mountable cameras to get a shearwaters-eye perspective of life at sea. In particular, this GPS tracking gives us the opportunity to quantify not only the space-use of these long-distance foraging behaviours but also the navigational performance of these birds when they make the decision to home. Through the nuanced analysis to these homewards movements, we can gain an insight into the cognitive processes that underpin their natural navigation across spatial scales, by quantifying the route decisions and homeward accuracy displayed by birds in a range of navigational contexts. All chapters of this thesis apply such analyses to this ongoing long-term GPS tracking dataset of breeding Manx shearwaters throughout the British Isles. This methodological chapter will serve as a general introduction to this dataset, detailing the breadth of GPS tracks it contains, the innovations in tracking technology that arose throughout this project, and how the available movement tracks were filtered and prepared prior to the analyses carried out in this thesis. Finally, it will present the available dataset of free-ranging Manx shearwater movements that have been analysed in this thesis, representing the largest repository of Manx shearwater tracking data to date.

The Manx shearwater

The Manx shearwater, *Puffinus puffinus*, is a ~400 g Procellariform seabird that is near-endemic to the British Isles (Brooke, 1990). During the breeding season (approximately May – September), these birds are faithful to their nest (burrow), and are central place foragers, routinely travelling hundreds of kilometres to pelagic foraging sites (Dean et al., 2015; Guilford et al., 2008). Shearwaters show high inter-annual fidelity to marine foraging sites, and individuals are consistent in their use of core foraging areas both within and between years (Dean et al., 2015; Jaggers, 2023). At the onset of homing, shearwaters show remarkable accuracy in their homeward movements (Padget et al., 2019). It is probable that Manx shearwaters, as seen in other Procellariiformes, use olfactory cues for broad-scale search behaviour (Kane et al., 2020), and their central eye placement and binocular vision supports the use of visual guidance (Darby et al., 2022; Lucas et al., 2024; Martin & Brooke, 1991). Shearwaters are well adapted to pelagic flight. Their wing morphology allows them to exploit at-sea vertical wind gradients (the shear layer) through shear soaring flight (Harris et al., 2025; Kempton et al., 2022). Whilst these adaptions allow for efficient flight over water, these long wings make flight more costly over land, and their back-set legs make take off difficult from the ground, putting them at risk of predation if they land (Brooke, 1990). As such, shearwaters routinely avoid flying over land, except at night to visit their nest (Brooke, 1990; Padget et al., 2019).

Recent work has shown that, like in other Procellariiformes, differences in reproductive roles between Manx shearwater sexes results in divergent foraging behaviour during the pre-laying period (April; Siddiqi-Davies et al., 2025). At this time, females travel further south towards the continental shelf and Bay of Biscay, whilst males remain close to the colonies (Siddiqi-Davies et al., 2025). After egg laying however, parental care is split roughly equally between the sexes (Brooke, 1990; Gillies et al., 2021), and the spatial divide between sexes disappears, with both sexes utilising the same foraging areas (Siddiqi-Davies et al., 2025). During incubation partners alternate stints of incubation and foraging (Gillies et al., 2021; Padget et al., 2018), whilst during chick-rearing both partners alternate

between short and long foraging trips, associated with chick and self-provisioning respectively (Gillies et al., 2022; Tyson et al., 2017). Following breeding, they embark on transhemispheric migrations, spending the winter off the coast of Argentina on the Patagonian shelf (Brooke, 1990; Guilford et al., 2009). These shearwaters are able to both adjust the timing of their migration to compromise between the completion of breeding and resource availability at the wintering site (Siddiqi-Davies, Wynn, Padget, Bond, et al., 2024), whilst also altering this wintering location in response to climatic conditions (Siddiqi-Davies, Wynn, Padget, Lewin, et al., 2024).

Deployment history

Beginning on Skomer Island, Wales, in 2004, the OxNav Manx shearwater tracking project now spans six colonies, with over 1,500 GPS devices deployed by the team in the past 20 years. The six colonies included within this dataset are as follows: Skomer Island [51°44'14.7"N, 5°16'55.6"W], Skokholm Island [51°41'37.8"N, 5°17'13.9"W] and Ramsey Island [51°52'26.6"N, 5°20'0.8"W], South Irish Sea, Wales; Lighthouse Island [54°41'43.0''N, 5°15'3.9''W], Copeland Islands, Northern Ireland; Rum [56°59'23.1''N, 6°17'11.0''W], Hebrides, Scotland; and Lundy [51°10'6.7''N, 4°40'32.5''W], Bristol Channel, England (**Figure 2.1**). The majority of GPS data within this tracking project has been collected on Skomer Island and Copeland (Lighthouse) Island (**Figure 2.2**), whilst other islands included in the tracking project are either more recent additions to the projects or are visited more sporadically (**Table 2.1**). Through collating and integrating this historical dataset into one bank of data, a total of 1,533 raw GPS files were available for processing in this thesis by the end of the 2024 field season. Whilst data collection across these islands is on-going, and indeed expanding, the dataset presented in this thesis will be capped to 2004-2024.

GPS devices were deployed on breeding adult Manx shearwaters, either during their incubation period (May-June), or chick-rearing period (July-August). This means that, as these were archival devices that must be physically retrieved for

the data to be downloaded, GPS devices could be deployed with high certainty that each individual will return to a known location following its foraging trip(s) for device retrieval. This also allowed for the close monitoring of breeding success and impact both during the deployment period and in the window following device retrieval. Whilst sex is determined in some colonies, such as Skomer, as part of the long-term monitoring efforts, the sex of GPS deployment candidates is not routinely assessed. Similarly, the age of birds is largely unknown within this dataset. Adult Manx shearwaters begin breeding at approximately five years old (Brooke, 1990), and unless they were ringed as a chick in their first year, discerning their age is not possible. Whilst in recent years known-age birds have been targeted for GPS deployments at the Copeland colony where historic ringing has created a decent proportion of breeders originally ringed as chicks (Padget et al., 2022), overall, too few tracks of known age birds exist in the extant dataset to be the focus of any of the analyses here. Therefore, neither age nor sex were used to identify candidates for GPS deployments, and these metrics were not carried into any analyses within this thesis. Instead, aspects such as burrow accessibility and location were the primary inclusion criteria for GPS candidates.

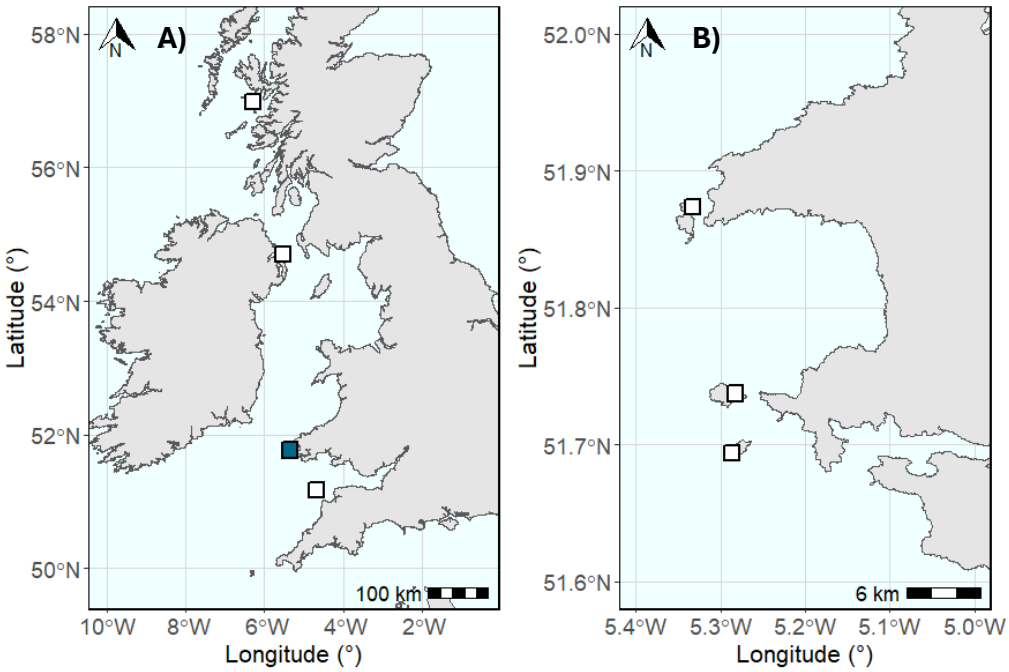


Figure 2.1. Maps displaying the locations of all shearwater colonies tracked within this dataset. Map **A**) shows the colonies across the UK, the blue point marks the colonies within the Pembrokeshire islands and are displayed in map **B**). From North to South, these colonies are Rum, Copeland, Ramsey, Skomer, Skokholm, and Lundy. See text for colony coordinates.

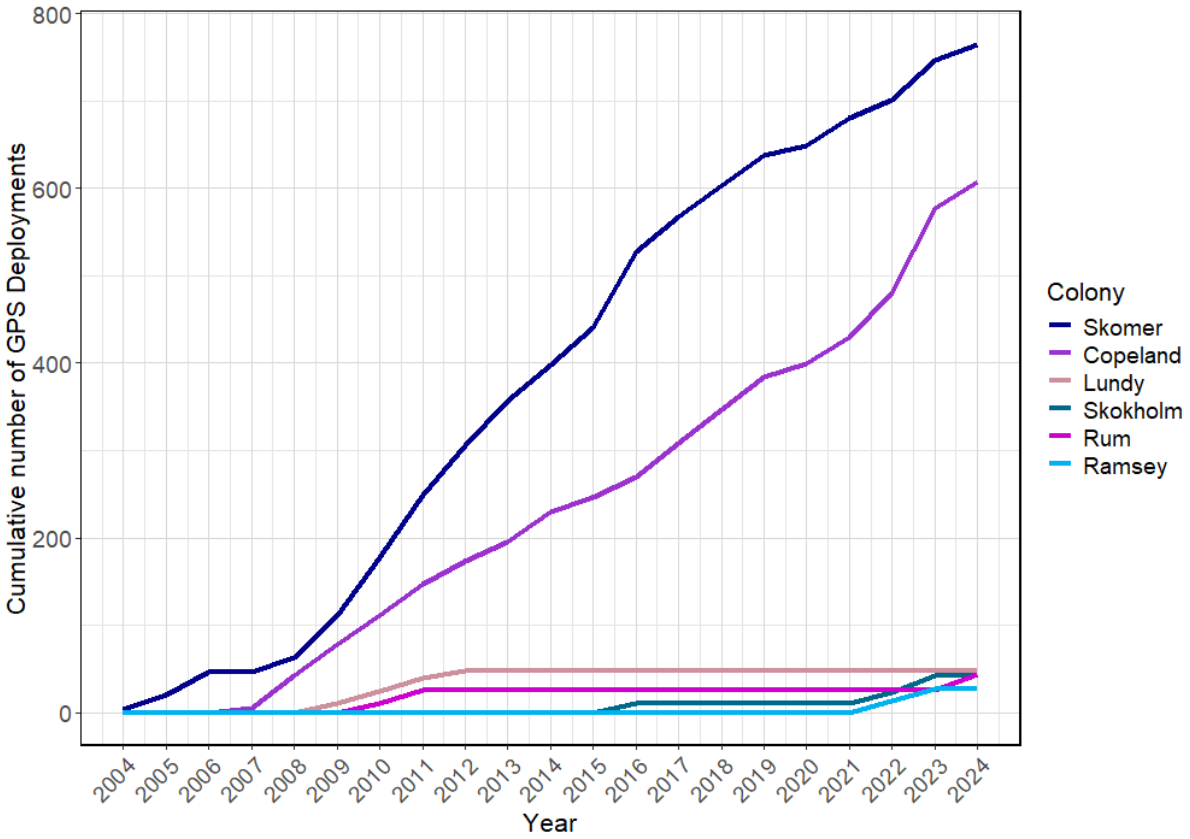


Figure 2.2. Cumulative number of GPS deployments for each of the six colonies included in this long-term dataset.

Table 2.1. Year of first deployment and the total number of GPS devices deployed from each colony (capped to the end of the 2024 field season).

Colony	**Year of first deployment**	**Total no. of GPS files**
Skomer	2004	765
Copeland	2007	607
Lundy	2009	48
Rum	2010	44
Skokholm	2016	42
Ramsey	2022	27

Technological advances

Throughout the project, the availability of GPS devices, and their capacity to record at higher frequencies or for longer periods of time, has substantially increased. Due to the relatively small body mass of Manx shearwaters (approximately 400 g), the maximum mass of tracking devices suitable for these species is rather constrained (under 20 g taking the standard upper limit of 5% of the subject's total body mass; Kenward, 2001; Portugal & White, 2018). Considering this mass threshold is also inclusive of all tag housing and any material used in the attachment, this limits the range of devices suitable for this task, especially in the earlier years of this project prior to the recent advances in miniaturisation of such equipment (Guilford et al., 2011).

In the initial years of this project, GPS devices were custom-built for these campaigns (see Guilford et al., 2008 for technical details on their construction), and these devices were capable of a total active operation time of just 55 minutes (weighing 17 g including all housing and attachment material). This vastly limited their utility for the tracking of long-distance pelagic movements and meant that fixes were set to take bursts of positional data with long gaps between these periods, maximising estimates of space-use whilst retaining the chance to identify behaviours during these fix bursts. From 2008 onwards, the project's primary GPS device switched to a commercially available tracker, originally intended for travel and sport uses, called the Mobile Action i-GotU (Allan et al., 2013; Dean et al., 2012). These devices were much more cost-effective, since they were commercially available, and could be stripped of their original housing and placed in heatshrink as a lightweight waterproofing solution for deployment on shearwaters. Smaller lithium batteries could be soldered onto these devices, maximising the trade-off between deployment mass and recording period (Allan et al., 2013). Finally, these devices came with an interface that made their frequencies and scheduling remarkably flexible, allowing for recording windows to be set only for active hours or periods in the future, further maximising the use of the limited battery life.

In more recent years, (from ~2021 onwards) there has also been sporadic use of industry-specific commercially available GPS devices, such as TechnoSmart's Axytrek. These devices are equipped with various animal tracking-specific features, such as built-in accelerometers, solar panels, and pre-sealed waterproof resin housing. However, the cost of these devices has limited their implementation across full campaigns.

The main advancement in the GPS technology employed within this tracking project is the development of the SnapperGPS devices by Dr Alex Rogers and his lab in the department of Computer Science at the University of Oxford (Beuchert & Rogers, 2021). The primary limitation of GPS tracking devices for small species such as the Manx shearwater lies in the trade-off between tag mass and the battery capacity required for long-term deployments. The need for substantial battery power stems from how GPS receivers determine position, through a process termed trilateration. Each time a device acquires a positional fix, its receiver powers up to detect timing signals broadcast by multiple satellites within the Global Navigation Satellite System (GNSS). By measuring the time delay of these signals and calculating its distance, or 'pseudo-range', to each satellite of known position, the device computes its own location as the intersection of these distance spheres. This signal acquisition and, in particular, processing stage is computationally intensive and therefore represents the major source of energy consumption in GPS tracking tags (Paxton et al., 2022).

The advancement made with these SnapperGPS devices, and indeed others in the industry such as those developed by Lotek (Forrest et al., 2022), is that this computation of position, which demands a high battery capacity, is calculated externally to the device post-retrieval, once the data is uploaded to a custom-built server (Beuchert & Rogers, 2021). During the position-fixing step of the snapperGPS, once they receive an array of signals from GNSS satellites, these satellite signals are digitised and stored locally for later processing, rather than computing the intersection of these signals onboard at the time of acquisition (Beuchert & Rogers, 2021). This allows these devices, whose batteries are already smaller than any previously used within this shearwater tracking campaign, to

run for significantly longer periods on significantly higher frequency schedules than any prior device (Beuchert & Rogers, 2021). This improvement to data quality, and duration, allows us to interrogate their movements with regard to their navigational performance with greater precision. Furthermore, this reduction in battery size allows for a sizeable reduction in the mass of these deployments, with the snapperGPS devices deployed in 2024 averaging a mass of 12.96 g, inclusive of housing and attachment material, reducing this deployment mass to ~3% of average body mass (Portugal & White, 2018). It is well established that the deployment of biologgers onto free-ranging animals can impact the expression of their natural behaviours (Barron et al., 2010; Bodey et al., 2017). Indeed, this has too been reported in the Manx shearwater, with the deployment of previously used i-GotU GPS devices having been shown to extend the length of their foraging trips (Gillies et al., 2020). Therefore, this reduction in mass presented with the SnappergGPS offers further support for their implementation into the tracking of far-ranging species (Portugal & White, 2018). These devices were piloted in the Manx shearwater tracking project as a collaboration with Dr Rogers' group in 2022 and have been widely used across the islands ever since, forming the core of the fleet of devices used in the OxNav tracking campaigns. For this, we would like to extend our thanks to Dr Alex Rogers, Dr Jonas Beuchert, and Amanda Matthes, who helped endlessly in implanting these devices.

Finally, a more recent addition to the devices within this dataset are the Ornitela remote GSM GPS. Their primary utility is not fully demonstrated in this thesis, but these devices allow for the remote download of data through connection to global cellular networks (Gould et al., 2024). This means that they do not need to be physically retrieved for the data to be accessible. Whilst this has facilitated increased tracking on some of the more remote islands such as Rum, the true potential for these devices lies in the tracking of migratory or non-breeding movements, which will no doubt be explored in future works from the lab group (see **Chapter 7, Future Directions**; Gould et al., 2024).

GPS attachment procedures

Despite a range of devices being employed in this tracking project, the general attachment procedure has been largely conserved. This will be detailed here and is also described for the first time in Guilford et al. (2008). In some seabirds, such as the Charadriiformes, tags are attached using harnesses (Thaxter et al., 2014), however with diving birds such as shearwaters, the changes in pressure experienced at depth compresses their bodies, making a harness that was fitted tightly on land pose a potential risk of entanglement during foraging (Phillips et al., 2003). Therefore, here tags are attached dorsally to the bird, sitting between the shoulders, using several thin strips of marine cloth TESA tape (**Figure 2.3**). When heatshrinked, device profiles are kept slim to streamline deployments, and additional tabs of heatshrink can be left at either end to provide additional attachment points. Each strip of TESA tape is seated underneath a small bunch of mantle feathers, upon which the device is placed, and the tape is tightly fastened around the device. It is not the adhesive of the tape that holds the device in place, but the compression between the device and the several bunches of mantle feathers. All deployments take place in a dark quiet room, under red light if required, with the bird's head placed in a bird bag during the procedure to minimise stress. Signs of stress were monitored throughout the procedure. These included increased body temperature, continued heavy panting, repeated vocalisations, and a general prolonged restlessness during tag attachment. If a bird was ever deemed too stressed to continue with a deployment, any attachments were removed and the bird was immediately returned to its burrow. Upon retrieval of a GPS device, the strips of tape are peeled away from the device and any feathers that may be adhered, the bird is then returned to its burrow. Taking the Skomer chick-rearing campaign of 2024 as an example, GPS deployments averaged 08:22 minutes, ranging from 05:00 to 12:00 minutes, whilst retrievals averaged 04:18 minutes.

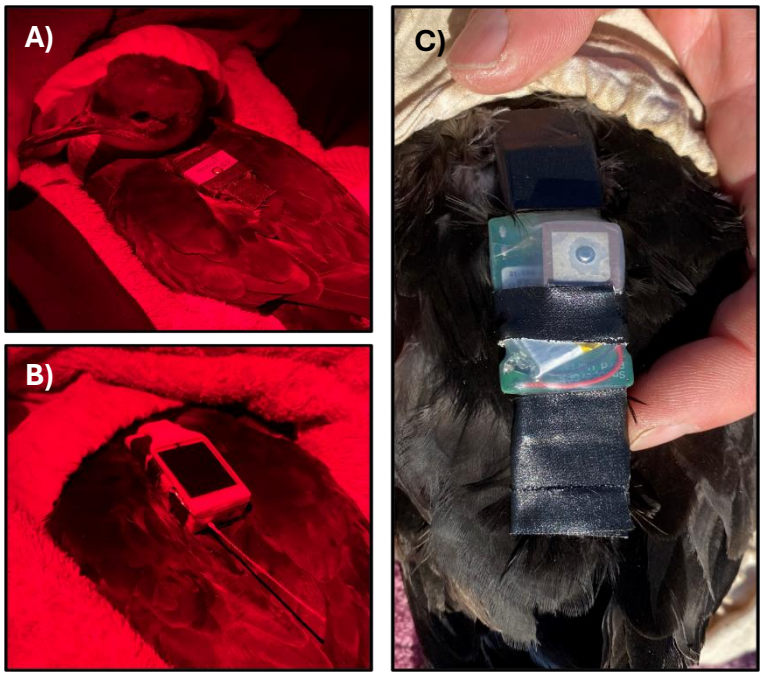


Figure 2.3. Deployments of **A**) a new style SnapperGPS device with a larger, more streamlined antennae, **B**) a TechnoSmart AxyTrek device with integrated solar panel, this is mounted on a panel that folds over the TESA strips so that it is not obstructed after attachment, and **C**) an old style SnapperGPS device.

Licensing and ethics

All tag attachment protocols, experimental designs, and monitoring regimes were authorised by the Zoology Animal Welfare and Ethical Review Board in 2022-2024, in accordance with the University of Oxford's policy on the use of protected animals for scientific study. All work conducted on the Skomer and Skokholm colonies was further authorised by Natural Resources Wales, Islands Conservation Advisory Committee for Skomer and Skokholm Islands. For work on Copeland Island, all team members held wildlife licences issued by the Northern Ireland Environmental Agency (NIEA). Work in Scotland was covered under Scottish Natural Heritage.

All bird handling was covered by an appropriate British Trust for Ornithology ringing licence. "Special methods" (any additional devices) were licenced by the British Trust for Ornithology after ethical review by the BTO's Special Methods Technical Panel (permit C/6981).

Track filtering

These devices, even with modern advancements, are not infallible. GPS errors may still result from a poor availability or distribution of GNSS satellites. In some cases, human error during the heatshrinking process allows seawater to enter the housing whilst at-sea, short-circuiting or damaging the device and corrupting any resultant data. Furthermore, older files within this long-term database contain GPS tracks that, whilst complete, are at a resolution too low for the analyses proposed in this thesis. Due to these avenues of potential error and variation in data quality, this database first needed to be passed through several quality filters before GPS tracks could be passed on to processing.

Firstly, GPS files were separated out into the individual foraging trips contained within them. This primarily applies to those deployed in chick-rearing where foraging trips tend to be much shorter and as such a bird is allowed to return to the colony several times before the tag is retrieved. As incubation trips are generally longer, these are preferentially retrieved in the first instance the bird is seen post-deployment, but this still leaves the potential for deployments to have spanned multiple trips if the bird was missed on its first return. These trips were split by identifying each return to the colony within a GPS file.

For a trip to be taken forward into an analysis within this thesis, it must have met the following criteria. The GPS scheduling (how often the device acquires a positional estimate) must not have exceeded 30-minutes, there must be a minimum of 50 fixes within the trip, and the bird must have reached a minimum distance of 25 km from its home colony during this time. These criteria were established to ensure that any one trip within the database taken forwards contained enough detail to be analysed with respects to its at-sea movements, and its ultimate homing behaviour.

Trip processing

The primary step in this data processing was the removal of GPS errors from within the trips. If during the position fixing step, a device does not have access to a sufficient array of satellites, either due to a physical obstruction (such as the bird itself) or because the bird is submerged at the time of fix, then the device can miscalculate its position in space. This can also occur when the array of available satellites is clustered in one region of the sky, making the intersection of their relative positions more challenging. These are often single-fix errors and can be rectified simply enough through removal. To do this, any fix with a reported speed (calculated as the distance travelled since the last fix divided by the time between these two fixes) above 80 km h^{-1} (as seen in the upper reported speed threshold of Guilford et al., 2008) was removed from the trip, and the surrounding speed values were recalculated (**Figure 2.4A**). In some instances, primarily where several GPS errors occur in sequence, the surrounding speed values became non-resolvable for the gap that is left in the trip once the errors are removed. In these cases, the trip was not taken forwards into any further processing.

Despite the initial deployments having set fix schedules (e.g. one fix every 15 minutes), the removal of these GPS errors, along with instances where a device may have failed to acquire a fix within its search window, meant that the time gaps between fixes in a trip were often nonuniform. To resolve this, all trips were then interpolated using a cubic-spline interpolation algorithm (Tremblay et al., 2006). This process produced a GPS trajectory with fixes at uniform 5-minute intervals, thereby standardising the sampling rate across all trips regardless of their original scheduling. The cubic-spline interpolation ensures that all original data points are retained within the reconstructed trajectory, while allowing the path to curve smoothly between them when estimating intermediate positions. Such curvilinear interpolations yield a more continuous, natural-looking movement path compared to the angular, piecewise connections typical of lower-resolution data or linear interpolations (**Figure 2.4B**; Tremblay et al., 2006). These curves enforce smooth transitions in velocity and acceleration, preventing abrupt changes in direction that would be unlikely during normal flight behaviour.

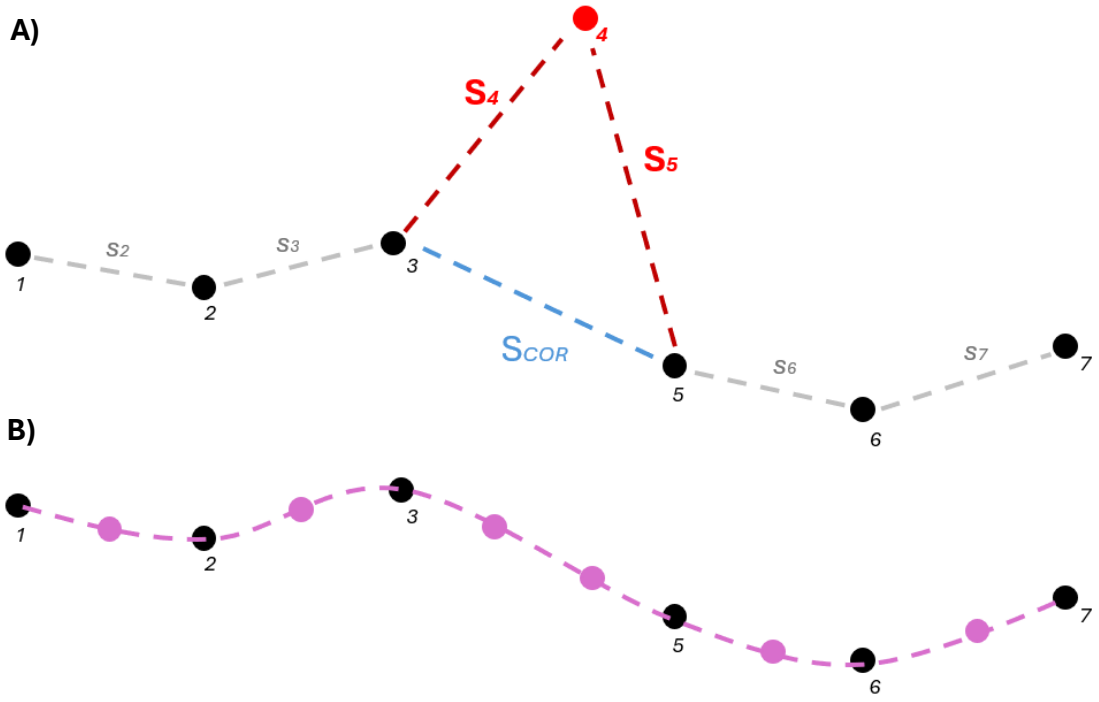


Figure 2.4. A schematic detailing **A**) the removal and correction of GPS errors and **B**) cubic-spline interpolation. In **A**) each fix is numbered, and the period of track used to calculate its associated speed value is labelled accordingly. Here, fix *4* is a GPS error (with a speed, S_4, above 80 km h^{-1}) and so is removed through filtering. This removes the error fix, along with its associated speed value, but we can see that the speed associated to fix 5, S_5, was computed in relation to the distance and time travelled away from this error and so is also incorrect. This speed is therefore recalculated with regards to the distance and time travelled since fix 3 (the blue dashed line) replacing S_5, with S_{COR}. In **B**) these now corrected fixes are interpolated using a cubic-spline algorithm, which allows the trajectory to bend (such as between fixes 2 and 3), rather than interpolating them linearly, retaining all original points.

Homing identification

In these free-ranging movements, the onset of homing is marked by a clear behavioural switch from non-directed mid- to low-speed movements, such as foraging or rest, to a directed bout of high-speed movement in the homeward direction. When plotting a track as its distance from the colony through time, this behavioural switch for homing is marked by a steep decline in this distance (**Figure 2.5A**). The onset of this decline can be taken as the point of homing, and for every trip in the database this was manually identified using visual inspections of the tracks plotted as in **Figure 2.5A**. Here, this homing point is marked in red, meaning all following behaviour is classified as homing behaviour.

This process of manual identification was validated using a subset of twenty tracks. These tracks were shuffled and randomly resampled each five times, blind with respects to any details of the trips themselves. I then reidentified the homing point from the distance plot for each trip a total of five times, and from this it was possible to calculate the mean homing point, and deviation from this, for each trip. This showed that I had 98% repeatability within the identification of consistent homing points (**Figure 2.5B**). Deviations were at most two fixes from the mean which, in the context of these tracks, constitutes very little variation (~10 minutes).

As this homing period, and their subsequent performance in this behaviour, is the primary focus of the analyses in this thesis, trips were only taken forward if they contained sufficient homing data. This included all trips that reached less than 5 km from their colony, as this was assumed to be sufficient proximity to their goal, or in larger trips where perhaps the tag had exhausted its battery during the homing period but had still captured significant homeward movement, a minimum reduction of at least 90% of the homeward distance was required for a trip to be retained.

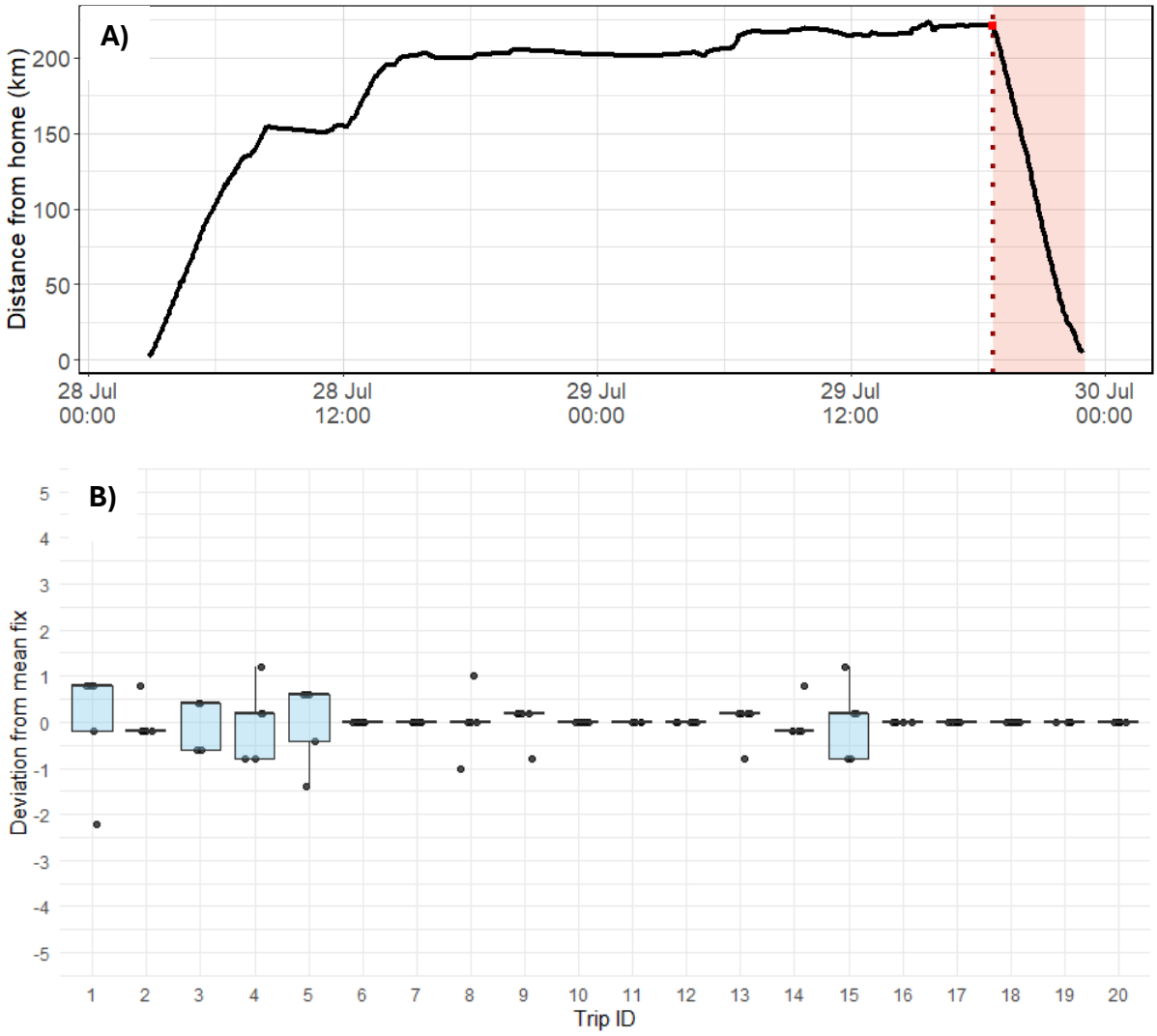


Figure 2.5. **A**) The changes in distance from home (km) in a trip through time. The point marked in red (along the dashed red line) indicates the point marked as the start of homing. This point marks the onset of a rapid decline in the distance to home (shaded in red), indicating homing behaviour. **B**) shows the deviation from the mean fix identified as the point of homing in the validation of the manual identification method of this point across twenty tracks, each resampled five times blind to the researcher.

Data availability

Once trips had passed through the quality filtering, been filtered for GPS errors and interpolated, and been identified as having sufficient homing data, they were then admitted into the pool of data ready for analysis. These trips were separated for each chapter as outlined in **Figure 2.6**.

This final dataset constituted 2,004 foraging trips originating from 1,110 GPS deployments. These deployments spanned 799 individual Manx shearwaters across the six colonies utilised within this long-term tracking project. To date, this is the largest collation of GPS data presented by the OxNav research group, representing the largest tracking effort of Manx shearwaters in the world (**Figure 2.7**).

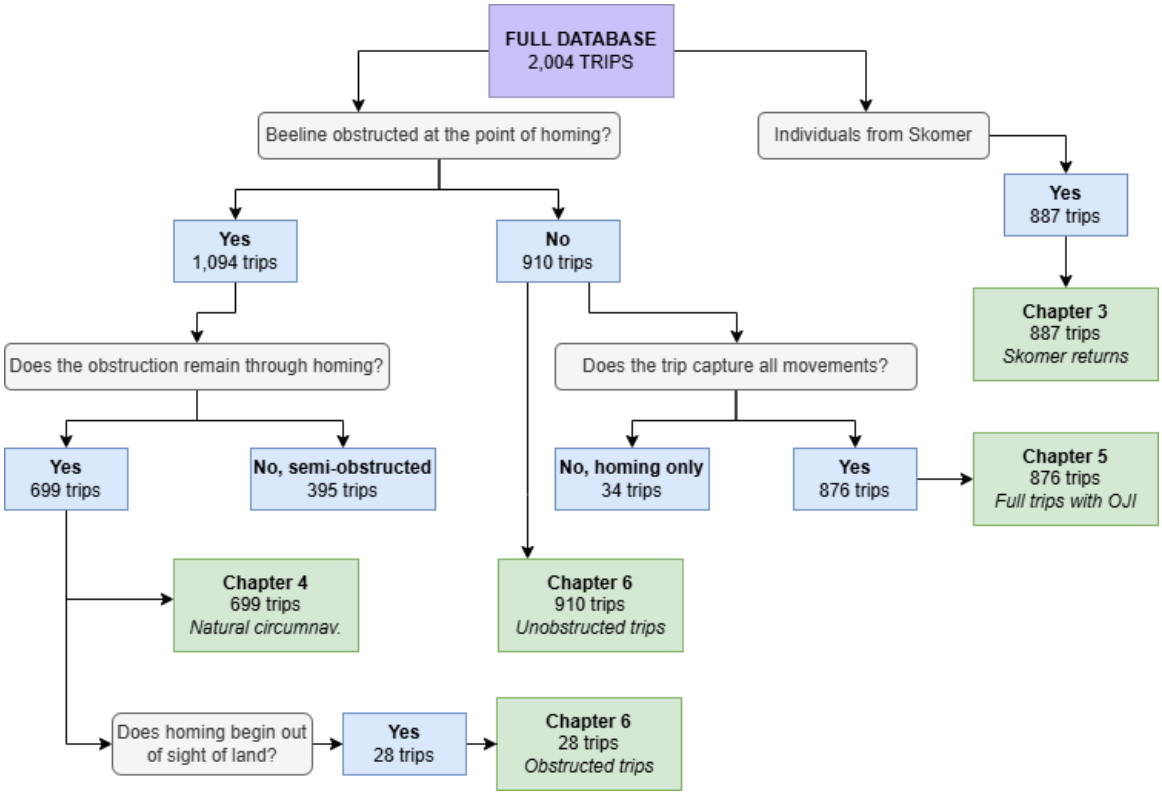


Figure 2.6. The allocation of the database to each chapter within this thesis. Further data subsetting was carried out within each chapter for specific models etc., but these details will be given in the methods sections of the chapters themselves.

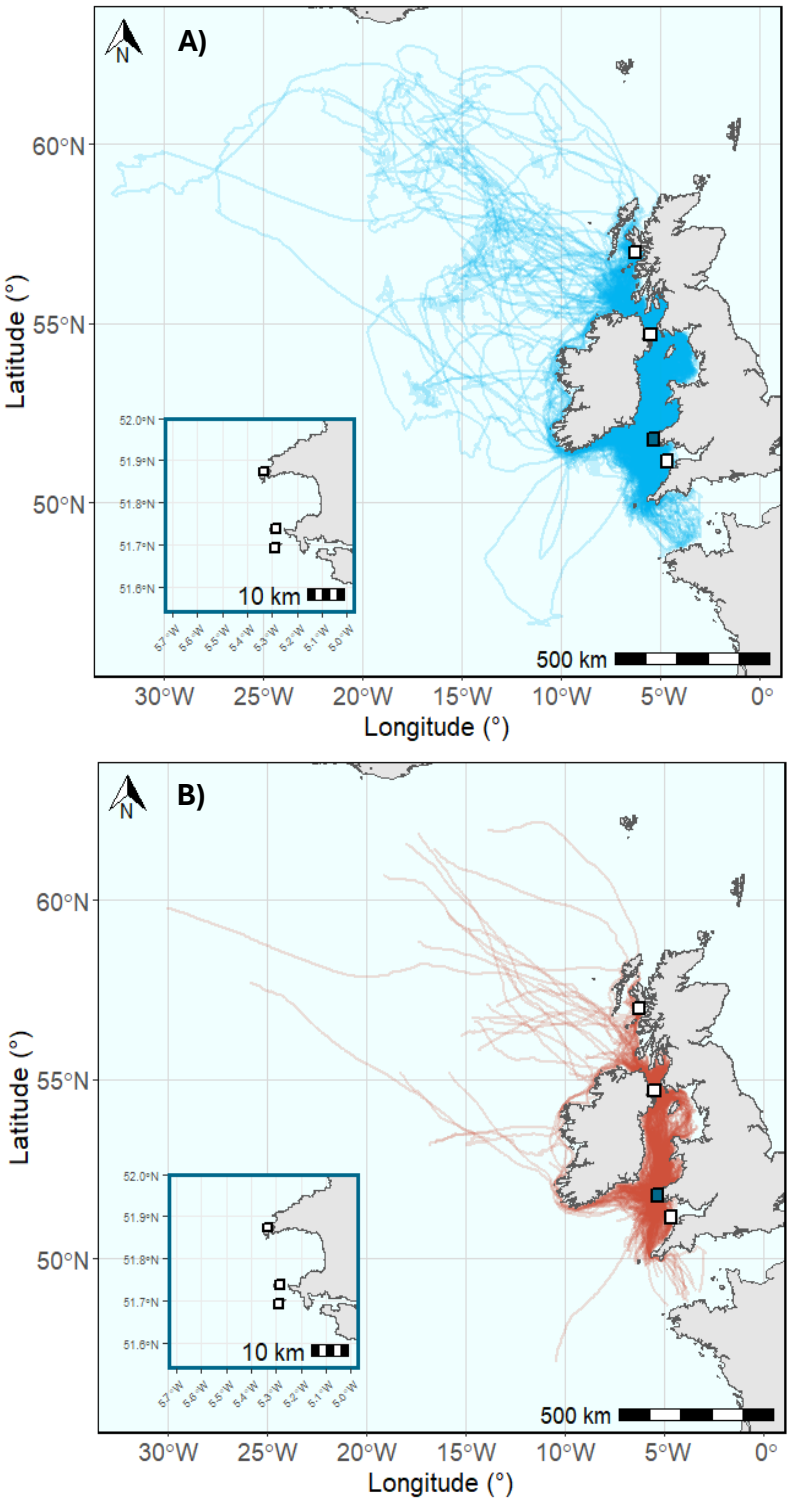


Figure 2.7. Maps displaying **A**) all 2,004 trips contained within the dataset employed within this thesis in blue, and **B**) their homing periods in red. White points indicate colony locations, the Pembrokeshire colonies are all located within the dark blue point, with precise locations shown on the inset.

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Chapter 3

Shearwaters make efficient navigational decisions, even at very fine scales



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Abstract

Seabirds are superb long-distance navigators, capable of navigating across entire ocean basins with remarkable accuracy. Whilst the mechanisms that facilitate these movements are increasingly well understood, it is unclear how accurately seabirds determine their position on finer scales. Here, we investigated local navigation in a pelagic seabird, the Manx shearwater (*Puffinus puffinus*), by displacing GPS-tracked individuals to different points around their colony island. Because shearwaters normally avoid flying over land, these coastal release sites present a choice of two over-sea routes by which the island could be circumnavigated that differ in distance. When presented with this task, we found that shearwaters preferentially adopted the shorter round-island route following release. This, we suggest, indicates that shearwaters are capable of learning to use the most efficient route even when the difference in payoff is very slight. We discuss the potential learning mechanisms that may underpin this navigational efficiency; speculate as to how birds might distinguish between routes where the absolute difference in payoff is minimal, but the relative payoff is large; and propose that, despite being known for their long-distance navigational ability, land-avoiding seabirds might present us with a surprisingly useful model for fine scale navigation.

Introduction

Manx shearwaters, *Puffinus puffinus*, routinely travel hundreds of kilometres across open ocean in search of food (Guilford et al., 2008). Constrained to return to their breeding colony as central place foragers, they must then be able to navigate effectively back home from these distant sites and have evolved to be extremely proficient at doing so (Matthews, 1953). Whilst long-distance, at-sea navigation is thought to be facilitated by detecting large-scale gradients in environmental cues (Gagliardo, 2013; Gagliardo et al., 2013; Holland, 2014; Phillips, 2006), it is unclear whether these cues would remain useful at smaller spatial scales (Lohmann & Lohmann, 2006; Mouritsen, 2018; Phillips, 1996; Wallraff, 2004, 2005). It is, then of some interest to determine a) how effective shearwaters' navigation systems are at local tasks and b) what is the mechanistic basis for this?

Our current best understanding of local area navigation is seen in the widely used model system of homing pigeons. Within an area of high familiarity, pigeons can refine their routes through repeated experience with the homing task, increasing their navigational efficiency with repeated releases from the same site (Bonadonna et al., 1997; Guilford & Biro, 2014; Meade et al., 2005). Furthermore, it appears that birds can recall these individually refined routes such that when displaced they will preferentially adopt these routes, even in cases where a more efficient alternative is available (Biro et al., 2004, 2006; Meade et al., 2005). Such route learning is also found in other taxa including insects (Collett et al., 2003; Collett, 2010; Menzel & Giovanni Galizia, 2024) and rodents (Alyan & Jander, 1994; Wijnen et al., 2024). This process of route learning and refinement is likely underpinned either by associative ('trial and error') learning, where animals encode navigational decisions with the reward of reaching home (or some proxy) or via some form of latent learning – i.e. route refinement without direct reinforcement when the navigational task is achieved, as seen in cognitive map models (Guilford & Burt de Perera, 2017; Wang & Hayden, 2021). If route improvements are learnt associatively, then for a route preference to form there should be a perceptible increase in the reward value, the associated positive

affective value, of executing a given route over alternatives (Guilford & Burt de Perera, 2017; Kahnt & Tobler, 2017; Pearce, 2008). At finer scales however, these distinctions in route value may become less salient (perceptible in a learning context), as the improvements offered by routes become less pronounced. Therefore, understanding navigational efficiency at this fine scale, particularly in a wild model, may give us insight into how route-learning within the familiar area is achieved.

Here, we look for evidence of these fine scale route efficiencies, investigating familiar area navigation in a species previously celebrated for its long-distance abilities. Shearwaters routinely avoid flying over land, meaning landmasses (islands and peninsulas) constitute an obstacle between a bird and its target (Brooke, 1990; Dall'Antonia et al., 1995; Padget et al., 2022). Therefore, by displacing shearwaters locally from their colony to nearby points around their home island's coastline, we provide shearwaters with a homing task where they must choose between two over-water routes, either way around the island back to their nest. Over very fine scales such as these, the two potential over-water routes a shearwater must choose between are similar in absolute distance but differ more substantially in relative cost. Hence, by releasing birds from the coast of their home island, we test whether they can detect these differences in route value and take the shorter route, even at this fine spatial scale. Based on this framework, we predict that shearwaters will preferentially select the lower cost route following release, as if they are sensitive to fine-scale differences in route value, their initial route choice should be biased towards the more efficient option.

Methods:

Data collection and displacement procedures:

This study took place on Skomer Island, Pembrokeshire, Wales, UK (51.737°N, 5.282°W), the largest colony of Manx shearwaters in the world (Perrins et al., 2019). The colony is monitored throughout the season, and so the breeding stage and occupants of study nests were known prior to the experiment. For this experiment, target birds were adults in an active breeding attempt; no preferences were made for sex, with both sexes included in the sample, and age was not known for any birds in the study sample. Each individual was only displaced once per field season to mitigate any potential cumulative impacts of repeated disturbance on their breeding attempt. No priority was given to birds who were displaced in 2022 when selecting for birds in 2023, but in instances where birds were viable candidates in both years (n = 2), their inclusion in both years was permitted.

During the chick-rearing periods of 2022 and 2023, nests were monitored during the night for the arrival of target adults, returning to their burrow to provision their chick. In 2023, the displacement procedure was also conducted during the incubation period (11th-16th May), where adults alternate stints in their burrows without leaving. During displacement nights in chick-rearing (5th-20th July), birds were removed from their burrows upon arrival, ideally before they began chick provisioning. The efficacy of displacements during chick-rearing has been demonstrated in related species, with the working assumption that birds retain their motivation to home when removed from their burrow before being able to feed their chick (Yoda et al., 2014). Similarly, previous work has shown that, during incubation, Manx shearwaters are highly motivated to home when displaced within the early stages of their incubation stints (Matthews, 1953; Padget et al., 2018). While still at the colony, 15g Mobile Action I-gotU gt-120 GPS loggers were attached dorsally using thin strips of tesa® marine tape to small bunches of mantle feathers, following a standard protocol outlined in Guilford et al. (2008). Devices were programmed to take fixes every second, providing high

resolution movement data, and were scheduled to begin recording once the displacement protocol had begun.

Birds were then transported by foot (1.8-2.1 km) in opaque, sectioned boxes with disposable paper towel linings and air holes, to one of two release points around the coast of Skomer island (**Figure 3.1A**). Total transport time did not differ between release sites and was consistent across individuals. Release sites were pseudo-randomised within each night to ensure both sites were represented within each night of data collection. Since we anticipated that the shearwaters would be reluctant to fly over land directly back to the colony, the chosen release sites presented two over-sea routes back (one clockwise and one counterclockwise around Skomer Island) of unequal circumnavigation distances depending on the route adopted following release (Padget et al., 2019, 2022). From either site the shorter route option (eastwards) could take less than 2km, whilst the longer route (initially westwards), would take around 5km. In 2023, the presence of multiple handlers at the field site allowed for the simultaneous release of birds from both sites within one displacement night, maximising the number of birds that could be released on suitable nights. Whilst in 2022, a smaller field team meant that only one site could be visited during each night.

Release procedures began as soon as both handlers had reached their sites. Birds were released singly from atop 30 m high coastal cliffs from an open hand allowing them to take flight immediately which allowed handlers to confirm they had flown out to sea from the coastal release site. This hand release also allowed handlers to approximately direct the bird's take-off 180° to the homeward beeline from either site, each only after the previous bird had vanished from sight. Wind speed thresholds of an average speed of 7 m s^{-1}, and gusts of 9 m s^{-1}, were applied to any displacement night, to both minimise welfare risks and release night confounds.

All tag attachment and displacement protocols were authorised by the Zoology Animal Welfare and Ethical Review Board in both 2022 and 2023, in accordance with the University of Oxford's policy on the use of protected animals for scientific study. All work was further authorised by Natural Resources Wales,

Islands Conservation Advisory Committee for Skomer and Skokholm Islands. GPS deployments were approved by the British Trust for Ornithology Unconventional Methods Technical Panel (permit C/6981).

Track processing:

Only complete GPS tracks of birds that returned to the colony during the same night were used for analysis. These tracks were then filtered using speed thresholds for GPS errors (above 80 km h^{-1}) and stationary bouts (0 km h^{-1}, bird sat on the water) and trimmed with a 50 m exclusion zone around both the release site and nest site, to ensure that only at-sea flight behaviour was taken forward in subsequent analysis.

To visualise general route differences whilst accounting for individual variation arising from the high-resolution tracks, a median route was calculated for each combination of decision and release site present in the results (e.g. shorter path taken from the northern site), using data from all birds within each combination. These were extracted by segmenting the island's coastline into radial polygons projecting from its centre, which encompassed all tracks, and then calculating the median latitude and longitude of all movement data within each of these polygon segments (**Figure 3.2A**). Here, the median was used in preference to the mean as it is less sensitive to outlying positions and uneven fix densities within segments across individuals and therefore provides a robust estimate of the central tendency of routes followed by the majority of individuals. For a polygon to contribute to the median route calculated, it must have contained tracks from at least three individuals, to not overrepresent specific individuals.

Route classification:

Tracks were assigned the route choices of 'long' or 'short' with respects to the route taken to circumnavigate the island following release. This was classified by identifying the median point along each track and assigning it to either a clockwise (e.g. 'short' if released from the Northern site) or anticlockwise (e.g. 'long' from the Northern release site) direction along the at-sea routes available post release. Some birds, despite homing on the same night, flew either out to sea

(n = 2) or directly over the island (n = 1) upon release, meaning that the classification criteria above could not be easily applied. Furthermore, by flying out to sea before homing, these birds altered the relative value of circumnavigation routes intended by the selection of release sites, meaning they could not be analysed with regards to the wider experimental design (but are still presented in **Figure 3.1C**). It should be noted however, that all three birds still made the 'correct' route choice from their respective release sites, so their inclusion would only strengthen the interpretations of this study.

Environmental covariates:

It is possible that choices in homing direction could be biased by birds actively trying to minimise the headwind encountered along their homing route. As such, at-sea wind conditions experienced following release were modelled to investigate how they may influence the appeal of the possible at-sea circumnavigation routes. Local weather measurements were not taken at release points, and so hourly (closest to the hour of time of release) wind speed (km h^{-1}) and wind direction (degrees) were extracted from Open-Meteo for the coordinates of each release site. This API provides spatially interpolated point estimates of weather variables from an underlying ~9 km ECMWF IFS (*European Centre for Medium-Range Weather Forecasts*) grid (Hersbach, 2023; Zippenfenig, 2023), and thus values represent area-averaged conditions rather than site-specific measurements. As such, fine-scale local variation in wind conditions may not be captured, but the data provide a consistent estimate of broad-scale wind patterns at the time and location of release. From this data, the head/tailwind component that would have been experienced along the initial flight paths of either route for each track at the time of release were calculated. As these routes are in opposite directions (eastwards or westwards) at the point of release, positive values of this metric corresponded to headwind on the shorter (eastwards) route, which consequently offered a tailwind on the initial (westwards) portion of the longer route. Negative values therefore corresponded to the opposite wind directions. Since forecast models such as that used here have limited spatial resolution (9 km in the ECMWF IFS), incorporating wind data along the entire route was not

possible, and so these values were calculated using the initial homeward direction from the median tracks calculated above (**Figure 3.2A**). However, since returns following release tended to occur rapidly, it is unlikely that wind conditions experienced would significantly vary temporally.

Additional environmental covariates, moon illumination and cloud cover, were modelled here, as illumination at night is known to influence the night-flying behaviour of shearwaters, and diurnal predators remain active on well-lit nights, reducing shearwater return rates (Siddiqi-Davies et al., 2024; Yamamoto et al., 2008). Moon illumination percentages were obtained from Time and Date AS (2025). These values are based on the standard astronomical definition of the illuminated fraction of the moon and give a broad estimate to how illuminated the moon is on any one night. Cloud cover was extracted through the Open-Meteo API detailed above, using the 'total' cover metric, which summed low, medium, and high cloud cover.

Analysis:

Summary statistics (distance, mean speed, and duration) were computed for each track, and each track was assigned a quadrant of the colony for its burrow position, as even this small difference in goal location (50 - 100 m) may well factor into route length calculations at this scale. Route choice likelihoods were tested using two-tailed binomial tests and the potential effects of covariates were modelled using binomial logistic regression models, where the response was route choice taken as a binary, for example:

$$\textit{Binary route choice} \sim \textit{Release site, family} = \textit{binomial}$$

Moon illumination and cloud cover were modelled together with an interaction term. Beyond modelling the covariates of route choice, route metrics between the long and short routes were compared using linear regression models.

Prior to modelling, the structure of these covariates and the proposed model assumptions were assessed to determine the suitability of these binomial logistic regression models. Route choice was coded as a binary response variable

(correct or incorrect), supporting the use of a binomial error distribution with logit link function. Contingency tables were inspected for separation between response and predictor levels. Several predictors produced complete or quasi-complete separation due to sparse route choice distributions, likely driven by the small sample size. Because this separation can result in unstable or biased maximum-likelihood estimates in standard logistic regression, Firth's penalised likelihood regression was implemented to obtain reliable coefficient estimates and finite likelihood-based confidence intervals (Heinze & Schemper, 2002). Where this Firth's penalisation was used, model stability was additionally assessed through inspection of profile penalised likelihood curves to identify irregular likelihood behaviour or unstable parameter estimation.

As many predictor variables in these models were categorical, assessment of linearity in these was not required. Where covariates were categorical variables, likelihood ratio tests were additionally used to assess the significance of factor effects on route choice. For models on continuous covariates, the linearity in the logit was assessed graphically. Cook's distance values were inspected to assess the influence of individual observations on the linear regression models, as with this smaller sample size observations had the potential to skew results (Cook, 1977). While several observations exerted moderate influence, no observations displayed extreme influence sufficient to justify exclusion.

To gain an insight into the potential familiarity with presented circumnavigation routes from these release sites, the long-term tracking database of birds from this colony (containing 887 foraging trips, processed as discussed in **Chapter 2**) was mapped and assigned to either a Northern or Southern circumnavigation trajectory based on their location at 1 km from colony. From this, a route ratio of circumnavigations along either the North or South side of the island was calculated.

Results:

Route choices in homing birds:

Across the 2022 and 2023 breeding seasons a total of 55 birds were displaced to one of the two release sites (16 in 2022, all during chick-rearing, and 39 in 2023, 9 of which were in incubation and 30 in chick-rearing). All birds were subsequently re-encountered at the colony following displacement and all GPS were retrieved. The 55 releases resulted in 49 usable GPS tracks, 29 of which homed immediately following release. 3 homing routes were unclassifiable (not clearly either route, **Figure 3.1C**), meaning 26 were taken to analysis. 20 returned along the shorter of the circumnavigation routes, whilst 6 took the longer route (a significant preference for the shorter route; two-tailed binomial test on 20/26, p = 0.009; **Figure 3.1A-B**).

Models of covariates found no evidence that release date (LRT $\chi^2(8) = 5.29$, p = 0.726), year (LRT $\chi^2(1) = 0.158$, p = 0.691), breeding stage (LRT $\chi^2(1) = 0.440$, p = 0.507), moon illumination (β = 1.146, SE = 1.739, p = 0.510), cloud cover (β = -0.057, SE = 0.040, p = 0.156), nor colony position of the target burrow (LRT $\chi^2(1) = 0.597$, p = 0.742) influenced the route decisions. Neither did instantaneous headwind component (km h^{-1}) along the shorter route predict the circumnavigation direction (β = -0.001, SE = 0.066, p = 0.984). However, release site did marginally influence the odds of correct route decision: birds released from the Southern site were more likely to adopt the longer route (6/17 homing birds) than from the Northern site, where we saw no instances (0/9 homing birds) of longer route adoption (LRT $\chi^2(1) = 3.97$, p = 0.046).

We found that the shorter routes were significantly associated with a lower total flight distance during homing (linear regression: t = 2.575, p = 0.017) and the flight-only homing duration (t = 2.645, p = 0.014) (**Table 3.1**, **Figure 3.2B**) compared to the longer alternatives.

Island circumnavigation in natural tracks:

The natural data showed that 77.41% (677/887, p = <0.001, 95% CI: 73.36-79.06%) of all return trajectories from tracked foraging trips approached the colony from the north side of the island (**Figure 3.3**).

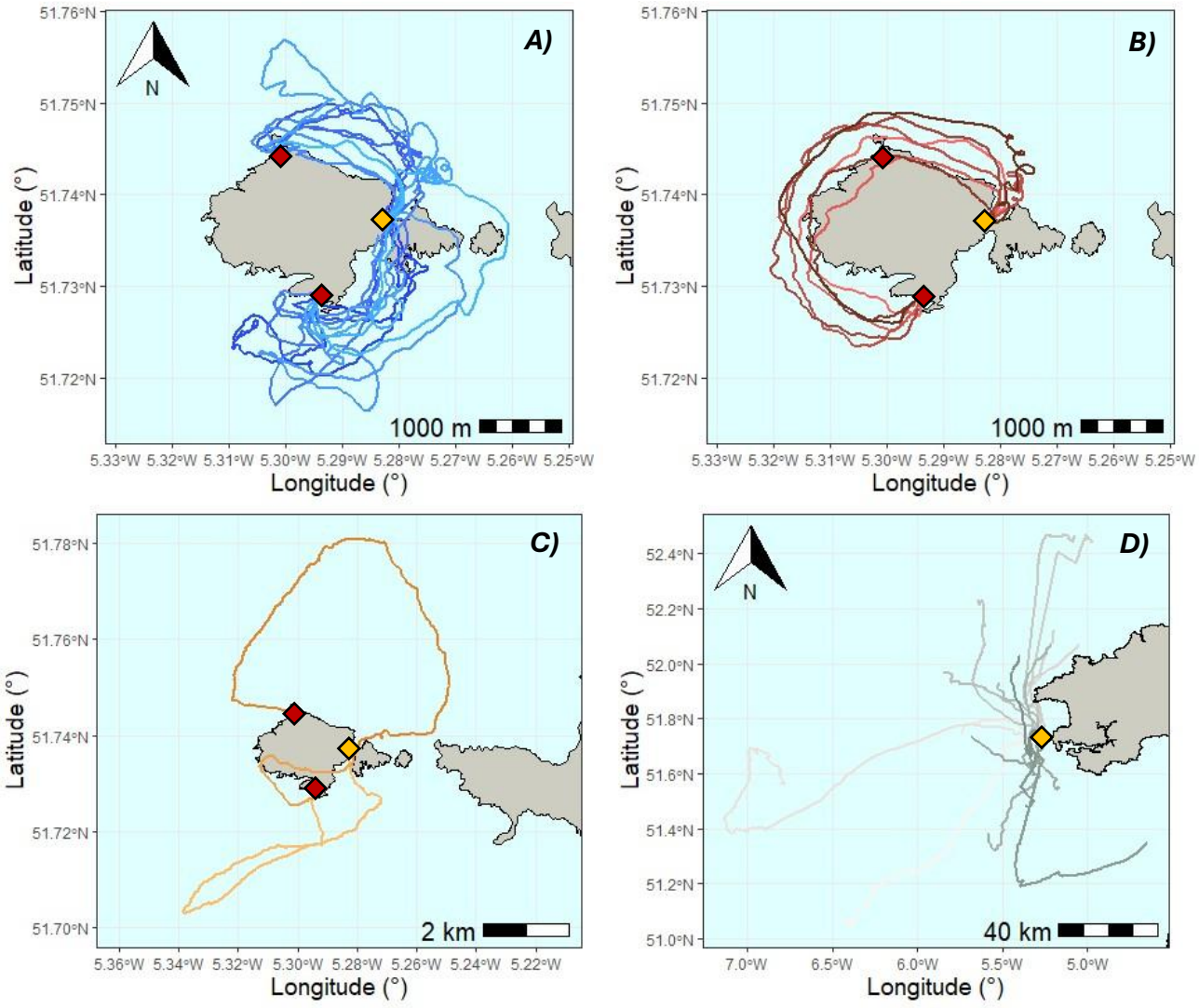


Figure 3.1. Maps showing the routes taken post-release by birds that: ***A)*** homed immediately along the shorter route (*n* = 20), ***B)*** homed immediately along the longer route (*n* = 6), ***C)*** homed but showed non-classifiable behaviour (*n* = 3), and ***D)*** did not home upon release (*n* = 20). The red points represent the two release sites, and the gold point shows the colony. Map in ***D)*** is zoomed out, see scale bars.

Table 3.1. Model outputs from linear regressions testing whether adopting the shorter or longer route influences homing trip metrics. P-values in bold with an asterisk indicate statistical significance between decision groups. * Flight-only homing direction refers to the time spent in flight post-release, as displaced birds often sit on the water initially following release.

Metric	Decision	Mean	SE	*t*	P
Absolute homing duration (*s*)	Short	665	141	0.778	0.444
	Long	893	293		
Flight-only homing duration (*s*)*	Short	405	64	2.575	***0.017****
	Long	749	344		
Total flight distance to home (*km*)	Short	4.392	0.494	2.645	***0.014****
	Long	7.109	1.027		
Flight speed *(km h^{-1})*	Short	42.058	2.291	-1.304	0.205
	Long	35.841	4.769		

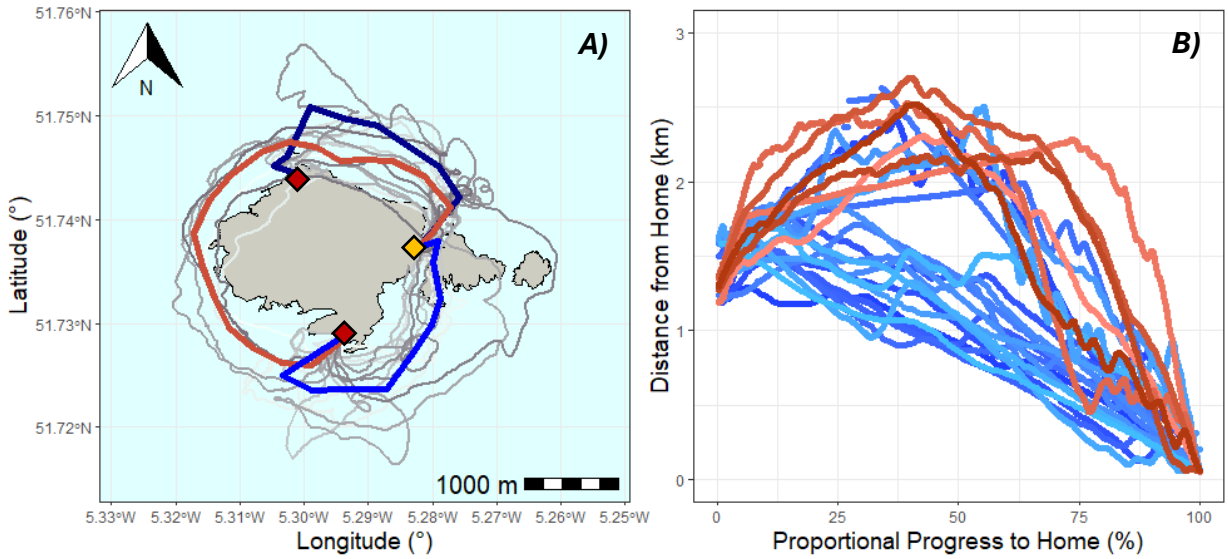


Figure 3.2. ***A)*** A map showing all tracks from birds that homed immediately post-release in grey, overlayed with the median routes taken from each release site with respect to the shorter (blues) or longer (red) route taken. ***B)*** The distance of each track from home (km) as each track progresses (measured as a proportion of their total flight distance) from release (0%) to return at the colony (100%), coloured as in *(A)* where red tracks represent those that took the longer route and blue those that took the shorter.

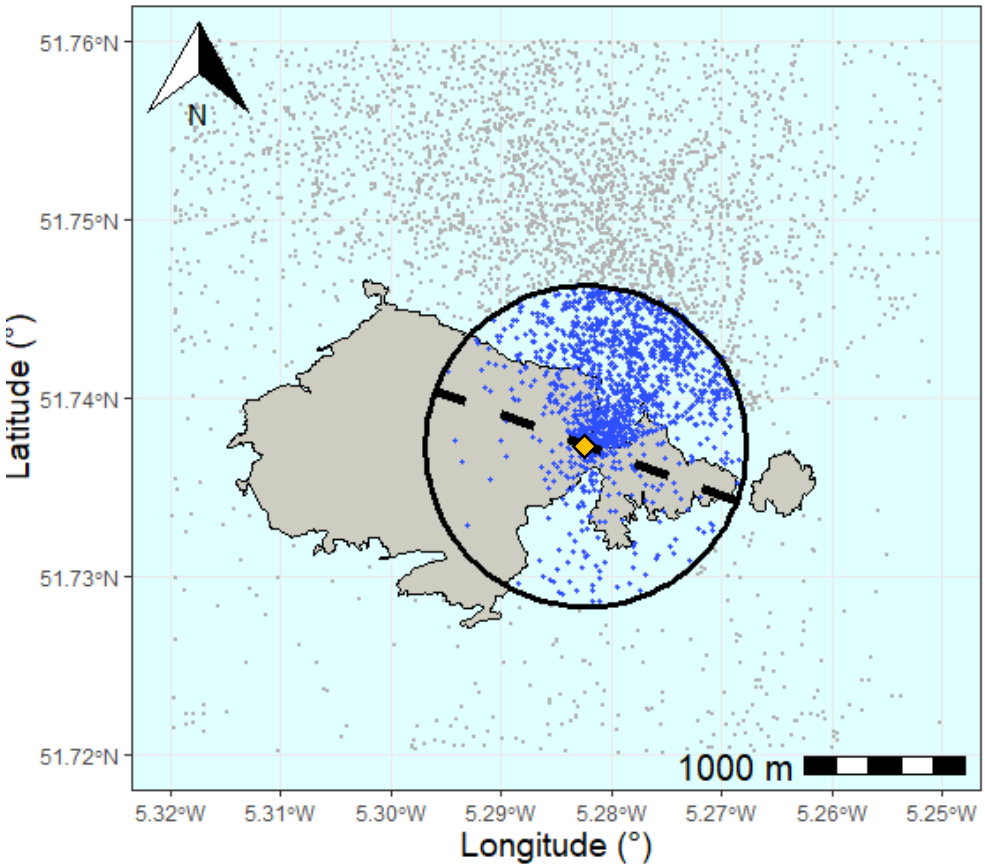


Figure 3.3. A map showing the historical free-ranging tracking data collected from birds breeding on Skomer (n = 887). The circle indicates a 1km radius from the colony, with the blue points showing fixes within this. For each track, the fix closest to this radius was taken and assigned either to approaching from the North or South based on which side of the diameter bisector line (dashed line) they fell on.

Discussion

In previous studies shearwaters have shown excellent orientation towards home when returning from natural foraging trips and following displacement to distant sites, far from their home colony (Padget et al., 2019, 2022), but few studies have investigated shearwaters' local scale route choices closer to the target. Here, we analysed various aspects of our local displacement tracks to understand some of the factors influencing local route efficiency and learning. We show that when displaced to nearby release sites on their home island, Manx shearwaters make efficient navigational decisions, discriminating between routes with small differences in absolute route length.

It seems our results reflect choices being made by the shearwaters upon release to adopt a certain route, rather than simply responding to immediate environmental conditions on release (e.g. adopting the route that offers optimal wind conditions; Harris et al., 2025), as we found the most likely confounding factors (wind direction and strength) did not predict route choice. If not a response to immediate wind conditions, these route choices imply that shearwaters knew which route was more efficient from both release sites.

These route efficiencies are likely achieved through prior learning acquired through the repeated adoption of these circumnavigation routes. More generalised navigational strategies such as those attributed to a bird's ability to home from an unfamiliar site following displacement (which likely uses large-scale environmental gradients to compare its currently perceived location with those associated to home to chart a course between the two) are unlikely to remain informative at such fine spatial scales (Lohmann & Lohmann, 2006; Mouritsen, 2018; Phillips, 1996; Wallraff, 2004, 2005). Furthermore, such maps should be constrained to provide animals only with a direct beeline home (Gagliardo et al., 2013; Padget et al., 2019). Therefore, the mechanism by which shearwaters make efficient decisions in this context, when instead faced with two indirect routes, almost certainly involves learnt route efficiencies formed through previous experience of the task (Griffin, 1952; Papi, 1990). The argument that these results reflect learnt responses is supported with further incidental

evidence from our historical tracking data which shows that the release site associated with more efficient route choices in our displacements (the North site) is also encountered more often in natural movements and so is likely more familiar to the birds than the alternative site (Meade et al., 2005). Indeed, the inefficient choice to take the longer route observed only from the Southern site is reminiscent of familiar area route loyalties in pigeons where, despite more efficient routes being available, individuals will instead move to recapitulate routes with which they are more familiar, which here appears to be the North side of the island (Biro et al., 2004; Meade et al., 2005).

Whilst the avoidance of within-year repeated releases in this experiment limits the inference we can draw on intra-individual route choices, the single instance of an individual homing following displacement in both 2022 and 2023 (EM34657) shows that this bird, whilst failing to adopt the shorter route in the first year, did so in 2023. Without knowing the age of this bird, it is hard to conclude the role of experience in this anecdotal finding, but it is plausible that this improvement in route preference could reflect an increase in experience with this fine-scale task between years.

It has been demonstrated in homing pigeons released from beyond impassable topographical features (such as mountains and large tracts of water) that, through repeated release, they are able to improve their subsequent performance with the navigational task, plausibly underpinned through learning and route refinement (Bonadonna et al., 1997). Furthermore, Cory's shearwaters displaced to the far side of Sicily, Italy, demonstrate efficient circumnavigation choices upon homing (Dall'Antonia et al., 1995), and Scopoli's shearwaters largely adopt the best route in the circumnavigation of Corsica, France, following displacement into the Mediterranean, demonstrating route knowledge within this localised area (Pollonara et al., 2015). In these instances, it is clear how such routes could be learnt associatively, as at these scales, differences in the benefits or costs of alternative route choices would plausibly be salient to these birds (Bonadonna et al., 1997; Dall'Antonia et al., 1995; Guilford & Burt de Perera, 2017; Pearce, 2008). It is likely that such learning also underpins the route efficiencies reported in this

study, and that this has likely been achieved through the repeated experience of this localised navigational task within natural movements. However, how this learning might operate in such contexts where the pay-off between route choices is potentially very small, in contrast to those shown in large-scale obstacle circumnavigations (Dall'Antonia et al., 1995; Padget et al., 2019, 2022), is worth careful consideration (Kacelnik et al., 2023). Whilst we cannot answer this directly from the results of this displacement, we can hypothesise how this learning may operate at such a fine scale.

First, we consider whether these routes could be learnt through generalisable associate learning in previous natural round-island movements, where the reward of reaching home sooner reinforces the route choice in future encounters (Guilford & Burt de Perera, 2017; Pearce, 2008). However, for this association to form, the difference in the perceived value between the two choices should be detectable (Guilford & Burt de Perera, 2017). In classical choice experiments this value would be apparent in the prescribed magnitude of reward received (Sutherland & Mackintosh, 1971), which here would translate to the reduction in flight time taken to reach the reward of arriving back at the nest. Whilst these routes indeed differ in such value, the detectability of this difference may be debatable, as at this spatial scale the temporal (and presumably energetic) costs of these routes are near identical in absolute terms (a difference between mean flight timings of just 344 seconds), particularly when considering the typical distances travelled by this species (Guilford et al., 2008; Padget et al., 2019), and so this similarity may impede generalised associative learning. Whilst this low salience between the absolute differences in route value may lead us to reasonably conclude that associative learning cannot underpin route efficiencies at these fine spatial scales, alternative cognitive representations of these differences in route value may facilitate their detection.

Whilst the absolute difference of route cost is low, we see that when considered relative to one another, the shorter routes offer a near 50% reduction in distance and subsequent flight time to reach the colony (**Table 3.1**), which marks a significant increase in route efficiency in the context of the task. Weber's Law is a

psychological phenomenon that states that the proportional contrast is of greater importance than the absolute contrast in the salience of a dichotomy (Brus et al., 2019) and could be invoked at this fine scale to explain how routes which offer high relative, but low absolute, differences in reward could still be learnt under a generalised associative framework, assuming these birds are capable of this relative comparison (Bateson & Kacelnik, 1995).

If these small-scale route efficiencies are not underpinned by generalised associative learning however, then it is instead probable that some kind of 'latent learning' is involved. Latent learning is broadly defined as the association of stimuli without direct reinforcement and employs a specially evolved cognitive module to pay attention to, and associate, primed stimuli without the apparent rewards required under an associative framework (Wang & Hayden, 2021). These modules have evolved to pay attention to specific stimuli, usually of significant fitness importance to the animal (Öhman & Mineka, 2001), at the cost of the generality of associative learning where any salient stimulus can be learnt. In the context of navigation, this led to the expectation of a module evolved for the detection of route efficiencies and the subsequent discovery of the cognitive map, which appears to facilitate the learning and recall of efficient routes and spatial information in absence of reward in a range of taxa (Singer et al., 2006; Toledo et al., 2020; Tolman, 1948; Wang & Hayden, 2021). This too could be present here where, despite the potential lack of salient rewards to associatively encode such fine scale route improvements, these birds are able to successfully adopt efficient routes around the island upon release.

Whilst offering an intriguing direction for discussion and future study, this nuance in the learning mechanisms of fine scale shearwater navigation is perhaps beyond the scope of this study. What we can conclude however, is that the route efficiencies demonstrated here by shearwaters when displaced at a fine spatial scale are likely achieved through learning mechanisms facilitated by a high familiarity with this localised circumnavigation task.

Here, we have shown that shearwaters are able to make efficient route choices, even at fine scales, and that this is unlikely to be underpinned by the generalised

navigation strategies such as the large-scale maps employed when homing over longer distances, but rather through familiarity with the task and the learning of optimal routes. Whilst it is plausible that these route efficiencies at the local scale could involve an evolutionarily primed module, such as the cognitive map of mammals, we cannot rule out the potential for associative learning without knowing if shearwaters are able to compare the relative of values of similar routes or are extremely sensitive to nuanced differences in route rewards. We therefore suggest that future studies should aim to manipulate the rewards of getting home (for example by delaying the entry to the nest for specific route choices) to switch their route preferences to gain further insight to the detection and learning of these small-scale route efficiencies.

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Chapter 4

Evidence for learning in the circumnavigation decisions of at-sea obstacles in free-ranging shearwaters



With contributions from Joe Wynn, Patrick Lewin, Joe Morford, Tim Guilford, and Oliver Padget. Additional thanks are extended to the contributors of the long-term Manx shearwater dataset.

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Abstract

Manx shearwaters, *Puffinus puffinus*, are impressive oceanic navigators, capable of locating their colony with pinpoint accuracy from hundreds of kilometres away. Whilst the calculation of this direct course to home, termed the beeline, is extremely precise, they fail to account for intervening landmasses between themselves and home, resulting in longer homing routes as they must then circumnavigate these obstacles when encountered due to their reluctance to fly over land. However, despite not initially accounting for these obstacles, shearwaters often adopt the shorter of the two available routes of circumnavigation when an island intercepts their homeward beeline. What do shearwaters understand about these obstacles, and their place in the space, if this knowledge is apparently not used at the time of beeline calculation? In this chapter, I look for patterns in the performance of shearwaters in this vast maze-like natural experiment to investigate evidence of route learning by using a large free-ranging tracking database of shearwater movements around the British Isles. First, I identify the circumnavigation routes available when a shearwater encounters an obstacle during homing, calculating the differences in flight distance between the routes, identifying which route they adopted during their outward journey, and estimating their familiarity with this task. By analysing shearwaters' performance at choosing the shorter route, I show that a shearwater's route choice improves with experience, and when the cost of adopting the longer of two routes increases. Finally, I introduce the concept of auxiliary outward journey information in the context of these results. These findings show that shearwaters appear to learn costly detours that they may take when encountering at-sea obstacles and probably have some allocentric map-like representation of landmasses that facilitates this efficient circumnavigation. Having to learn routes such as this might be one reason for the delayed onset of breeding in many species with long distance foraging trips in the marine environment.

Introduction

The role of Manx shearwaters, *Puffinus puffinus*, as a model of avian navigation has grown rapidly owing to advantages over traditional homing pigeons and other species confined to exhibit spatial behaviour in a laboratory or domestic environment. Long-distance movements of seabirds allow us to investigate this remarkable behaviour in more ecological contexts (Gagliardo et al., 2013; Guilford et al., 2008; Padget et al., 2019). These seabirds frequently travel hundreds of kilometres across open ocean to reach foraging grounds, travelling both above and through a fluid medium, and often out of sight of any visual landmarks (Guilford et al., 2008). Yet, at the point at which they decide to return home, they determine the direction and distance to their colony with high accuracy, producing a direct course termed a beeline (Matthews, 1953; Padget et al., 2019).

This initial orientation appears to be blind to intervening obstacles such as islands or peninsulas (Padget et al., 2019). Meaning that, rather than anticipating an obstruction to this beeline and adjusting their trajectory accordingly to instead adopt the shortest at-sea flyable route around such obstacles, birds instead fly directly towards them and must then circumnavigate them once it becomes apparent that their beeline is no longer viable (Padget et al., 2019, 2022). The consequence is that the resulting trajectory home is less efficient than theoretically possible, hinting that whatever mechanism is used in the formation of this beeline is constrained not to encode intervening obstacles. The computation of the beeline home is therefore probably achieved via true navigation (see **Chapter 1**), a process where the values of intersecting environmental gradients detected at the bird's current location are compared against learnt values close to home, producing a beeline between the two without the aid of goal emanating cues or outward journey information (Guilford & Burt de Perera, 2017; Holland, 2014; Padget et al., 2019).

Even in the absence of this anticipation, shearwaters indeed appear able to determine the more efficient route to circumnavigate these landmasses during natural movements. This could be achieved by either using knowledge of these

landmasses and the routes available around them (Dall'Antonia et al., 1995; Padget et al., 2022; Pollonara et al., 2015), or by recapitulating the outward journey (Padget et al., 2022; Papi et al., 1973; Wehner & Räber, 1979).

If route knowledge is used here, it must be acquired through learning, facilitated by repeated encounters of these circumnavigation tasks during natural movements (Bonadonna et al., 1997; Collett, 2010; Meade et al., 2005; Tello-Ramos et al., 2022). There is strong evidence from both laboratory and field studies that show animals can refine and update their navigation through repeated exposure to a task. Rodents show improved performance in maze tasks over time (Morris, 1984; Tolman, 1948; Wijnen et al., 2024) whilst homing pigeons exhibit more direct flight paths when repeatedly released from the same site, suggesting route learning and refinements to their spatial memory (Biro et al., 2004; Guilford & Biro, 2014; Meade et al., 2005). Furthermore, when released from beyond novel topographic obstacles we find that pigeons are able to refine their routes of circumnavigation through repeated releases, further contextualising this route refinement in face of such obstructions (Bonadonna et al., 1997).

Two major hallmarks of route learning should exist in this data if shearwaters learn to circumnavigate obstacles through repeated experience. First, shearwaters should make more efficient navigational decisions when circumnavigating obstacles with which they are more familiar (Bonadonna et al., 1997; Guilford & Biro, 2014). Second, contrasting routes of bigger consequence should be learned more readily. Evidence from controlled learning experiments would suggest that animals are more attentive to, and more readily learn a preference for, stimuli that convey a greater reward, or cost, than available alternatives (Bower & Hilgard, 1984; Claudi et al., 2022; Kacelnik et al., 2023; Treviño, 2016). In shearwaters, it may then be that landmasses which have larger discrepancies between the flight distances of their circumnavigation routes (i.e. where route values are more salient) are more readily integrated into their allocentric representations of space, as wrongly adopting an inefficient route

around such obstacles would be more costly (Guilford & Burt de Perera, 2017; Padget et al., 2022).

Alternatively, it could be that, rather than learning an array of obstacles and their associated routes, it is cognitively less intensive to recapitulate the route adopted on their outward journey (Padget et al., 2022). Whilst the use of path integration processes, such as those seen in insect species (Muller & Wehner, 1988), are challenged in navigation at the scales covered during shearwater movements (but see **Chapter 5**; Biegler, 2000; Guilford et al., 2008; Padget et al., 2019), shearwaters may still recall auxiliary information gathered on the outward leg of their foraging trip to facilitate their return. For example, recalling the egocentric position of an obstacle when passed on the outward journey (e.g. the landmass was on my left), and reversing this during homing (e.g. so keep the landmass on my right), would ensure sufficient circumnavigation (Able, 2001; Padget et al., 2022).

To investigate these potential mechanisms of obstacle circumnavigation, in this chapter I look for evidence of learnt route efficiencies and the role of outward journey information in free-ranging Manx shearwater movements when homing from beyond a landmass. Specifically, I look for evidence of experience-mediated improvements in obstacle circumnavigation, the potential influence of outward journey information on route choice, and whether increasing discrepancies between route values produce stronger preferences for the more efficient route. Specifically, I predict that shearwaters will more readily adopt the shorter route of obstacle circumnavigation when the discrepancy between this and the alternative is larger.

Methods

Data availability and processing

Breeding Manx shearwaters were tracked using on-board GPS loggers across six colonies around the British Isles (**Figure 4.1B**; Skomer Island [51°44'14.7"N, 5°16'55.6"W], Skokholm Island [51°41'37.8"N, 5°17'13.9"W] and Ramsey Island [51°52'26.6"N, 5°20'0.8"W], South Irish Sea, Wales; Lighthouse Island [54°41'43.0''N, 5°15'3.9''W], Copeland Islands, Northern Ireland; Rum [56°59'23.1''N, 6°17'11.0''W], Hebrides, Scotland; Lundy [51°10'6.7''N, 4°40'32.5'' W], Bristol Channel, England) between 2004 and 2024 during both the incubation (May-June) and chick-rearing (July-August) periods of their breeding season as part of an ongoing long-term monitoring effort. All devices were attached dorsally to the birds using TESA marine tape, following the protocols outlined in Guilford et al. (2008) and no device weighed more than 4% of the bird's total body mass (Portugal & White, 2018). Devices were scheduled to take fixes at a range of intervals throughout this tracking effort (from 1-60 minutes).

Individual foraging trips were separated by each return to the colony. Data quality filters were applied to ensure foraging trips contained sufficient detail for analysis. For a trip to be taken forward, GPS fix intervals could not exceed 30-minutes, there must be a minimum of 50 fixes, and the bird must have reached a minimum distance from the colony of 25 km. Trips were filtered for speed to remove GPS errors, excluding any fixes travelling above 80km h^{-1} (as seen in the upper speed threshold of Guilford et al., 2008). These trips were then interpolated to 5-minute intervals using a cubic spline interpolation algorithm (Tremblay et al., 2006).

The onset of homing marks a clear behavioural switch between non-directed mid speed foraging movements, or rest, and a continuous, directed bout of movement in the homeward direction (Padget et al., 2019). This produces a steep decline in the distance from home, and the start of this decline can be taken as the point at which the bird began to home. I identified these points manually, through visual inspection of the relationship of distance from home through time, blind with

respect to details of each trip. This manual identification was validated using a subset of tracks, randomly resampled and identified, with individual researchers having above 98% repeatability (see **Chapter 2** for more details). Only trips that contained a complete (or near complete, >90% reduction in distance from home from the onset of homing) homing period were taken into the analysis.

After all filtering, there were 2,004 foraging trips originating from 1,110 GPS deployments across 799 individual shearwaters available for analysis (**Figure 4.1A**).

Obstacle identification

Intervening obstacles were identified along the trajectory of each homing period in the dataset. This was achieved by first downsampling the homing data so that there was at least 5 km of movement between each fix (to reduce computational demand). Then, for every fix, a beeline was projected from each location to the home colony, defined as the Great Circle arc between the bird's current location and the colony, as in Padget et al. (2019), calculated using the 'distHaversine' function in the 'geosphere' R package. Each constructed beeline was then run through a geometric interception ('st_intersect' from the 'sf' package) with all known landmasses within the bounds of the tracking dataset, retrieved as shapefiles from the Natural Earth public database (accessed through the 'rnaturalearth' package).

Since we know that shearwaters do not anticipate obstacles along the homeward beeline at the onset of homing (Padget et al., 2019), for a landmass to be registered as an obstacle to this projected beeline, it had to be visible from the current location of the bird (**Figure 4.2A**). This visibility was calculated by computing the maximum visibility radii from all points of elevation within each landmass shapefile and assessing whether the bird's location fell within this area of visibility. To avoid an oversensitivity to obstacles along this beeline, a threshold was set where a landmass must both continually intervene the beelines and be visible for four continuous fixes of the homing period for it to be retained as an obstacle. If multiple obstacles were encountered sequentially through a homing

trajectory, these were identified and processed separately as individual circumnavigation decisions.

From the 2,004 individual foraging trips present within the available dataset, 1,094 (54.46%) of these began homing from beyond some form of landmass obstruction. After the quality filtering described above, there were 789 instances of obstacle circumnavigation present for analysis, originating from 699 foraging trips spanning 450 individual shearwaters (**Figure 4.1**).

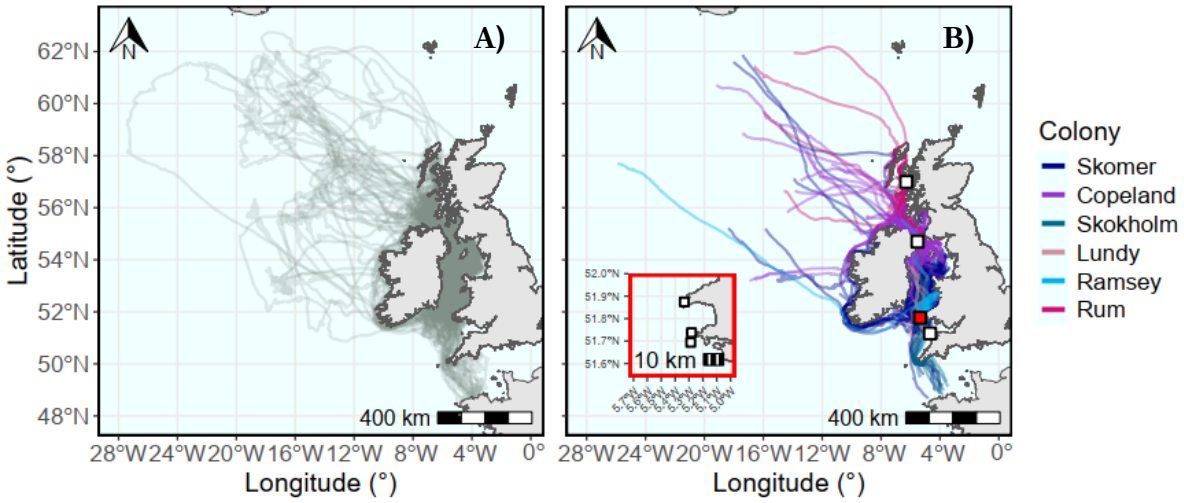


Figure 4.1. Maps of the British Isles showing **A**) the full database available for this study and **B**) the homing trajectories of all foraging trips within this dataset that begin homing from beyond an obstacle. Trips are coloured by colony, which are indicated on the plot by white squares. The Pembrokeshire colonies can be seen in the zoomed inset plot due to their proximity.

Circumnavigation route calculation

For each landmass identified as an obstacle to the bird's homeward beeline, the potential routes of circumnavigation were calculated around it. To do this, I identified the point at which the obstructed homeward beeline intersected the target landmass, using the beeline taken from the first fix at which the obstacle was visible, and this point was termed the learning point (red square; **Figure 4.2B**). This point was used as the reference for circumnavigation calculations as, presumably, when a given bird encounters an obstacle for the first time it continues along its projected beeline until it cannot, and then makes novel movements to circumnavigate the landmass following that (Padget et al., 2019). Therefore, any representations of route value that it may form from experience with this task will plausibly have stemmed from this initial point of beeline intersection.

From this learning point it was then possible to calculate the circumnavigation route in either direction (clockwise or anticlockwise). We calculated two representations of potential circumnavigation routes from this learning points, first as the absolute coastal distance, taking the cumulative distance of the obstacle shapefile along its perimeter from the point closest to this learning point to the point closest to the home colony (solid lines; **Figure 4.2B**). This method represented a 'coast following' route, incurring all the inefficiencies of the obstacle's geography, including inlets and bays, as seen in movements made following displacement (Padget et al., 2022). The second representation of routes was computed by creating a convex hull of the landmass (dashed lines; **Figure 4.2D**, see **Supplementary Materials S4.1** for additional details regarding these hulls) which accounted for potentially shorter routes if birds anticipated the shape of the obstacle and avoided moving into bays, as seen in the natural movements in Padget et al. (2022). Both representations of routes were trimmed to the first point at which the beeline home becomes unobstructed again, assuming that at this point the bird would adopt this updated beeline rather than continuing along the coastline of the obstacle.

To assign which circumnavigation direction the homing trajectory then followed, the bird's track was isolated between the learning point and point where the bird's beeline was no longer obstructed by the present landmass, and the nearest neighbour distances between this section of homing and the two circumnavigation directions were computed, with which had the greater proximity to the bird's path being taken as the direction of circumnavigation (**Figure 4.2C**). This was repeated for the outward journey (the flight period away from the colony at the beginning of the foraging trip), so that this could be compared to the return direction.

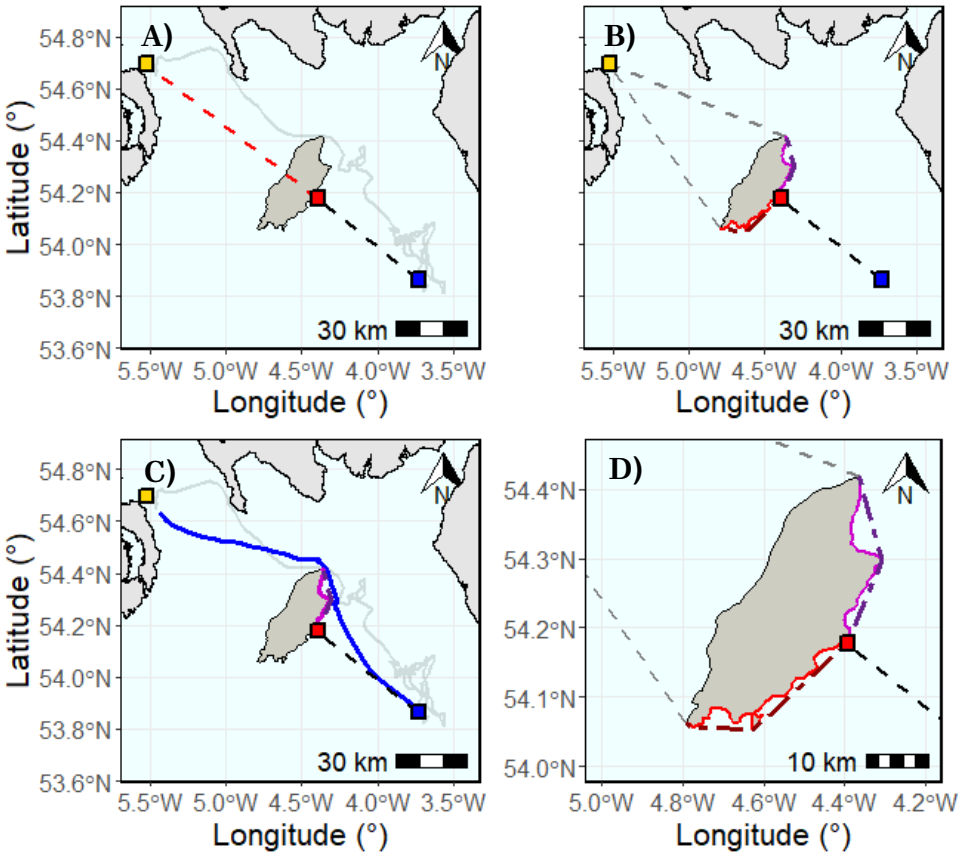


Figure 4.2. A schematic showing obstacle identification and route calculation for a foraging trip. In **A**) the homeward beeline to the Copeland colony (dashed line) is obstructed by the Isle of Man. This point of intersection, the learning point (red square), is used to calculate circumnavigation routes in both directions as in **B**), solid lines indicate coastal routes, and dashed lines indicate convex hull routes. These routes end their circumnavigation once the beeline becomes clear again (grey dashed lines). Finally, in **C**) the real homing trajectory (blue) is compared against these routes to identify which the bird took. **D**) shows the coastal and convex hull routes as in **B**) but are zoomed to aid visualisation. The route taken on the outward journey is shown in **A**) and **C**) in grey.

Metrics and analysis

Each instance of obstacle circumnavigation was categorised by the bird's success in adopting the shorter of the two possible circumnavigation routes. Route choice likelihoods of then adopting this shorter route were tested across the dataset using two-tailed binomial tests. There could be various drivers of route preferences in these circumnavigation tasks, and so I extracted and modelled multiple metrics. Route choice likelihood was used as the response variable in all binomial linear regression models to test predictions.

First, the experience level an individual has with a given circumnavigation task, or how many times it has encountered a given landmass, could likely influence its route decision. Whilst the dataset used here does not have sufficient intra-individual tracking to deduce individual levels of experience, it can be used to derive a colony-specific population level proxies of experience. To do this, I calculated the expected encounter rate, as the number of instances of circumnavigation, of each landmass as a function of colony across the data, and modelled this against choice likelihoods:

Route choice ~ Expected encounter rate + (1|Ring) + (1|Colony) + (1|Landmass ID)

Secondly, if this route choice is underpinned through learning, then it is likely that the difference in reward (reduction in route distance) would predict the strength of route preferences between obstacles. The distance of each available route was calculated by summing together the distance of the circumnavigation around the obstacle in that direction, and the resultant distance back to the colony once the beeline became unobstructed. The difference between these distances for the two route options (clockwise and anticlockwise) was then calculated as both the absolute value, subtracting one from the other, and the proportional value, expressed as the difference in route distances divided by the distance of the shorter route, to account for various plausible representations of stimuli salience in comparative learning models (Brus et al., 2019; Kacelnik et al., 2023). These values were first scaled (to improve model interpretability) before being modelled against the route choice likelihoods for both the coastal and convex hull

projections of routes. I then used Akaike's Information Criterion (AIC; Akaike, 1974) to compare candidate models and determine the best supported representation of routes (coastal or hull) and route difference values (absolute or proportional). AIC balances model fit against model complexity, with lower AIC values indicating models expected to minimise information loss (Burnham & Anderson, 2002). AIC was selected for model comparison as the objective here was to compare the relative support for a set of biologically plausible candidate models describing route choice behaviour, rather than to identify a single 'true' model, as is emphasised more strongly by Bayesian Information Criterion (Burnham & Anderson, 2002).

Coastal route models are given here, see **Supplementary Materials S4.2** for the convex hull equivalents:

Route choice ~ scaled (absolute coastal difference) + (1|Ring) + (1|Colony)

Route choice ~ scaled (proportional coastal difference) + (1|Ring) + (1|Colony)

Once the model with the strongest support was identified through AIC comparison, the same model structure was repeated on a subset of the data that excluded instances of circumnavigation around the landmass of Great Britain, as this obstacle is of a disproportionate scale to all others, and could potentially overrepresent the effect in the data (**S4.2**).

Finally, it is plausible that, rather than identifying which circumnavigation route is shorter, birds instead recapitulate the route adopted on their outward journey. Therefore, a model was constructed testing whether both the shorter route available and the outward route taken predicted the homing route chosen (this model was also repeated on a subset of data excluding Great Britain; **S2**):

Homing route ~ outward route + shorter route + (1|Ring) + (1|Colony) + (1|Landmass ID)

Results

Obstacle occurrence

A mean of 1.27 (± 0.74_{SD}) obstacles were encountered per trip (ranging from 1 to 8), with this significantly varying between colonies (F = 39.28, p = <0.001), owing to birds from Rum encountering more obstacles than any other island, probably due to its position amongst the Hebrides (**Table 4.1**). Birds adopted the shorter route when circumnavigating an obstacle 91.13% of the time in this dataset (719/789 instances), showing a significant preference for the shorter route (p = <0.001, 1-sample proportions test).

Table 4.1. The number of trips, birds, and mean number of obstacles encountered per trip as split by colony. *** indicates a significant difference in number of obstacles compared to all other colonies using an ANOVA model.

Colony	**No. of trips**	**No. of birds**	**Mean Obstacles per trip (±SD)**
Copeland	188	137	1.19 (0.51)
Lundy	5	4	1.00 (0.00)
Ramsey	28	14	1.18 (0.61)
Rum	31	22	***2.90 (1.89)*** ***
Skomer	431	264	1.20 (0.55)
Skokholm	16	9	1.31 (0.60)

Landmass encounter rate

The expected encounter rate of obstacles as a proxy for experience significantly increased the likelihood of a given bird adopting the shorter route (β = 0.005, *SE* = 0.002, *z* = 2.601, *p* = 0.009). This result is illustrated in **Figure 4.3** which shows that, whilst not statistically tested, birds from the Copeland colony that encounter the Isle of Man more frequently always adopt the shorter route when returning from beyond it. On the contrary, in the single instance that a Skomer bird encountered this obstacle, the bird was unable to correctly identify the shorter route. Substantial variation was observed between landmass ID (SD = 1.44) in this model, indicating consistent differences in route choice likelihoods across the landmasses encountered in the dataset. Effects persisted with the exclusion of Great Britain from the database (**S4.3**).

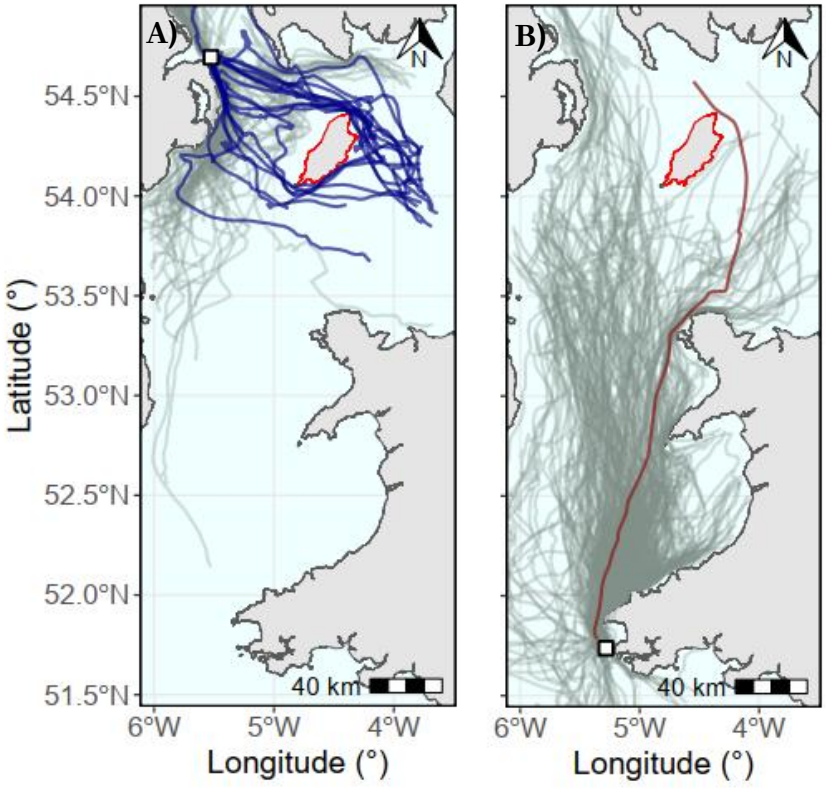


Figure 4.3. Two plots showing all homing data in grey and the trajectories from birds that circumnavigate the Isle of Man (outlined in red) from **A**) Copeland, with 14 instances of circumnavigation, which all birds adopt the shorter route (blue lines), and **B**) Skomer, with a single instance of circumnavigation where the bird took the longer route (red line).

Route reward differences

All models of route representation and value significantly predicted the observed route choice likelihoods when modelled individually (See **Supplementary Materials S4.2** and **S4.3**). However, the model structure using absolute route value differences between coastal representations of routes had the best fit (AIC = 349.0), with competing models having significantly higher AIC values ($\Delta AIC \geq 7.0$), indicating weaker support. Therefore, the coastal absolute model will be prioritised in the main text, with full results from all models provided in **S3.** This model indicated that increasing absolute route differences significantly improved the likelihood of birds adopting the shorter circumnavigation route ($\beta = 1.893$, SE = 0.258, $z = 7.350$, $p < 0.001$). Effects persisted with the exclusion of Great Britain from the database (**S4.3**). By simulating this model output across the range of absolute route difference values seen in the dataset we can see that, even at very low values, birds have a higher than chance likelihood of adopting the shorter route (~75%, **Figure 4.4**). Since coastal representations of routes were in all cases better fits for the data than convex hull representations (**S3**), I further compared the perceptions of coastal route value differences by modelling both the absolute and proportional values within a single model (M_8). In this, the absolute values remained the better predictor ($\beta = 1.570$, SE = 0.353, $z = 4.443$, $p < 0.001$), whilst proportional values were no longer significant predictors of route choice likelihoods ($\beta = 0.667$, SE = 0.628, $z = 1.062$, $p = 0.288$). This is likely a product of high collinearity between these two perceptions of route values ($r = 0.779$).

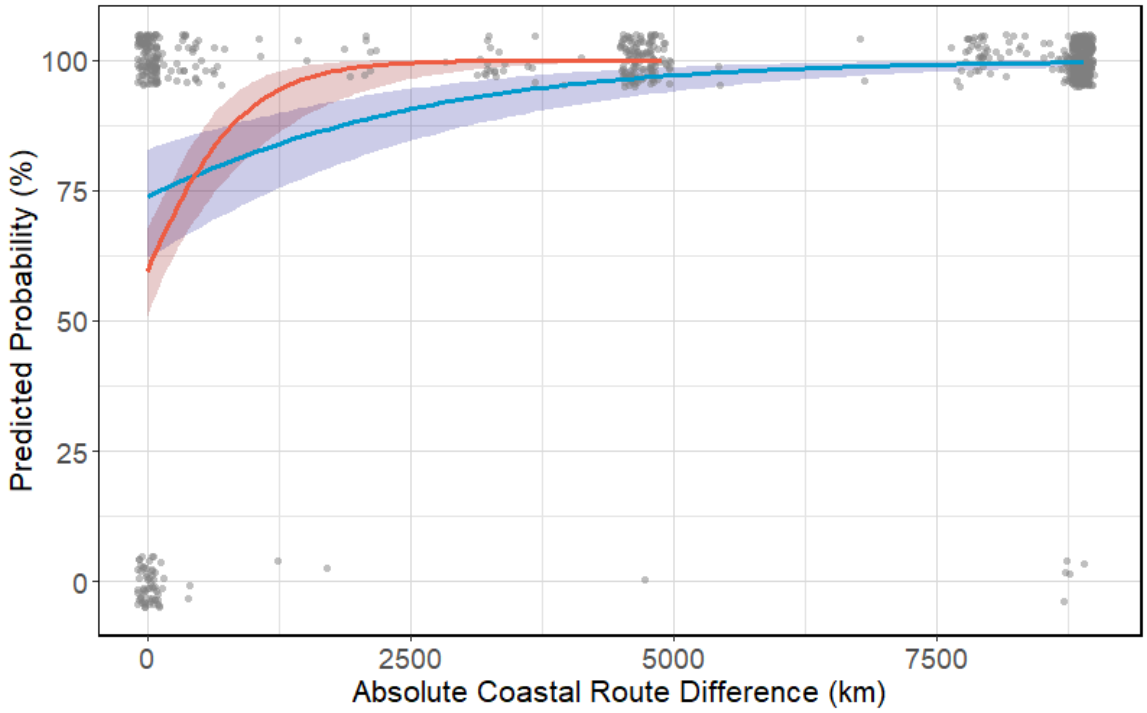


Figure 4.4. The relationship between the absolute distance (km) between coastal routes of circumnavigation and the probability of a shearwater adopting the shorter route. The blue line indicates the likelihood and relationship for the full dataset within this model, whilst the red line uses a model that excludes all instances of Great Britain, to ensure there is not overrepresentation. These probabilities were calculated using the predicted likelihoods taken from the model outputs.

Outward journey recapitulation

Both the route taken on the outward journey, and which route was shorter at the time of homing strongly increased the odds of a bird returning via a given route. However, which route was shorter had a much stronger effect on ultimate route choice than which was adopted on the outward route (**Figure 4.5**). For example, birds that had taken route B on the outward journey were ~13 times more likely to return via B ($\beta = 2.568$, SE = 0.337, $z = 7.622$, $p < 0.001$, **Figure 4.5**), but birds for which route B was the shorter option were ~42.6 times more likely to return via B ($\beta = 3.752$, SE = 0.431, $z = 8.705$, $p < 0.001$, **Figure 4.5**). The correlation between fixed-effect estimates was low between these two predictors ($r = -0.056$), indicating minimal collinearity. Effects persisted with the exclusion of Great Britain from the database (**S4.3**).

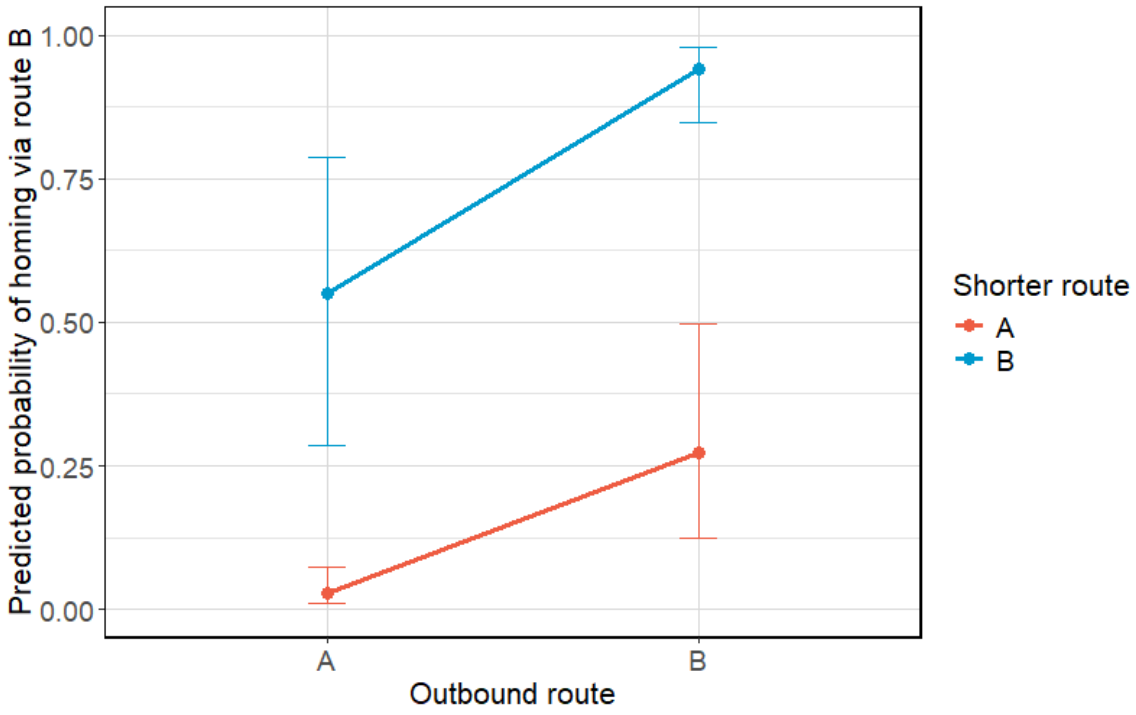


Figure 4.5. The influences of both outward journey route and which route is the shorter option at the time of homing, on the probability of homing via a specific route, given here as the probability of adopting route B. Error bars show the approximate 95% confidence intervals for the predicted probabilities from the fixed-effects portion of the model.

Discussion

Previous studies have shown how, during natural movements, shearwaters are able to circumnavigate intervening obstacles to their homeward course efficiently but have failed to distinguish between outward journey route recapitulation and some sort of route-learning as the underpinning mechanism (Dall'Antonia et al., 1995; Padget et al., 2019, 2022; Pollonara et al., 2015). Here I provide the first empirical evidence for which of these cognitive processes is most likely to facilitate efficient route decisions when encountering obstacles. While correlative, the relationships presented here support the involvement of learning in this navigational decision making, primarily facilitated through experience with the task and the salience within the reward values of route dichotomies, with residual influences of the route adopted on the outward journey.

This study shows that the colony-specific encounter rate of obstacles predicts the likelihood of birds making efficient circumnavigation decisions around them. Despite the lack of inference of individual-specific experience within this dataset, this colony-level proxy likely still represents a significant estimate of an individual's familiarity with obstacles. Several studies have shown both intra- and inter-annual consistency in foraging ground attendance by individuals tracked from the same colonies (Avalos et al., 2017; Dean et al., 2012, 2015; Jaggers, 2023). Furthermore, with available sources of colony-specific information about foraging locations, it seems plausible that individuals from the same colony will have shared knowledge of local foraging grounds, and as a result the obstacles that intervene between these and their home (Padget et al., 2018; Richards et al., 2019; Weimerskirch et al., 2010).

This result is supported by other findings in avian models that demonstrate increasing experience with a navigational task facilitates the learning and refinement of homing routes, as well as hippocampal development, both shown to mediate improvements in homing performance (Biro et al., 2004; Bonadonna et al., 1997; Cnotka et al., 2008; Flack et al., 2014; Gagliardo et al., 2014; Meade et al., 2005). Perhaps central to this concept of route refinement, and to future investigation of this in shearwaters, is the tendency for route efficiency to

asymptote after multiple encounters with the task (Meade et al., 2005). By the time shearwaters are of breeding age and subsequentially candidates to be tracked in this dataset, they are likely to have already spent multiple years foraging within these localised areas as non-breeders, learning about the spatial structure of these obstacles and resultant circumnavigation routes (Brooke, 1990; Perrins et al., 1973; Wynn et al., 2025). When opportunities allow for the tracking of both immature and adult seabirds, it has been shown that immatures rapidly learn efficient navigational choices (Wynn et al., 2020; Yoda et al., 2017), perhaps explaining the high efficiency I find in the circumnavigation decisions here, as all tracked individuals are adults. Alternatively, rather than this expected encounter rate relating to an assumed familiarity with a given obstacle through repeated encounters, it could instead infer the recency with which the obstacle was last encountered, which, whilst still mediating effective route choices, would represent different underpinning cognitive mechanisms (Reed, 2018; Sutton & Barto, 1998; Worthy & Maddox, 2014).

In path integration, outward journey information is integrated to produce a homeward vector (Wehner, 2003), but such a vector would, like the beeline produced from true navigation processes, be blind to intervening landmasses (Padget et al., 2019). Therefore, path integration could not provide information as to which obstacle circumnavigation route was most efficient. However, this does not mean that some information collected by a shearwater on the outward journey might inform and improve homing performance. Such "auxiliary outward journey information" (Padget et al., 2022), rather than providing a homeward vector, could help to guide movement decisions at key points during homing, such as obstacle encounter. This guidance could arise from the recognition of landmarks experienced during the outward journey (Collett & Zeil, 1997; Guilford & Biro, 2014; Holland, 2003), or by remembering the side land appeared on this outward leg and inverting this egocentrically to recapitulate this route (Padget et al., 2022).

However, if this OJI was the primary source of knowledge facilitating obstacle circumnavigation, we would expect all birds to recapitulate their outward routes,

but this is not the case. Instead, I found that a significant proportion of individuals depart from the route taken on their outward journey in favour of a now shorter alternative. This implies that they have an allocentric understanding of these obstacles beyond simplified egocentric representations recalled from their outward journey (Alvernhe et al., 2012; Collett et al., 2007; Toledo et al., 2020). Indeed, these results show that, whilst the route adopted on the outward journey influences route choices during homing, that which offers a shorter circumnavigation option has a much stronger effect. That being said, we find the greatest likelihood of correct route adoption when the route that offers the shortest flight distance is also that which was adopted on the outward journey. Therefore, it is likely that, whilst the learnt relationships between these routes are more informative to homing decisions, these shearwaters likely incorporate some information attended to on the outward journey for route guidance. This is reinforced in the finding that displaced Manx shearwaters, who are denied outward journey information, make costly circumnavigation decisions that are never seen in this natural dataset (Padget et al., 2022).

Here I show that the likelihood of adopting the shorter route of circumnavigation is predicted by increasing discrepancies between the reward values of route options, supporting the theory that associative learning is involved in this decision process. Under a generalised associative learning framework, we would expect route preferences to be more apparent when the reward of the shorter route, here seen as a faster return to the colony and reduced flight cost, far exceeds the alternative (Bateson & Kacelnik, 1995; Guilford & Burt de Perera, 2017; Pearce, 2008). With larger landmasses, this comparison of route values to distinguish the more efficient choice seems very plausible, as large discrepancies in flight energetics or arrival time between routes would be salient to the bird.

With smaller landmasses however, or in instances where alternate routes are similar in length, the detectability of such differences in route value may become less apparent (as discussed in **Chapter 3**; Kacelnik et al., 2023; Mackintosh, 1974). This is why multiple representations of route reward value were included in my models. Whilst the absolute value fits in most generalised associative

frameworks, the proportional value tested a principle termed Weber's Law, which could explain how route preferences may still develop when the absolute values in route reward seems functionally indistinguishable. This law states that it is the proportional disparity between alternatives, rather than the absolute difference, that more significantly affects the perceived salience of a dichotomy (Brus et al., 2019). Other species have been shown to be sensitive to these proportional differences in rewards and timings when faced with experimental choice tasks (Bateson & Kacelnik, 1995; Gibbon, 1977; Kacelnik et al., 2023; Namboodiri et al., 2014; Roberts, 1981), whilst pigeons have been shown to encode relative, but not absolute, geometry in spatial learning (Kelly & Spetch, 2001). Whilst these proportional values were significant predictors in this analysis, the absolute values had a stronger predictive power, especially where both perceptions of route value were included in the same model. Whilst this result does not support the use of Weber's Law, the support for differences in route values being both perceivable and influential to shearwaters during this decision-making process is widely evident.

An unexpected finding here was that, even with very low absolute route differences, shearwaters appear more likely than chance to adopt the shorter route (~60-75% at route differences around 1 km, **Figure 4.5**). Whilst this level of comparison may appear implausible under a purely associative framework, owing to the presumed low salience of such route differences, results from **Chapter 3** would suggest that these birds are able to detect fine-scale improvements in routes, at least in areas with which they are highly familiar. As discussed in Guilford & Burt de Perera (2017), perhaps, with the extensive repetition of these circumnavigation tasks in natural movements, shearwaters are able to associatively learn such fine-scale route improvements (see **Chapter 3**). Equally, it is plausible that the need for effective navigation may have favoured the evolution of a specific cognitive module to detect and associate primed stimuli without direct reinforcement, such as the cognitive map (O'Keefe & Nadel, 1978; Singer et al., 2006; Toledo et al., 2020; Tolman, 1948; Wang & Hayden, 2021).

Whilst this study has presented strong evidence for the role of learning in obstacle circumnavigation tasks within free-ranging Manx shearwater movements, we do not yet know which models of learning, or cognitive representations of route value, facilitate this. I demonstrate here that birds are more likely to adopt the efficient route of circumnavigation around obstacles that they plausibly encounter more frequently, and when the discrepancy between route value dichotomies is greater, which fits within a generalised associative framework of learning. I also demonstrate that even when route discrepancies are small, birds often make efficient navigational decisions, indicating a high capacity to distinguish route discrepancies, or potentially the presence of additional cognitive modules to facilitate such. Finally, I demonstrate the involvement, but not reliance upon, auxiliary outward journey information in aiding route decisions. Future studies should prioritise tracking immature birds, in attempts to witness the development of route preferences and learning in the wild and should carefully consider experimental displacements which could allude to the underlying learning mechanisms within these route choices.

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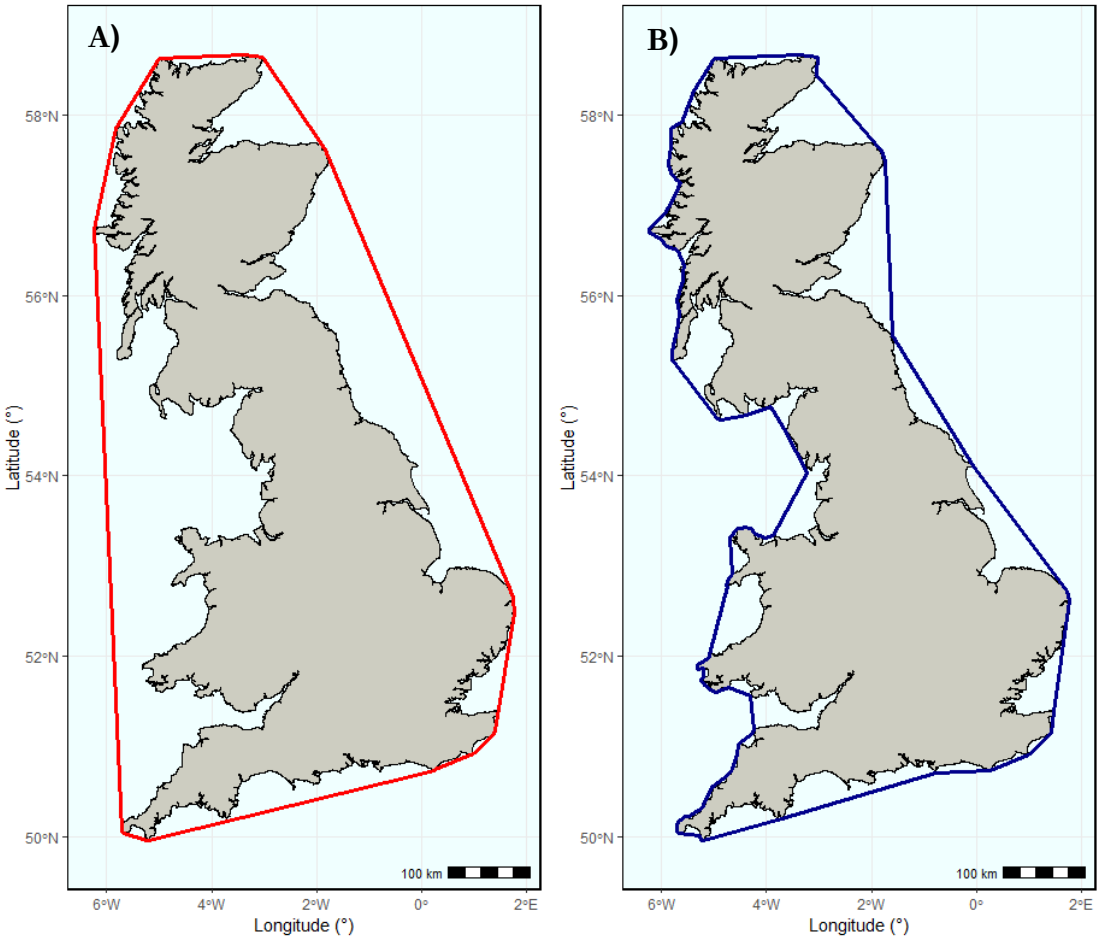
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Supplementary Materials

S4.1 – Convex hull calculations

For all islands except the landmass of Great Britain, the convex hull was calculated using the 'chull' function in R from the 'grDevices' package. Due to Great Britain's shape and scale, the convex hull created by this function spanned from Kintyre in Scotland to Land's End in Cornwall (**S4.1A**) which made this hull nonapplicable to the data, particularly in instances where birds began to home from areas within this hull, such as the waters near Liverpool. Instead, a more detailed hull was made manually by identifying points along the primary coastline of Great Britain, producing a simplified shape which would create routes that avoid bays and inlets whilst conforming to the general geometry of the landmass (**S4.1B**).



S4.1. Two plots showing the **A**) convex hull created by the 'chull' function in R, and **B**) the manual hull created and used for analysis.

S4.2 *– Model structures*

$\mathbf{M_1}$ – Expected encounter rate:

Route choice ~ Expected encounter rate + (1|Ring) + (1|Colony) + (1|Landmass ID)

$\mathbf{M_2}$ – Expected encounter rate (excluding Great Britain):

Route choice ~ Expected encounter rate + (1|Ring) + (1|Colony) + (1|Landmass ID)

$\mathbf{M_{3\text{-}4}}$ – Coastal route representations of route differences:

Route choice ~ scaled (absolute coastal difference) + (1|Colony)

Route choice ~ scaled (proportional coastal difference) + (1|Colony)

$\mathbf{M_{5\text{-}6}}$ – Convex hull route representations of route differences:

Route choice ~ scaled (absolute hull difference) + (1|Colony)

Route choice ~ scaled (proportional hull difference) + (1|Colony)

$\mathbf{M_7}$ – Coastal route representations of route differences (excluding Great Britain):

Route choice ~ scaled (absolute coastal difference) + (1|Ring) + (1|Colony)

$\mathbf{M_8}$ – Coastal route representations of route differences (merged model):

Route choice ~ scaled (absolute coastal difference) + scaled (proportional coastal difference) + (1|Ring) + (1|Colony)

$\mathbf{M_9}$ – Outward journey and the shorter route:

Homing route ~ outward route + Shorter route + (1|Ring) + (1|Colony) + (1|Landmass ID)

$\mathbf{M_{10}}$ – Outward journey and the shorter route (excluding Great Britain):

Homing route ~ outward route + Shorter route + (1|Ring) + (1|Colony) + (1|Landmass ID)

S4.3 *– Model results*

These models cannot be compared as M_2 uses a subset of the data, but comparison between them does indicate the persistence of the effects with the exclusion of Great Britain from the database.

Model	Estimate (β)	SE	z-value	p-value	Odds Ratio (e^{β})
M_1	0.005	0.002	2.601	0.009	1.005
M_2	0.029	0.010	2.983	0.003	1.029

M_7 cannot be compared to $M_{3\text{-}6}$ as it uses the subsetted data, however its significance indicates the persistence of the effect of the best fitted model, M_3, with the exclusion of Great Britain from the database. M_8 contained fixed-effects for both route value representations, and so two fixed-effects are reported.

Model	AIC	ΔAIC	Fixed effect	Estimate (β)	SE	z-value	p-value	Odds Ratio (e^{β})
M_3	349.0	0.0	-	1.855	0.241	7.685	< 0.001	6.392
M_4	377.8	28.8	-	3.325	0.811	4.098	< 0.001	27.80
M_5	356.0	7.0	-	1.941	0.273	7.120	< 0.001	6.967
M_6	383.2	34.2	-	2.439	0.492	4.960	< 0.001	11.46
M_7	-	-	-	2.364	0.488	4.848	< 0.001	10.63
M_8	351.5	2.5	*Abs*	1.570	0.353	4.443	< 0.001	4.806
			Prop	0.667	0.628	1.062	0.288	1.947

These models cannot be compared as M_{10} uses a subset of the data, but comparison between them does indicate the persistence of the effects with the exclusion of Great Britain from the database.

Model	Fixed Effect	Estimate (β)	SE	z-value	p-value	Odds Ratio (e^{β})
M_9	*Outward*	2.568	0.337	7.622	< 0.001	13.037
	Shorter	3.752	0.431	8.705	< 0.001	42.583
M_{10}	*Outward*	2.214	0.397	5.574	< 0.001	9.154
	Shorter	1.921	0.454	4.233	< 0.001	6.825

Chapter 5

The role of outward journey information in the homing performance of the Manx shearwater



With contributions from Joe Wynn, Patrick Lewin, Joe Morford, Tim Guilford, and Oliver Padget. Additional thanks are extended to the contributors of the long-term Manx shearwater dataset.

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Abstract

While in mobile animals allocentric 'maps' have received most investigation, this is unlikely to be their only source of positional information. Outward journey information (OJI) – spatial information acquired by an animal about its own movements as it moves away from a reference location (its home) – is another way an animal can compute the direction and distance it must travel to navigate home successfully without a map. Path integration, for example, provides an animal with a homeward vector without the need for a map, as a path integrating animal would continually update a vector home by integrating the translations and rotations of its outward journey. Such an egocentric log of movement would allow a wild navigator to orientate home without learning about the navigational task and without any other spatial representation. Despite being central to invertebrate and mammalian navigation, path integration has been all but ruled out in the navigation of wide-ranging animals such as pelagic seabirds because of the inevitable accumulation of error which, over such vast distances, would render accurate homing impossible. Here I challenge this assumption and explore several theoretically plausible mechanisms that exist which could reduce error accumulation in path integration at these scales, such as the resetting of inaccurate vectors against visual landmarks. Consequently, in this chapter I investigate how properties of the outward journey, such as path length and tortuosity, influence the homing performance of Manx shearwaters, using a large-scale dataset of free-ranging movements captured throughout the British Isles. Here, I find that increasingly tortuous trajectories in the outward journey significantly predicts a reduction in the accuracy of homing, but that these birds, even after substantially tortuous movements, remain well orientated along a homeward course. These results comprise, for the first-time, evidence of the role of OJI in a long-distance flying species. In light of this I then discuss the cognitive processes that shearwaters may be employing in their navigation and, given the evidence for the role of OJI presented here, the likely hierarchical organisation of navigational mechanisms in this decision-making process.

Introduction

For any animal that moves through its environment, navigation emerges as a fundamental behavioural process, allowing animals to locate resources, return to nesting or breeding sites, and complete large-scale migrations with remarkable precision (Nathan et al., 2008; Wiltschko & Wiltschko, 2003). A range of cognitive processes have evolved with which animals achieve this efficient navigation (Wiener et al., 2011) and perhaps the earliest to emerge, is path integration (Wang, 2016). Whilst many processes rely on learnt spatial relationships with environmental cues to inform an animal of its position relative to a goal, through path integration, an animal is able to navigate by monitoring its own movements with limited to no experience of the area within which it is navigating (Able, 2001; O'Keefe & Nadel, 1978; Papi, 1990; Wang, 2016; Wehner, 2003).

In path integration, animals continually update their current location relative to a reference point, such as a nest, through the integration of movement vectors executed along their outward journey, maintaining a constant homeward vector that can be enacted once the animal wishes to return to this reference point (Able, 2001; Wehner, 2003). Rather than then recapitulating the outward route in full, this homeward vector allows the return along a straight-line trajectory (Collett & Collett, 2000). The inputs that update an animal's path integrator about its movement vary across taxa. Animals may use external, allothetic cues such as optic flow within their environment or the position of the sun to judge their direction and speed of progress (termed allothetic path integration; Able, 2001; Merkle et al., 2006; Muller & Wehner, 1988; Wehner, 2003; Wehner & Srinivasan, 2003). Alternatively, inputs may be idiothetic (internal) signals of self-motion, such as step-counting or feedback from the vestibular system, tracking their inertial movements through space throughout their outward trajectory (termed idiothetic path integration; Merkle et al., 2006; Ronacher & Wehner, 1995; Wittlinger et al., 2007).

Desert ants, one of the best studied path integrating animals, combine an idiothetic odometer (which monitors stride count and internal turn signals) to monitor distances, whilst using an allothetic compass (based on celestial or geomagnetic cues) to measure changes in direction, which together can be used to update the

homeward vector (Andel & Wehner, 2004; Wehner, 2003; Wittlinger et al., 2007). By contrast to the odometer of desert ants, honeybees judge their movement using the optic flow of features moving through their visual field during flight as a measure of distance travelled (Collett, 2019; Srinivasan, 2015), in tandem with the sun's azimuth as an external reference with which to derive direction (Collett, 2019). In vertebrates, trigger fish have been demonstrated to estimate distance allothetically like bees, by monitoring the optic flow of visual cues caused by their own movement (Sibeaux et al., 2022). In domestic geese, visual cues were shown to act as allothetic reference points during passive displacements, where goslings with access to such cues during the outward route could derive the correct homeward direction upon release, while those who were denied visual information during displacement could not successfully home (Saint Paul, 1982).

Path integration, whilst widespread, is a unique case of a more general navigational phenomenon, the use of outward journey information (OJI). To be navigationally useful, outward journey information does not need to be a detailed and accurate log of the rotations and translations resulting in a complete homing vector as those implied above. For instance, OJI could provide additional information to improve other navigational mechanisms if animals remembered simple aspects of outward movements which could be used on the homing leg, recently termed 'auxiliary outward journey information' (see **Chapter 4**; Padget et al., 2022). For example, knowledge from the outward journey that an animal departed its reference location to the West could be reversed so that homing was directed Eastwards, which would plausibly return the bird to at least an area in which it is familiar (Saint Paul, 1982; Wiltschko & Wiltschko, 2009).

There are many examples of cases where OJI appears to be important, although this has not always been the main conclusion of studies which show it. While concluded as evidence for olfactory map use, the role of OJI was evident in homing pigeons that, when denied olfactants during the outward journey, had poorer initial homeward orientations than controls, implying that sampling olfactants during transport on the outward journey improved homing ability (Baldaccini et al., 1982; Ioalé et al., 1983; Wallraff & Foà, 1981; Wallraff & Sinsch, 1988). Furthermore, detours taken on the

outward journey can predict orientation errors upon release, termed the ‘detour effect’, implying that olfactory information perceived on the outward journey factors into subsequent homing decision, even during passive displacements (Papi et al., 1973, 1978). Although these investigations into the homing pigeon do not support the use of path-tracking processes, since these olfactants can only provide positional information once they have been learnt in a familiar area (Morford et al., 2025), they do show that this avian model is attentive to stimuli perceived during outward movements (Wallraff & Sinsch, 1988).

Whilst path integration allows an animal to maintain a homeward vector throughout the outward journey, the imperfect integration of step vectors accumulates error continually, particularly in the absence of external references (Benhamou et al., 1990; Biegler, 2000; Etienne & Jeffery, 2004). This directional error then accumulates as the trip grows in complexity, with the error accrued in the integration of a given step being proportional to the distance travelled in that step (Biegler, 2000; Cheng et al., 1999). This makes path integration a risky navigation strategy for a far-ranging species, but that isn’t to say that this error accumulation cannot be offset.

Ants that occupy cluttered environments have also evolved to attend to visual landmarks, when available, and these appear act independently to path integration, allowing them to mitigate against the error accrued through path integration by switching to landmark guidance (Bühlmann et al., 2011; Collett & Graham, 2004; Menzel & Galizia, 2024; Wehner et al., 1996). In rodents, which path integrate primarily with inertial cues, experiments in which the integrated vector is put into conflict with visual information reveal that these systems operate in tandem, with visual references exerting a greater control on the neurophysiological systems of orientation than the positional information derived from their own movement (Etienne & Jeffery, 2004; Knierim et al., 1996; McNaughton et al., 1996). Furthermore, these rodents are able to reset their integrator, reducing or eliminating a discrepancy between their integrated estimation of their position and external sources of position-fixing, namely landmarks, that convey their current location with greater certainty (Biegler, 2000; Etienne et al., 1998; Gothard et al., 1996). If an animal is capable of piloting, this being the process of determining its current position relative

to a goal and directing a course to it by first inferring its position in relation to available landmarks with known spatial relationships to the goal, then it is plausible that it could reset its integrator whenever such landmarks are present (Biegler, 2000; Etienne et al., 1998). Furthermore, the frequency with which this animal could then reset its integrator is effectively infinite during movements where recognisable landmarks persist (Biegler, 2000).

Despite comprising a mechanism for complete homing navigation, path integration is generally assumed to be a more basal navigation process, important primarily in insects, on which alternate strategies can be layered upon once the cognitive architecture exists to support allocentric representations (Biegler, 2000; O'Keefe & Nadel, 1978; Wang, 2016; Wehner, 2003). If such alternatives are sufficiently accurate, then there is no need to continue integrating one's own movements (Biegler, 2000). However, if error can also arise in the calculation of a homeward course from such alternatives, then the averaging of homeward vectors derived from several navigational processes must surely prove advantageous, especially in far-ranging species.

A suite of navigational mechanisms has been shown to be involved with avian navigation. Through true navigation processes, likely underpinned through large-scale olfactory or magnetic gradients, they are able to determine their position relative to a goal and chart a course to such using only information perceived at the point of homing (Gagliardo, 2013; Holland, 2014; Kishkinev et al., 2021; Phillips, 2006). They have also been shown to use learnt visual cues to successfully home when experimentally denied olfactory signals (Bonadonna & Gagliardo, 2021; Gagliardo et al., 2013; Pollonara et al., 2015). One might assume that such processes may supersede the directional guidance of path integration, making it appear as if this process is no longer useful (Able, 2001; Papi, 1990; Wallraff & Sinsch, 1988; Wehner, 2003). Indeed, when displaced, which actively denies OJI and any capacity to path integrate, avian species are still able to successfully home (Biro et al., 2004, 2007; Gagliardo et al., 2013, 2020; Meade et al., 2006; Padget et al., 2017, 2019; Pollonara et al., 2015; Wallraff & Sinsch, 1988). However, with the theoretical capacity to reset this integrator through landmark-mediated guidance as seen in

other taxa, path integration may persist in an evolved preference for system redundancy; this being the possession of multiple navigational processes that can be either integrated or substituted to facilitate homing in a range of situations. (Biegler, 2000; Bregy et al., 2008; Buehlmann et al., 2018; Graham et al., 2010; Müller & Wehner, 2010; Wehner, 2003; Wiener et al., 2011).

A detailed examination of homing in relation to the outward journey is, therefore, lacking in a wide-ranging species despite knowledge that the pre-requisites for path integration are plausibly retained. The Manx shearwater is a highly mobile pelagic seabird, remarked for its long-distance movements and superb navigational abilities (Padget et al., 2019). This species offers a surprising model to test for the prevalence of path integration processes. Despite the capacity for error accumulation in their pelagic movements, especially considering these are largely made through and above fluid media (Egelhaaf, 2022; Heinze et al., 2018), much of the Manx shearwaters' breeding ranges are rich with topographical features, potentially providing a basis for the recalibration of integrators while traversing long distances (Biegler, 2000; Etienne et al., 1998; Guilford et al., 2008). Therefore, in this chapter I investigate how variation in the characteristics of outward movements influences the ultimate homing error of shearwaters during their natural foraging movements. Through quantifying the complexity of outward movements, using metrics such as path length and cumulative tortuosity, this chapter models error in the homing orientation of free-ranging shearwaters under different predictions of path integration, using a large database of GPS-tracked Manx shearwater movements. I predict that finding evidence of such error accumulation will prove challenging in these wide-ranging movements. However, by considering the availability of visual cues at the point of homing, I test whether outward movements made out of sight of land, presumably beyond any landmarks that could serve to reset or dilute integrator error, with the expectation that these will disproportionately contribute error to the orientation of subsequent homing. These findings provide new insights into the cognitive mechanisms underpinning seabird navigation and expand our understanding of how multiple navigational strategies may be integrated in a single species.

Methods

Data availability and processing

As part of on-going monitoring efforts, breeding Manx shearwater were tracked using miniature GPS loggers across six colonies around the British Isles; five of which are presented here (**Figure 5.1B**: Skomer Island [51°44'14.7"N, 5°16'55.6"W], Skokholm Island [51°41'37.8"N, 5°17'13.9"W] and Ramsey Island [51°52'26.6"N, 5°20'0.8"W], South Irish Sea, Wales; Lighthouse Island [54°41'43.0"N, 5°15'3.9"W], Copeland Islands, Northern Ireland; Lundy [51°10'6.7"N, 4°40'32.5" W], Bristol Channel, England). Birds were tracked during two key stages of their breeding cycle, the incubation period (May-June), and the chick-rearing period (July-August). All GPS devices were mounted dorsally, attached to mantle feathers using TESA marine tape, in protocols outlined in Guilford et al. (2008) and no device weighed more than 4% of the bird's total body mass.

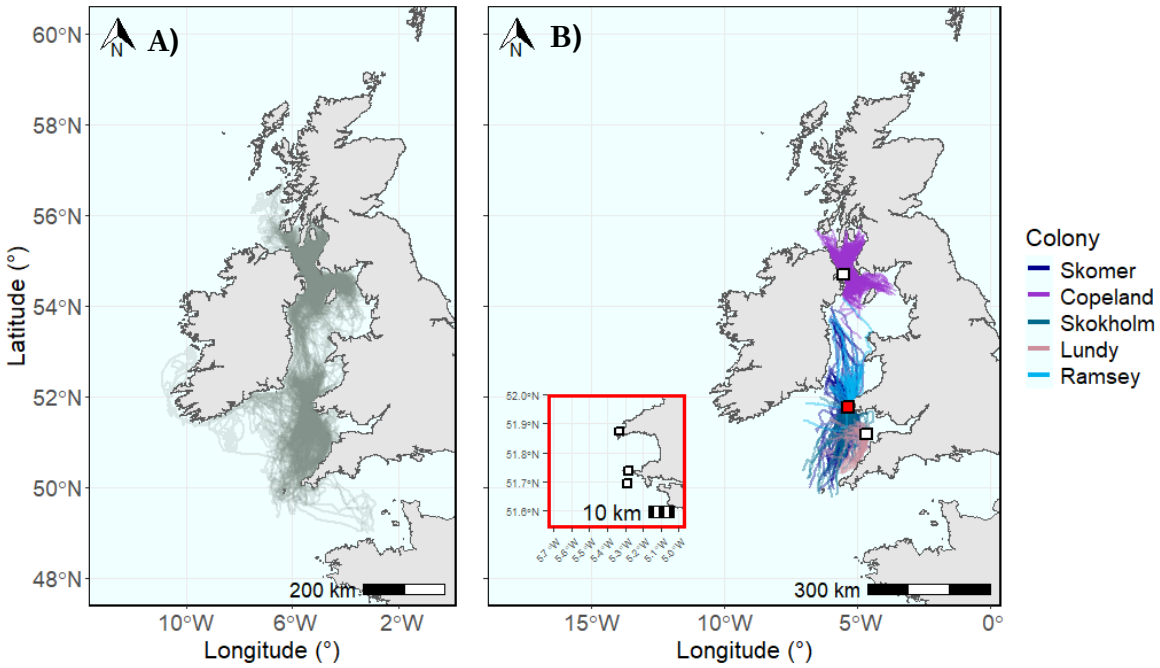


Figure 5.1. Maps of the British Isles showing **A**) the full trips used this study and **B**) the homing trajectories of these foraging trips, which all begin homing from a point with an unobstructed beeline home. Trips are coloured by colony, which are indicated on the plot by white squares. The Pembrokeshire colonies can be seen in the zoomed inset plot due to their proximity.

Individual GPS deployments often contained multiple foraging trips, which were separated and processed separately. Each trip was passed through quality filters before analysis, ensuring each trip contained the full movement path that reached at least 25 km from the colony, had a GPS resolution of 30-minutes or higher, and contained at least 50 fixes. If these criteria were met, trips were then filtered by inter-fix speeds to remove any GPS errors, excluding any fixes above the stated upper speed threshold of Manx shearwaters of 80 km h^{-1} as given in Guilford et al. (2008). Once any present errors were removed, trips were interpolated to 5-minute intervals using a cubic spline interpolation algorithm (Tremblay et al., 2006).

When a shearwater begins to home, there is a clear detectable switch in the movement data between mid-speed foraging movements, or rest, and a continuous bout of movement in the homeward direction (Padget et al., 2019). These rapid homeward movements produce a steep decline in the distance from home across the track, and the onset of this can be taken as the point that the bird began to home. This homing point was identified manually, through visual inspection of this distance from home through time, blind to all other track information, and this identification was validated with a subset of tracks, showing 98% repeatability of the identified homing point (See **Chapter 2**).

After all filtering, there were 2,004 foraging trips originating from 1,110 GPS deployments across 799 individual shearwaters available for analysis. Despite their lack of anticipation for intervening landmasses along the homeward beeline, such obstacles still force shearwaters to depart from their intended course (Padget et al., 2019). As such, only trips that began homing along an unobstructed beeline were taken forth in this analysis, to ensure any deflection in the homeward orientation was not an artifact of such obstruction. This left 876 unobstructed trips for analysis, from 431 individual shearwaters (**Figure 5.1**).

To ensure only homing periods with uninterrupted beelines were analysed here, intervening obstacles were identified along the homeward beeline from the first point of homing per GPS track to their respective home colony. This beeline was defined as the Great circle arc between the onset of homing and the colony, as in Padget et al. (2019), and run through a geometric interception ('st_intersect' from the 'sf' package)

with all known landmasses within the bounds of the tracking dataset, retrieved as shapefiles from the Natural Earth public database (accessed through the 'rnaturalearth' package, see **Chapter 4** for further details). Only tracks for which this beeline returned no intervening landmasses were taken forwards into analysis.

To give a measure of homeward directedness, the initial homing bearing of each trip was calculated as the bearing between the onset of homing and the first GPS fix after the bird reached 20 km from this point. This was then subtracted from the bearing calculated between the homing point and the home location, the homeward beeline. The window used here to calculate this deflection is smaller than that stated in other shearwater studies, as they involve displacements and so use a larger window to account for any escape behaviour following the displacement procedure (Padget et al., 2022). Since this study investigated natural movements, we can assume that the direction adopted at the point of homing is independent of any nonspecific effects seen in experimental releases, and a result of only the bird's perceived homeward direction.

If the onset of homing is marked by the point at which the bird switches to directed, continuous homeward movement, then presumably error in the information used to determine this homeward course could occur at any point before this decision point. Therefore, here the outward journey was labelled as all movement post colony departure up until this point of homing, including periods of foraging and rest (**Figure 5.2**).

Justification and calculation of movement metrics

I consider three aspects of a shearwater's movement path that could contribute to error accumulation and homeward deflection if path integration on the outbound journey contributes to homing. First, error in path integration processes accumulates with distance travelled, because each movement adds noise to the internal estimate of the homeward vector (Muller & Wehner, 1988). Second, tortuosity, the degree to which an animal's path deviates from a straight line, then compounds this error accumulation with the addition of angular components (Chatterji & Layne, 2024; Wehner & Srinivasan, 2003). Finally, a longer duration path

may allow memory decay to introduce temporal drift in the accumulation of self-motion cues (termed leaky integration; Vickerstaff & Di Paolo, 2005), and may produce further error from external perturbations, such as changes in wind speed, which are superimposed onto the perceived signals of self-motion (Harris et al., 2025).

Total path length was calculated as the cumulative distance travelled during the outward journey by summing the distance between GPS fixes, whilst total outward time was calculated as the duration of the trip (in hours) from colony departure to the point of homing. As outward movements are not obviously goal oriented as in homing and often contain periods of search or non-orientated behaviour, indices of straightness, such as path sinuosity, are not appropriate for the quantification of angular deviations (Benhamou, 2004). Therefore, to quantify the geometric complexity of these outward movements, tortuosity was calculated as it captures information about turning behaviour and step-length variation along the trajectory irrespective of a goal location. This tortuosity was quantified from sequential GPS fixes by computing the bearings and subsequent turning angles between successive locations using the *geosphere* package in R and follows Benhamou (2004) in using turning-angle statistics and step-length filtering to characterise tortuosity. Here, unweighted tortuosity was calculated as $1 - R$, where R is the mean resultant vector length of the turning angles (see equation below).

$$R = \sqrt{(\bar{\cos}\,\theta)^2 + (\bar{\sin}\,\theta)^2}$$

A weighted measure of tortuosity was also calculated which applied the same formula but weighted each turning angle by multiplying it against the mean length of its adjacent step segments (in kilometres), giving greater influence of the overall tortuosity value of the outward journey to longer bouts of movement. In both cases, tortuosity ranges from 0 (perfectly straight path) to 1 (highly sinuous or random turning). Tortuosity, either weighted or unweighted, was then summed across the entire outward journey to give a cumulative measure of tortuosity for each trip.

Model selection

Using the full outward journey of GPS trips, the stated predictors of homing deflection were modelled using generalized linear mixed-effects models (GLMMs) with a beta error distribution and logit link, termed beta regressions, implemented using the R package 'glmmTMB'. Where needed, metrics were logarithmically transformed and scaled to improve model interpretation. Beta regression models were chosen as the response variable, homing deflection, has values bounded between 0-180, and is heavily skewed for smaller values, owing to the bird's propensities for well-orientated movement.

First, the best measure of tortuosity (unweighted or weighted) was decided by including both as a fixed effect in a single predictor model and comparing the AIC scores, finding that the weighted measure best fit these data. From this, the three key predictors of outward journey information use: path length, (weighted) tortuosity, and time, were modelled against the resultant homing deflection of these foraging trips using non-nested beta regression models, accounting for random variation within individuals nested within colony, with the following model structures:

A) *Initial homeward deflection ~ Weighted summed outward tortuosity + (1|Colony/Ring)*

B) *Initial homeward deflection ~ Total outward path length + (1|Colony/Ring)*

C) *Initial homeward deflection ~ Total outward time + (1|Colony/Ring)*

These models were then interpreted individually and compared using AIC scores to find which predictor best explained the observed variation in homing deflection.

Modelling outward journey metrics in periods out of sight of land

If path-tracking mechanisms are being employed to monitor self-motion during the outward journey, then there is evidence to suggest that the availability of visual cues may be important (Müller & Wehner, 2010; Wehner & Müller, 2010). Without these

additional sources of spatial information, animals may be left unable to reset or correct their outward movement vector for error accumulating from the misrepresentation of self-movement vectors (Biegler, 2000; Müller & Wehner, 2010). Therefore, a second set of models were constructed which isolated periods of movements that were made during outward movements that directly preceded the point of homing (**Figure 5.2** for visualisation).

This land visibility was calculated by computing the maximum visibility radii from all points of elevation within each landmass shapefile and assessing which, if any, of the GPS fixes both during outward and homeward movement fell within these areas of visibility. The dataset was then subset for instances where birds began homing out of sight of land, and metrics were recalculated specifically for the section of the outward journey from the last point of land visibility to the point of homing (**Figure 5.2B**). The models ran on these subsections had the same structure as those above but included only periods of movements made out of sight of land:

D) *Initial homeward deflection ~ Weighted summed outward tortuosity since the last point of land visibility + (1|Ring)*

E) *Initial homeward deflection ~ Path length since the last point of land visibility + (1|Ring)*

F) *Initial homeward deflection ~ Time since the last point of land visibility + (1|Ring)*

The smaller sample size in this subset meant that the nested random effects did not contain enough variation to converge within the model, and so only bird ID (ring) was included.

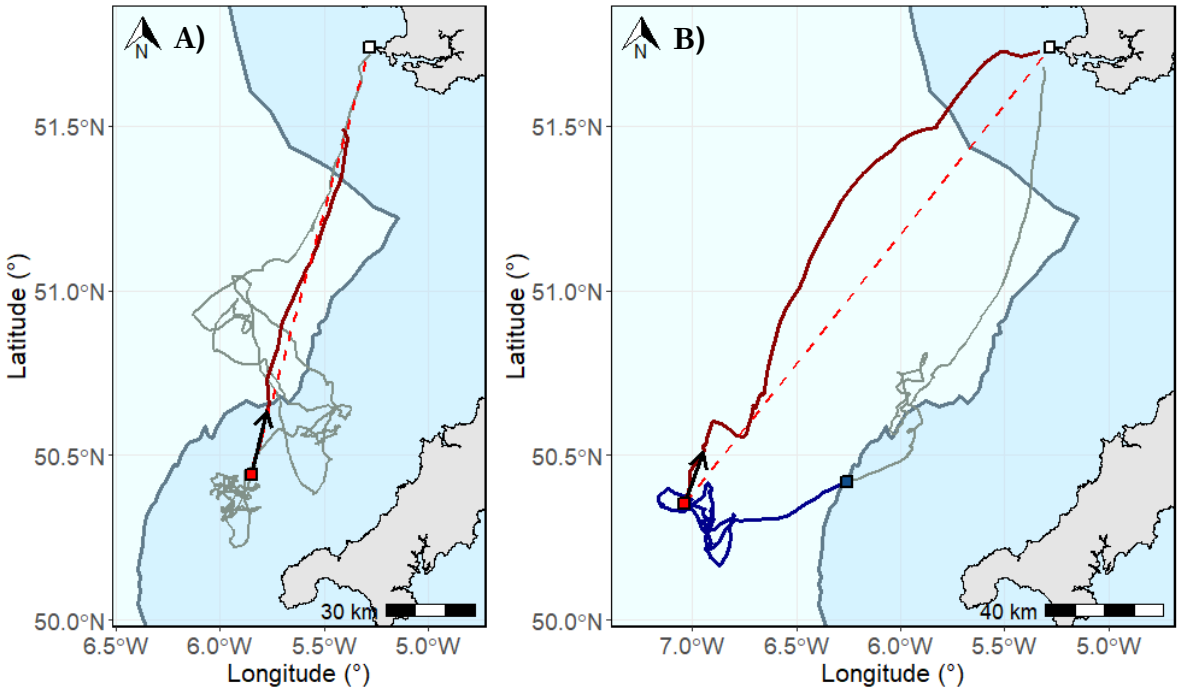


Figure 5.2. Maps showing two GPS tracks of birds from Skomer Island (white square). As an example, the visibility radius of Great Britain is underlaid on the maps in blue. Outward movements are shown in grey, and in **B**) outward movements made outside of the visibility radius prior to the points of homing are shown in dark blue but are not present in **A**) as homing was initiated within sight of land. The homing point is indicated by a red square, with the resultant beeline indicated by a red dashed line. Actual homing movement is shown in dark red (solid line) and the initial homing vectors (first 20km) are shown as black arrows.

Results

Foraging trips lasted on average 299.89 hours (SD = 189.60 hours), covering a range of total distances from 54.11 to 3458.69 km. Trip distances were highly variable and right skewed, with half of trips exceeding 250 km whilst some exceeded 3000 km. The requirement here for unobstructed beelines appeared to cap the distance that could be travelled, as all instances of far-off foraging into the North Atlantic then faced an obstructed beeline to re-enter the British Isles and so were excluded from this analysis. In this subset, birds began homing on average 67.80 km from home (SD = 42.04 km), with an average deflection from the homeward beeline of 16.26 ° (SD = 13.31 °), showing strong preferences for this beeline direction.

Predictors within the full outward journey

Using AIC comparisons on the non-nested models ran with the outward journey metrics of all trips, it was found that the tortuosity model had the greatest predictive power against initial homing deflection (AIC values given in **Table 5.1**). Increasing cumulative tortuosity through the outward journey showed a significant positive relationship with ultimate homing deflection (**Figure 5.3A**; $\beta = 0.103 \pm 0.027$, $z = 3.760$, $p = < 0.001$), as did increases in total path length (**Figure 5.3B**; $\beta = 0.091 \pm 0.027$, $z = 3.380$, $p = < 0.001$). The total time spent on the outward journey did not predict homing deflection (**Figure 5.3C**; $\beta = 0.044 \pm 0.028$, $z = 1.580$, $p = 0.114$). The outputs of the models are displayed in the first half **Table 5.1**, whilst the modelled effect sizes of these significant effects are reported in **Table 5.2**.

Predictors in movements made out of sight of land

In the non-nested models ran against the outward journey metrics of movements made out of sight of land preceding homing, there were no strong predictive effects of the modelled characteristics of these outward movements against the homeward deflection (**Figure 5.4**; full model reports in the latter half of **Table 5.1**). It was found that the path length of these periods had marginally better predictive power over resultant homing deflection, but this influence had no significant effect (**Figure 5.4B**; $\beta = 0.116 \pm 0.110$, $z = 1.052$, $p = 0.293$).

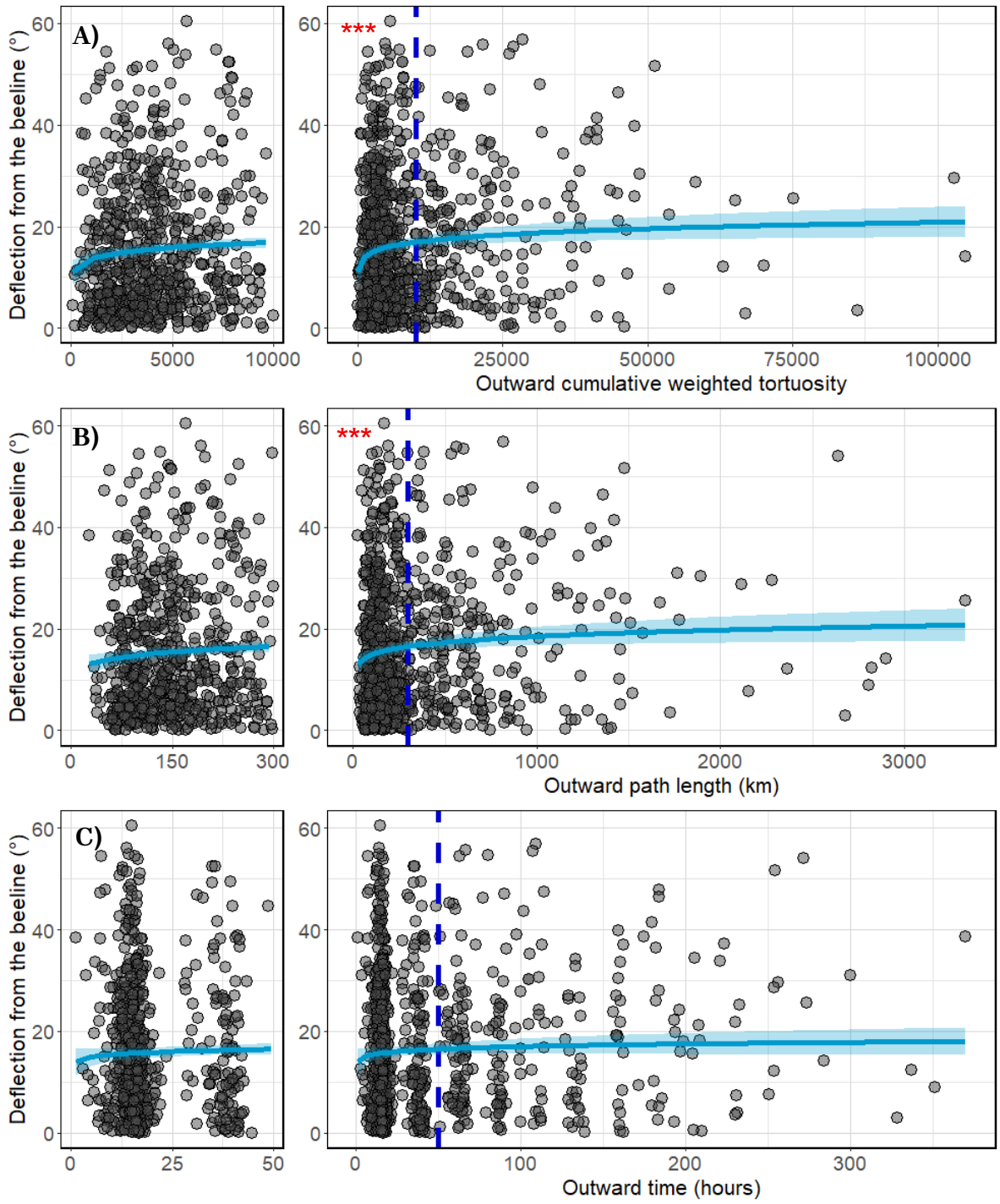


Figure 5.3. Relationships between metrics of the outward journey and deflection from the homeward beeline. Metrics are calculated from the full outward trip. In each row, the left-hand panel shows a zoom of the initial portion of data from the right-hand panel (marked by the dark blue dashed line). **A**) cumulative weighted tortuosity, **B**) path length (km), and **C**) the duration of the outward journey (hours). Asterisks indicate significance in the relationship across the full range of data for the corresponding metric.

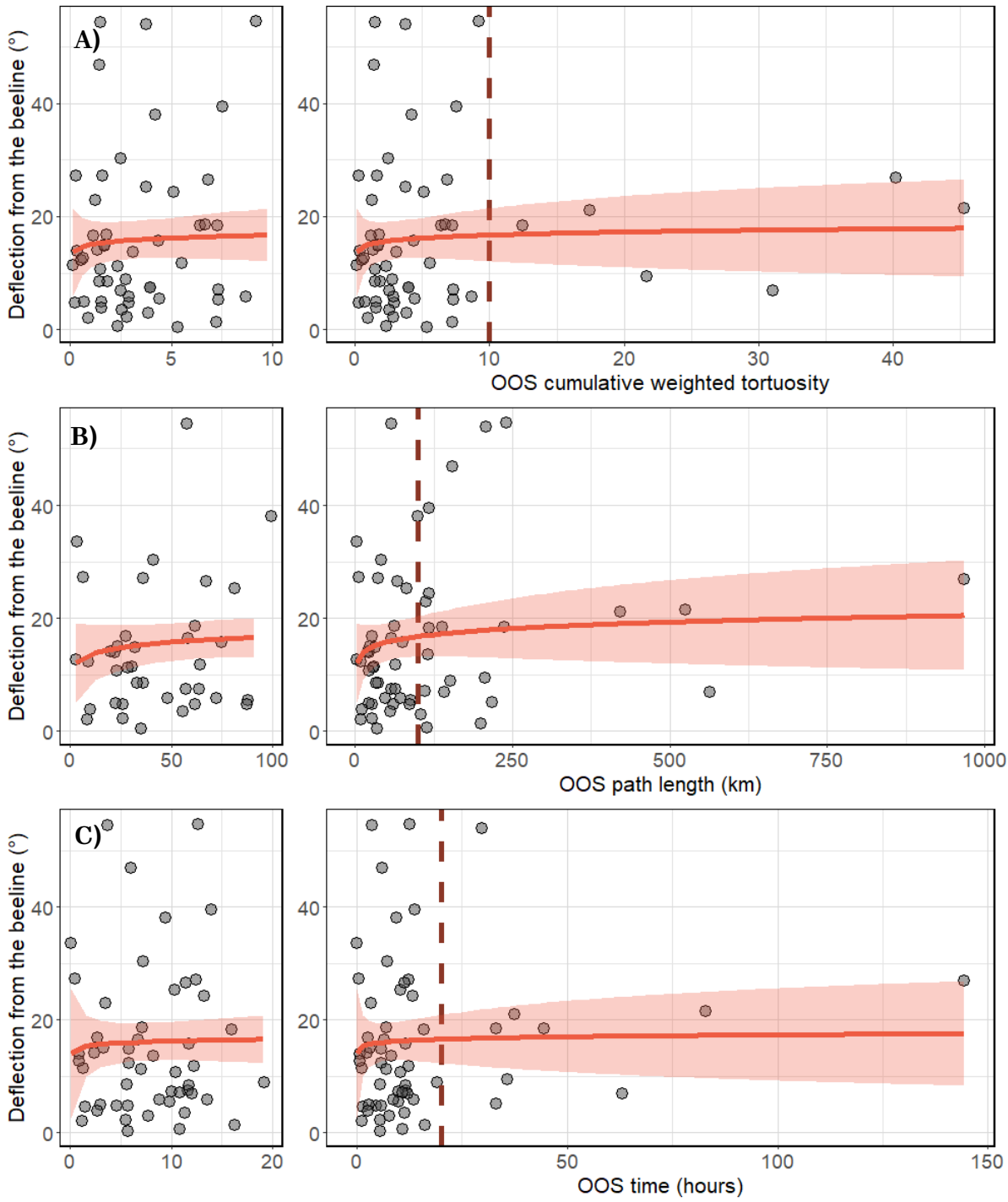


Figure 5.4. Relationships between metrics of the outward journey and deflection from the homeward beeline. Metrics are calculated from periods where birds were out of sight of land preceding the onset of homing. In each row, the left-hand panel shows a zoom of the initial portion of data from the right-hand panel (marked by the dark red dashed line). **A**) cumulative weighted tortuosity of movements since land was last seen, **B**) path length since land was last seen (km), and **C**) the time spent out of sight of land in this period (hours).

Table 5.1. A table detailing the model metrics and parameters for each tested within this analysis. The data column refers to the section of the outward journey modelled, with OOS referring to the 'out of sight' subset as discussed in the methods. See the main body for the structure of each model corresponding to the 'Model' column. P-values in bold with an asterisk indicate significance.

Data	Metric	Model	β	SE	Z	P	AIC
Full	Tortuosity	A	0.103	0.027	3.760	<**0.001***	-2498.1
Full	Path length	B	0.091	0.027	3.380	<**0.001***	-2495.1
Full	Time	C	0.044	0.028	1.580	0.114	-2486.5
OOS	Tortuosity	D	0.060	0.108	0.556	0.578	-164.5
OOS	Path length	E	0.116	0.110	1.052	0.293	-166.2
OOS	Time	F	0.040	0.119	0.339	0.735	-165.2

Table 5.2. A table reporting the modelled effect sizes of the significant effects seen in Table 5.1. For each model, the predicted deflection at the lowest and highest values of the predictor are reported, with the corresponding 95% confidence intervals.

Data	Metric	Model	Low Prediction [95% CI]	High Prediction [95% CI]
Full	Tortuosity	A	11.09 [8.99 – 13.65]	20.96 [18.12 – 24.18]
Full	Path length	B	13.11 [11.43 – 15.02]	20.76 [17.78 – 24.18]

Discussion

Here we have shown for the first time in a free-ranging, highly mobile navigator that outward journey information is used to inform homing behaviour. Despite path integration probably being crucial to primitive locomotion and navigation, its role in the navigational performance of far-ranging animals such as birds is often not considered. These results demonstrate that as the outward journey of Manx shearwater foraging movements becomes increasingly long and tortuous, the bird's ability to accurately adopt the homeward beeline at the later onset of homing is reduced. These relationships would suggest that elements of outward movements are being integrated into the decision-making process when determining a homeward course, likely in path-tracking processes such as path integration.

In insect models, it is well evidenced that increasingly complex movements made on the outward journey negatively impact the accuracy of their resultant homeward vector (Collett & Collett, 2000; Muller & Wehner, 1988; Wehner, 2003; Wehner & Müller, 2010). Similarly, it has been demonstrated in several crustacean species that increasingly tortuous movements made on the outbound journey can lead to a breakdown of path integration, causing these marine invertebrates to either switch to landmark guidance, or in their absence, begin search behaviour to find their home (Chatterji & Layne, 2024; Herrnkind & McLean, 1971; Patel & Cronin, 2020). In no previous demonstration of path integration has a species been reported to traverse such vast distances as those captured in the shearwater movements here whilst successfully integrating their outward vectors with such little error manifesting in their homeward direction. Given the scale of foraging movements within this dataset, including highly tortuous trips that span across several weeks, the reported effect size of the key predictor, tortuosity, is relatively small (**Table 5.2**). It is highly unlikely that a navigational system relying only on this integration of outward movements would produce such little error, given the turbulent and pelagic environment within which they move, coupled with the distances and complexities of the movements they make (Chatterji & Layne, 2024; Heinze et al., 2018; Sommer & Wehner, 2004; Wehner & Srinivasan, 2003). Whilst these results demonstrate that outward journey information is indeed influential in the homing performance of the Manx shearwater,

is it far more plausible that this OJI is being integrated concurrently to the operation of other processes, such as the use of large-scale maps, as previously demonstrated in both their natural movements and ability to home following distant displacement (Matthews, 1953; Padget et al., 2019, 2022). If, in this weighted comparison of several cognitive processes, these maps act as the primary informant, as demonstrated when this map-sense is experimentally denied (Gagliardo et al., 2013; Padget et al., 2017; Pollonara et al., 2015), then it is unsurprising that, although we find a statistically significant effect of tortuosity, this effect is modest and does not substantially limit these birds' ability to home, albeit reducing their accuracy.

This ability to integrate the resultant vector of multiple systems has been demonstrated in several species. In the navigational system of rodents, it was reported that they average the vectors generated from both idiothetic path integration, and that provided by the availability of allothetic visual cues (Etienne & Jeffery, 2004; Knierim et al., 1996; McNaughton et al., 1996). Similarly, clock-shifted pigeons moving within a familiar area show, whilst greatly reduced, predictable deflections during homing along stereotypic routes guided through salient visual cues, implying that this misinformed compass still weighs into these directional decisions (Biro et al., 2007; Gagliardo et al., 2005; Wiltschko et al., 1994). This too has been demonstrated in the coast-following behaviour of Manx shearwaters, that clock-shift themselves during rapid longitudinal movements (Lewin et al., Unpublished). Such examples demonstrate the integration of vectors produced through multiple simultaneous navigational processes, even in instances where such vectors may be partially in conflict (Wystrach et al., 2015). This may then explain why, despite the errors assumed in path integration at this scale of movement, I find that shearwaters remain well-orientated to home, as the resultant error-prone vector of path integration is offset through its comparison with vectors produced through alternate, more accurate, processes such as large-scale maps.

Alternatively, it may be that this path integration vector is not as error prone as we may assume. As discussed, several species are capable of offsetting this integration error in the presence of visual landmarks, either by switching to landmark guidance, or using landmarks as a means of resetting or recalibrating the path integration

system (Buehlmann et al., 2018; Collett & Graham, 2004; Etienne & Jeffery, 2004; Knierim et al., 1996). If this is indeed the case, then a vector derived from the integration of outward movements may, in fact, be viable in deriving the homeward direction during natural navigation of these wide-ranging seabirds, it may simply be more accurate than path integration at this scale is assumed to be capable of. Under this assumption though, we would then expect that movements made out of sight of land before homing, which cannot be offset with through vector resetting with landmarks, would accrue disproportionate homeward error (Biegler, 2000; Etienne et al., 1998). Yet, we find no evidence for such error arising from those movements here. Whilst this might be a product of the small sample size of birds that begin homing out of sight of land, or the reduction in data produced from the further sub-dividing of such tracks for only these movements made out of sight of land, there is also potential cognitive explanations for such a finding.

Inherent to successful navigation, which we would expect to arise under natural selection, is the selection of processes that produce minimal error (Gould, 2017; Wynn & Liedvogel, 2023). Or alternatively, the conservation of multiple strategies such that, in light of error arising in one system, alternatives can be employed to facilitate successful homing (Biro et al., 2004; Buehlmann et al., 2020; Gagliardo, 2013; Pollonara et al., 2015). Whilst multiple systems are integrated in rodent models, this averaging fails when visual cues are altered such that the vector they provide is irreconcilable against that produced from inertial path integration, and this conflicting visual vector is ignored (Alyan & Jander, 1994; Etienne et al., 1996; Etienne & Jeffery, 2004). Perhaps then, this explains the lack of evidence for error expression from movements made out of sight of land in this investigation. If these movements indeed are generating disproportionate, irreconcilable, error in the vector of path integration, then perhaps this is recognised by the shearwater at the point it is compared against that produced by other processes, and as such is excluded when averaging a course across multiple navigational processes (Cheng et al., 2007; Etienne et al., 1998; Etienne & Jeffery, 2004). Generally, perhaps this vector derived from path-tracking processes is not in itself, a reliable enough source of positional information to solely derive a homeward course in such wide-ranging

movements. If this were achievable, we should expect that the anosmic Scopoli's shearwaters in Padget et al. (2017) could, in absence of olfactory cues, instead derive a homeward course from their self-directed outward movements, but this is not the case. Their ability to home successfully when compared to the anosmic Cory's shearwaters displaced to far-off sites in Gagliardo et al., (2013) does support the use of an alternative homing strategy however, but as their initial orientation was significantly poorer than controls until they were within coastal areas, this is more plausibly landmark guidance than that derived from outward journey vectors. Perhaps then, in far-ranging species such as shearwaters, outward movements are monitored as a means of verifying the directional information derived from the olfactory map, but they in themselves cannot be solely employed to determine the direction to home (Biegler, 2000).

This investigation finds evidence for the influence of outward journey complexity on the subsequent accuracy of homing in free-ranging shearwater movements, a finding that was not found in Padget et al. (2019). It is likely that, with the increased number of tracks available in this updated dataset (876 here compared to 369 in Padget et al.), coupled with a modelling structure better suited to orientation data (beta regressions), and more intuitive measures of tortuosity (Benhamou, 2004), that this study represents a more thorough investigation into these hypotheses (Padget, pers. Comms., 2025).

Here we have demonstrated that Manx shearwaters are attentive to the movement characteristics of their outward journey and appear to be factoring these into the calculation of their subsequent homeward course. This, coupled with the errors apparent when denied OJI (Padget et al., 2022), support the role of outward journey information in the processes underlying navigation in this pelagic seabird. However, it is unlikely that these path-tracking processes are the sole determinant of the homeward course, and evidence from anosmia studies may suggest that this integrated vector alone may not be sufficient in guiding homing at such vast scales (Padget et al., 2017). Future work should now focus on identifying specifically which cues are being encoded, and in what cognitive mechanisms, during these outward journeys. Nuanced displacement paradigms (see **Chapter 7**, **Future Directions**),

coupled with experimental manipulations, either through the temporary denial of a sense, or through a clock-shift procedure to induce increased errors, should be employed to address such questions of the use of outward journey information.

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Chapter 6

Investigating the role of visual landmarks in the homing performance of free-ranging Balearic and Manx shearwaters



With contributions from Joe Wynn, Patrick Lewin, Joe Morford, Tim Guilford, and Oliver Padget. Additional thanks are extended to the contributors of both the long-term Manx shearwater dataset and Balearic shearwater tracking project.

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Abstract

In this chapter, I investigate the role of topographical features in the homing performance of free-ranging *Puffinus* shearwaters. Despite the ability of such shearwaters to remain well-orientated when homing out of sight of land, likely through a combination of allocentric 'maps' and outward journey information (**Chapter 5**), there are several reasons to expect that visual topographical information may also inform navigational decisions in natural movements when available. First, stable visual landmarks are important for other taxa – in pigeons, homing is more efficient when released from sites within a familiar area where they can make use of visual information. Even in pelagic seabirds, studies of homing of *Calonectris* shearwaters have demonstrated that topographical features provide navigational information in the absence of olfactory cues, when available. Finally, despite the popularity of large-scale gradient maps among researchers, it is unreasonable to assume that such gradients could be used for fine-scale navigation for which stable visual landmarks are ideally suited. Despite evidence suggesting that visual landmarks aid navigation in a range of contexts and species, there has yet been no quantification of this in the natural homing behaviour of *Puffinus* shearwaters. Therefore, here I examine whether the availability of topographical information affects the accuracy of free-ranging homing in Balearic, *Puffinus mauretanicus*, and Manx, *Puffinus puffinus*, shearwaters. Through these two case studies, I investigate several hypotheses of how landmarks may improve homing accuracy but find only marginal evidence for the availability of, or familiarity with, visible topographical features producing such improvements. In light of these findings, and those shown in related species, I propose how the likely hierarchical organisation of navigation mechanisms, and the necessity for redundancy in such processes, may inhibit the detection of landmark use in the natural homing behaviour of these pelagic seabirds.

Introduction

Several investigations into the navigation of shearwater species have provided evidence that from distant sites they are able to use true navigation to home, most likely based on learning of largescale environmental gradients (Gagliardo et al., 2013; Matthews, 1953; Padget et al., 2017, 2019, 2022; Pollonara et al., 2015). Despite explaining how these shearwaters are able to exhibit remarkable homeward orientation from far-off sites, true navigation cannot be reasonably expected to be the only process involved in navigating back to a precise location across all spatial scales (Able, 2001; Gagliardo, Pollonara, Casini, et al., 2020; Guilford & Biro, 2014; Holland, 2003; Menti et al., 2023; Papi, 1990). There are several additional reasons that we might expect to find evidence of additional navigational mechanisms. First, using multiple cues or cognitive navigational mechanisms generates redundancy. Certainly, there is evidence that Scopoli's shearwaters (*Calonectris Diomedea*) deprived of their olfactory sense are able to successfully home as long as they have access to stable topographic cues (Gagliardo et al., 2013), despite showing poor homeward orientation in pelagic movements, by using available topographic cues once reaching coastal area (Padget et al., 2017; Pollonara et al., 2015). Second, we must consider the precision required of navigational strategies across the scales that animals must navigate (Able, 2001; Phillips, 2006; Wiltschko & Wiltschko, 2023). Many studies report that large-scale olfactory maps, as seen in the homing pigeon, also form a core process of shearwater navigation (Gagliardo, 2013; Gagliardo et al., 2013; Padget et al., 2017; Pollonara et al., 2015). There are multiple theories around how such maps may be structured cognitively (Guilford & Burt de Perera, 2017; Morford, Lewin, et al., 2025; Morford, Wynn, et al., 2025; Wallraff, 2005), and each confers its own limitations as to at what spatial scales error in the position-fixing step may constrain homing accuracy (Phillips, 2006; Wiltschko & Wiltschko, 2023). If the resolution of the map is uniform, as discussed by Wallraff (2005), then it would be expected that at proximal scales to a goal, the accuracy in deducing a homeward direction solely from a gradient map would be impaired due to constraints in the perceivable resolution of the comprising gradients (See

Supplementary Materials S6.1 for details). It is of no surprise then, that it is at these proximal scales that we find the most evidence for the role of visual cues, namely landmarks, as a potentially alternative source of directional information (Braithwaite & Newman, 1994; Collett et al., 1992; Gagliardo et al., 2020; Holland, 2003; Toledo et al., 2020).

As an animal explores its environment, it can learn the spatial relationships between stable landmarks and a goal location, such that recognizing these landmarks later allows it to recall previously used routes from its current position to the goal (Guilford & Biro, 2014; Guilford & Burt de Perera, 2017; Holland, 2003). This representation, known as a familiar area map, may improve navigational accuracy at local scales or add redundancy to the animal's broader navigational systems (Guilford & Biro, 2014; Healy et al., 2003; Holland, 2003). Whilst these spatial relationships all must be learnt through experience, there are several possibilities for how they can be represented cognitively.

These relationships may be stored independently of a compass mechanism (e.g. "fly between those two islands to get home"), such as those described in pilotage behaviour and widely demonstrated in homing pigeons (Baker, 1984; Biro et al., 2004, 2007; Holland, 2003). Alternatively, the positions of familiar landmarks may be stored alongside landmark-associated compass bearings (e.g. "home is North of those two islands"; Holland, 2003; Papi, 1992; Wallraff et al., 1994) such as in the mosaic map proposed by Wallraff (1974). The capacity for pigeons to follow familiar routes under clock-shift procedures suggests the cognitive representation of such allocentric relationships between visual landmarks is indeed compass-independent (pilotage; Biro et al., 2007), although the existence of both map structures, and the potential for their simultaneous operation, is also plausible (Armstrong et al., 2013; Biro et al., 2007; Gagliardo et al., 2005; Guilford & Biro, 2014). This allocentric structure of landmarks could further be stored in such a way that supports both self-position fixing and vector calculation to the goal, whilst allowing for the computation of novel shortcuts between known locations (Bennett, 1996; Toledo et al., 2020). This construct is termed a cognitive map, being first described by Tolman (1948) and later refined by O'Keefe & Nadel

(1978) and has been largely demonstrated in bats and rodents (Geva-Sagiv et al., 2015; Moser et al., 2008; Toledo et al., 2020; Tolman, 1948; Tsoar et al., 2011). However, observing evidence of such novelty in movements is inherently difficult without knowing the complete history of an animal's past movements (Bennett, 1996; Harten et al., 2020; Wynn et al., 2025).

Despite such evidence for a range of map-like representations, animals do not need to embed visual landmarks in maps for them to aid in navigation. In their simplest form, a visual landmark close to the goal can act a beacon with which an animal can direct its homewards movements towards (Able, 2001; Geva-Sagiv et al., 2015). Rather than informing desert ants of their position in space through allocentric relationships, landmarks are encoded as panoramic views of visual arrays along familiar routes and simply instruct ants when to enact what orientation, through comparisons of their current view against these learnt panoramas and their associated orientations (Collett, 2010; Collett et al., 2007, 2025; Collett & Collett, 2002; Lionetti et al., 2023; Wehner et al., 2006). This recognition of the geometric array of landmarks in their visual field is also reported to be used by ants to locate the nest (Graham et al., 2003; Islam et al., 2022; Narendra, 2007; Wystrach et al., 2012). This view-based guidance is also reported in honeybees and potentially is retained as the alternative strategy to map-like representations in insects given their compact neural capacity (Collett & Collett, 2002; Kheradmand & Nieh, 2019; Zhang et al., 1999). Similarly, whilst taxonomically and neurally closer to other bird species, the expression of landmark use in hummingbirds is more analogous to that widely seen in insect models (Pritchard & Healy, 2018). As in ants, hummingbirds seem to use landmark arrays in close proximity to the goal in view-matching processes, rather than extracting vectors or bearings as we may expect in the maps described in other avian models (Pritchard et al., 2015, 2016).

Irrespective of how they are represented cognitively or through what process they relay positional information during homing, it is apparent that visual landmarks have wide applicability in the mechanisms underpinning animal navigation (Holland, 2003; Wiener et al., 2011; Wiltschko & Wiltschko, 2023). It appears that

the use of such visual cues can be best detected in experiments which either manipulate the landmarks themselves, or manipulate the sensory capacity of the focal species, forcing an animal to draw upon its learnt representations of landmarks in the absence of other cues (Collett, 1992; Etienne & Jeffery, 2004; Holland, 2003; Pritchard & Healy, 2018). Shearwaters are highly mobile seabirds that cover vast distances across open oceans, and presumably the only source of stable visual information available to them is through the recognition of topographical features such as coastlines and islands. Since these landmasses cannot be manipulated directly, several studies have denied these seabirds of their olfactory sense, using zinc sulphate or surgical intervention, to reveal the use of topographical features during homing (Dell'Ariccia & Bonadonna, 2013; Gagliardo et al., 2013; Padget et al., 2017; Pollonara et al., 2015; Shallenberger, 1975). Despite this evidence for landmark use in anosmic shearwaters, there has been little evidence for such processes in natural homing. It was demonstrated that streaked shearwaters rely on coastal topography more after sunset, presumably as a substitute for directional information in place of the sun compass (Shiomi et al., 2019), but as discussed in Pollonara et al. (2015), this localised coast following does not confirm the use of a larger scale allocentric map based on familiarity with topographical features. Therefore, in this chapter I investigate the question of landmark use in the navigation of highly mobile free-ranging *Puffinus* shearwaters by conducting two complementary case studies: an initial exploratory analysis on Balearic shearwaters, *Puffinus mauretanicus*, followed by a more comprehensive test using a larger Manx shearwater, *Puffinus puffinus*, dataset. Through these case studies I investigate the role of visual landmarks, here presented as coastal topographical features, on the homing performance of these free-ranging shearwaters at a range of spatial scales. This study aims to quantify the role of these landmarks on the mediation of efficient homing in natural movements of shearwaters, without any experimental manipulations in sensory capacities or homing location. By quantifying the role of such cues in natural movements, we can begin to frame our understanding of wild bird navigation processes in natural contexts.

General Methods

Data availability and processing

This chapter utilised free-ranging tracking data from two on-going shearwater monitoring projects. First, data was used from GPS tracked Balearic shearwaters breeding in the Sa Cella colony on Mallorca (**Figure 6.1A**, 39°36'19.47"N, 2°21' 21.96"W). These critically endangered seabirds were tracked during their incubation periods (March to April) from 2016 to 2019. Due to limitations in colony access, as well as special considerations of tracking impact with regards to their endangered status, the Balearic shearwater database is significantly smaller than the second dataset used here. The second dataset was sourced from GPS tracked breeding Manx shearwaters, tracked across six colonies around the British Isles (**Figure 6.3B**, Skomer Island [51°44'14.7"N, 5°16'55.6"W], Skokholm Island [51°41'37.8"N, 5°17'13.9"W] and Ramsey Island [51°52'26.6"N, 5°20'0.8"W], South Irish Sea, Wales; Lighthouse Island [54°41'43.0''N, 5°15'3.9''W], Copeland Islands, Northern Ireland; Rum [56°59'23.1''N, 6°17'11.0''W], Hebrides, Scotland; Lundy [51°10'6.7''N, 4°40'32.5'' W], Bristol Channel, England). The Manx dataset contains tracks from both the incubation (May-June) and chick-rearing (July-August) periods of their breeding season, with tracks spanning from 2004 to 2024. Both projects are on-going, but data is capped to 2024 at the point data preparation began for these analyses.

In both species, devices were attached dorsally to mantle feathers using TESA marine tape (attachments followed standardised protocols outlined in **Chapter 2** and Guildford et al., 2008) and all device masses were under 4% of the bird's total body mass. Devices were scheduled to take GPS fixes at a range of intervals, as changes in device capacities through the years allowed for increasing resolutions (from 60-minute intervals down to one-minute).

Individual GPS deployments often contained multiple foraging trips, particularly the chick-rearing trips in the Manx tracking data, incubation trips are often longer, and the bird remains in the burrow upon return, so the tag will often have been retrieved before a second trip begins. In instances where a single GPS file

contained multiple trips marked by a return to the colony, trips were separated at the point of this return and processed separately. Before analysis, all trips were checked for the data quality, specifically: That the GPS resolution was at least 30-minutes or higher, each trip contained at least 50 GPS fixes, each trip reached a minimum of 25 km from the colony, and that each trip recorded either the entire foraging trip, or at least 90% of the subsequent homeward movements (taken as the distance between the onset of homing and the colony). Trips that met these criteria were then filtered by their inter-fix speeds to remove any GPS errors, removing any fixes recorded as travelling above the upper speed threshold of Manx shearwaters of 80 kmph as given in Guilford et al. (2008). The same speed filter was applied to both species. After any errors were removed, trips were interpolated to 5-minute intervals using cubic spline interpolation algorithms (Tremblay et al., 2006).

When a shearwater begins to home, there is a clear detectable switch in the movement data between mid-speed foraging movements, or rest, and a continuous bout of movement in the homeward direction (Padget et al., 2019). These rapid homeward movements produce a steep decline in the distance from home across the track, and the onset of this can be taken as the point that the bird began to home. This homing point was identified manually, through visual inspection of this distance from home through time, blind to trip details, and this identification was validated with a subset of tracks, showing 98% repeatability of the identified homing point (see **Chapter 2**).

Landmark identification

Within the breeding ranges of both species, all known landmasses were collated as shapefiles from the Natural Earth public database (accessed through the 'rnaturalearth' package). For each of these, the area within which they would be visible to a shearwater was then calculated by computing the maximum visible distance of all points of elevation within each shapefile (accessed through the 'elevatr' package) and extracting the outermost values of these as a radius of visibility. These distances were computed using the 'horizon' function in the 'geosphere' package which, for a point of given altitude, computes the distance of the horizon along a tangent line of sight. This does not account for variation in an individual's flight height but given their preference for shear-soaring and known proximity to the sea surface (Kempton et al., 2022), they are extremely unlikely to fly at heights that would make these visibility estimations unreliable. Any error produced through the lack of flight height quantification is likely masked by the resolution of the GPS data, as the variation in the true point of emergence of these visible landmarks is likely within the distance covered between individual fixes (~2-5 km). To then identify when these landmarks became visible to individuals during their homing flights, all GPS fixes were intersected against the visibility radii of all landmasses within their breeding ranges (using 'st_intersect' from the 'sf' package) which meant that, for each fix, all visible landmasses (or lack thereof) were identified.

Predictions and Case Study overview

One indication that a shearwater may be using spatial information derived from visual landmarks to guide their homing flights would be a reduction in deviations of the bird's trajectory from the homeward beeline with the availability of such landmarks at the onset of homing, or their later emergence during homeward movements. The following two case studies test this prediction, first using data from Balearic shearwaters, and then expanding the analysis to a larger Manx shearwater dataset to address limitations identified in the initial study.

Case study I: Balearic shearwaters

Balearic shearwaters: Study rationale

Balearic shearwaters, *Puffinus mauretanicus*, are a Procellariform species that breed throughout the Balearic Islands, in the Mediterranean Sea, from March to early July (Guilford et al., 2012; Pérez-Roda et al., 2017). Despite uncertainties in their current taxonomic status (Ferrer Obiol et al., 2023; Sangster et al., 2026), their populations within these breeding islands are reported to be consistently low, facing threats from bycatch in fisheries and climate change, and as such are currently listed as Critically Endangered (Arcos, 2011; Genovart et al., 2016; Luczak et al., 2011; Mouriño et al., 2003). In light of these low population estimates and recognised threats, understanding both their movement behaviours and the cognitive processes that may underly these is crucial for better predicting changes in their movements in the future (Louzao et al., 2012; Pérez-Roda et al., 2017). For example, recent work has highlighted rapid changes in the spatial and temporal structure of their migratory behaviours, revealing that the cognitive mechanisms underlying these long-distance movements may facilitate this plasticity in the face of climate change (Lewin et al., 2024). Therefore, here we look to further this knowledge on the cognitive processes that underpin these movement decisions, investigating the role of visual information in the homing behaviour of this species.

In this case study, movement data collected from free-ranging individuals is used to analyse the role of landmark availability in the homing accuracy of unmanipulated Balearic shearwaters. The results of this analysis, and its limitations, informed refinements to the hypotheses and design of the second case study in this body of work, investigating such questions in the Manx shearwater.

Balearic shearwaters: Methodology

After the quality filtering detailed in the general methods for this investigation (as in **Chapter 2**), there were 26 Balearic shearwater foraging trips available for analysis, originating from 29 GPS deployments across 27 individuals (**Figure 6.1A**). The number of trips available for analysis is less than the total number of deployments as some birds did not travel sufficiently far to be analysed with respect to homing behaviour, whilst other devices failed before the bird had begun to home. Here, the only landmasses included within the ranges of the available GPS tracks were the Balearic Islands themselves (**Figure 6.1B**).

To analyse if landmark emergence produced changes in the homing performance of Balearic shearwaters, their homeward deflection was modelled in periods preceding and following the emergence of the first landmark. Homeward deflection was calculated for each fix as the difference in the instantaneous bearing between the current fix to the next, and the Great Circle arc, termed beeline (Padget et al., 2019), between the current fix and the home colony. This was then averaged across 20 km windows either side of the point of landmark emergence (**Figure 6.1B**), and these values were compared using a mixed-effect beta regression model, accounting for random intercepts from individuals:

$$\textit{Homeward deflection} \sim \textit{Presence or absence of visible landmarks} + (1|\textit{Ring})$$

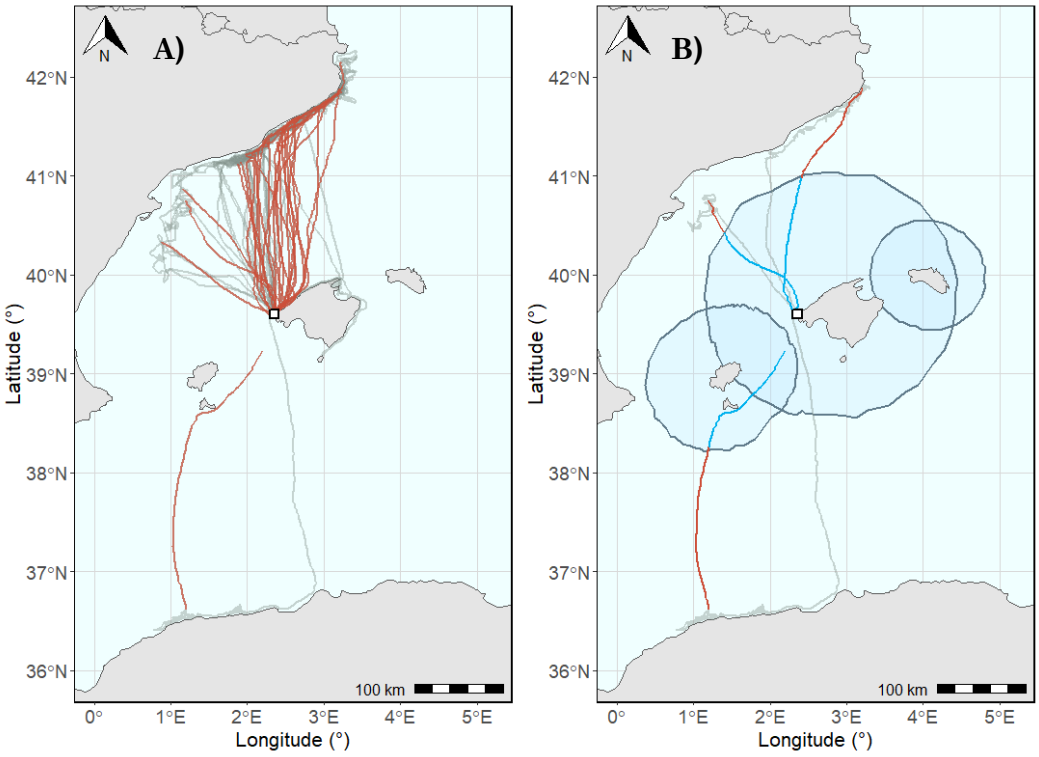


Figure 6.1. Maps of the tracked individuals in the Balearic dataset. In **A**) all tracks available for this investigation (n = 26), with outbound movements and foraging in grey and homing flight highlighted in red. In **B**) the visibility radii of the three large Balearic Islands are visualised, with example GPS tracks showing the non-homing behaviour in grey, homing made out of sight of land in red, and homing made in sight of these landmarks in blue. In both maps, the colony is indicated by the white square.

Balearic shearwaters: Results

In the 26 tracks available in this analysis (**Figure 6.1A**), birds went on foraging trips of an average length of 868.05 km (SD = 228.15 km), ranging from 493.39 km to 1451.60 km, reaching an average maximum distance from the colony of 243.52 km (SD = 50.13 km). These foraging trips lasted an average duration of 237.98 hours (approximately 10 days, SD = 77.19 hours), indicative of the longer movements seen in incubation trips as opposed to chick-rearing movements.

At the onset of homing behaviour, birds adopted a course with an average deflection of 18.98 ° from the beeline (SD = 15.93 °), ranging from 0.56 ° to 47.38 °. When investigating the changes in homeward orientation in the 20 km sections of movements before and after the emergence of landmarks, no significant changes were detected in the beta regression ($\beta = 0.189 \pm 0.147$, $z = 1.285$, $p = 0.199$). The mean deflection in the window before landmark emergence was 7.19 ° (SD = 6.05 °), and the estimated change after landmarks became visible was small (+1.32 °, SE = 1.09 °, **Figure 6.2**).

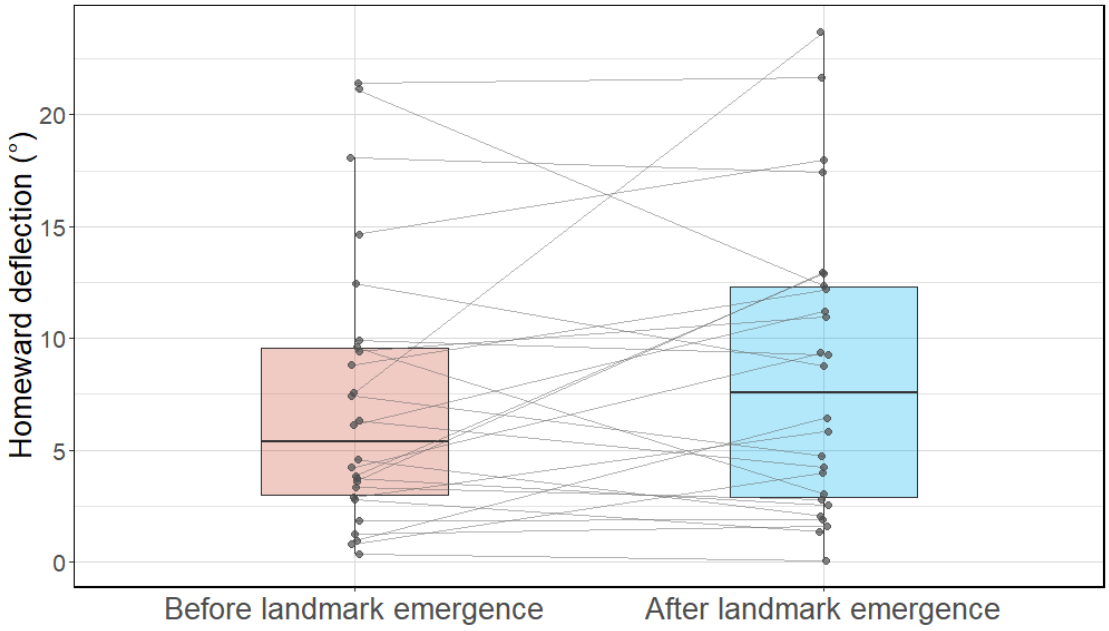


Figure 6.2. A boxplot showing the average homeward deflection in 20 km windows both before (left, red) and after (right, blue) the emergence of landmarks along the homing trajectory of Balearic shearwaters. The overlaid points with connecting slopes show the individual paired values within the dataset from each homing trip.

Balearic shearwaters: Discussion and data limitations

This analysis did not detect any effect of landmark emergence on the orientation of homeward movements in free-ranging Balearic shearwaters. Whilst it is entirely plausible that this lack of effect could indicate an absence of topographical landmark use in the homing processes of these shearwaters, it is more plausible that this dataset does not capture the breadth of data and natural contrasts needed to fully investigate this hypothesis in natural navigation. Here I will briefly highlight some of these limitations.

Firstly, almost all of the tracks, except the single bird that foraged in the South of the Mediterranean, began homing from along the Spanish coast, and intercept the same visibility radii, Mallorca, at analogous points (**Figure 6.1A**). This homogenises the data and limits the inferences that can be drawn from it with regards to landmark use. Secondly, this was not thought of at the time of analysis, but a post-hoc interrogation revealed a seemingly obvious flaw of these tracks that home from along the coast of Spain: the birds can see mainland Spain. Initially, landmarks were thought of as reference points that emerge on the homeward trajectory that could inform the bird of any refinements in its orientation with respect to the colony. However, reciprocal bearings, these being bearings taken against landmarks in the opposite direction to the intended course, could be used to remain orientated during these pelagic movements (Genz, 2008). In fact, when homing following successful foraging trips, ants walking backwards whilst dragging food items will routinely pause to look forwards and correct their trajectory, before returning to the food item and using rear-visible celestial cues to maintain a homewards orientation whilst walking backwards (Pfeffer & Wittlinger, 2016; Schwarz et al., 2017).

By encoding the position of the Catalonian coastline in an allocentric 'map' formed through experience, with or without associated compass-bearings, a shearwater could acquire simplistic directional information (such as "fly away from the coast", or "fly South of the coast") that would bring the bird closer to, and within visible range of, its home colony (Guilford & Biro, 2014; Guilford & Burt de Perera, 2017; Holland, 2003). Such use of the Catalonian coastline to provide

directional guidance has already been demonstrated. As discussed in Padget et al. (2017), anosmic Scopoli's shearwaters homing from foraging sites along this coastline were, whilst orientated worse than controls, relatively directed in their movements towards the Balearic archipelago, later adopting coast following to reach their goal. In contrast, anosmic Cory's shearwaters released in entirely pelagic sites showed no significant orientation and failed to home (Gagliardo et al., 2013). Therefore, perhaps these Scopoli's shearwaters, who routinely forage along the Catalonian coast, have learnt spatial relationships between this coastline and their home island, or archipelago, and are recalling them to facilitate successful homing in absence of olfactory information (Padget et al., 2017). It is plausible then that the Balearic shearwaters investigated here may too have learnt such relationships with this topographical feature, facilitating efficient orientation from the onset of homing. When applying such theories and mapping the visibility radii of the Spanish and Algerian coasts on to the available tracks in this case study, we see that there are in fact now no instances in which these Balearic shearwaters home out of sight of land (**Figure 6.3A**).

Nevertheless, evidence for landmark use could still be detected, even if birds do not begin homing in the absence of visual cues to provide the natural contrast originally sought after here. In Pollonara et al. (2015), anosmic shearwaters remained poorly orientated for much of their movements in sight of land, and it was only upon recognising specific topographical features that they became homeward orientated. If, during their natural movements, these Balearic shearwaters were to encounter a range of landmarks, it is plausible that we may detect how the change in landmark quantity, and the availability of specific landmarks, could influence orientation. However, the landmark array encountered by these Balearic shearwaters, across a relatively local area, is too limited, and homogenised between individuals, to produce such testable variation.

Given the discussed limitations in this Balearic dataset with regards to testing hypotheses of landmark use, it is here that I expand the analysis into the Manx dataset (**Figure 6.3B**). This dataset contains over 2,000 foraging trips, which

encounter nearly 200 landmarks across their ranges within and around the British Isles. Additionally, many of these foraging movements are out into the North Atlantic (**Figure 6.3B**) and begin homing from out of sight of any landmarks. Therefore, this dataset contains more natural variation in landmark availability to investigate the proposed hypotheses of their role in mediating homing performance.

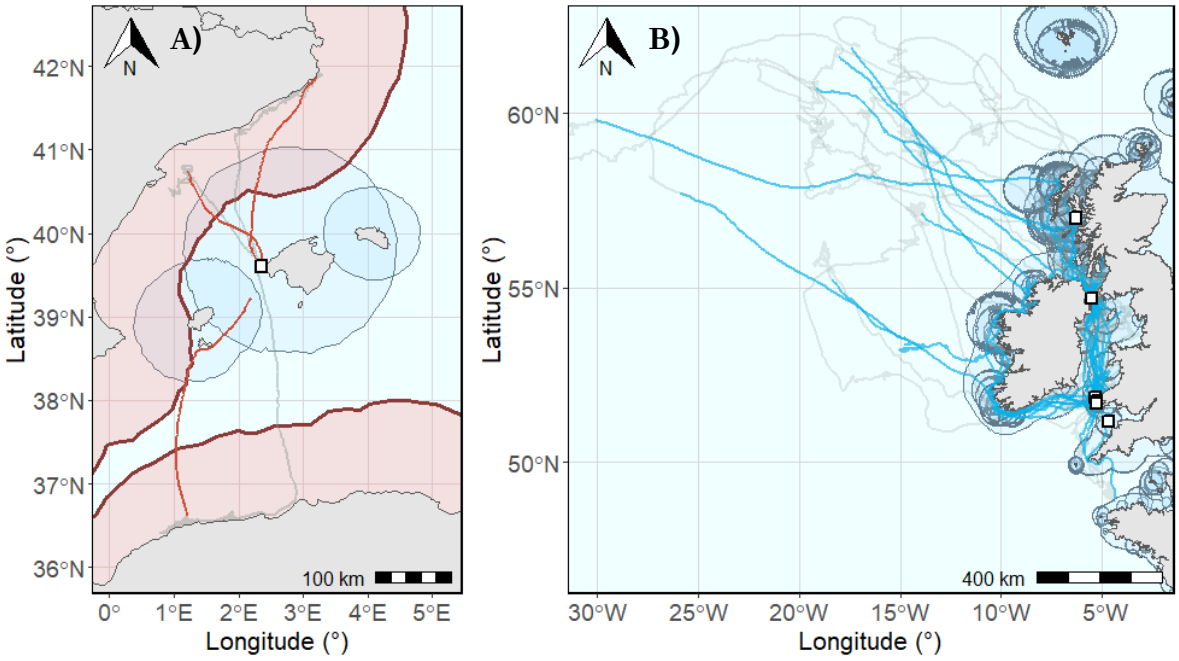


Figure 6.3. ***A***) A replotting of the example data presented in **Figure 6.1A**, but with the additional visibility radii of both the Spanish and Algerian mainland. With these accounted for, it is clear that no birds home from out of sight of land, and it is only during a brief stint of the bird homing off the coast of Algeria that a bird enters a pelagic area out of sight of landmarks. To contrast, ***B***) shows the larger scale of pelagic movements captured in the Manx dataset, as well as the vast array of visible landmasses (199) contained within the dataset. Only ~5% of the available data is presented here, to make the map more interpretable.

Case study II: Manx shearwaters

Manx shearwaters: Study rationale

The previous case study investigating landmark use in the homing behaviour of Balearic shearwaters highlighted the need for expansive datasets when investigating nuanced hypotheses in natural tracking data. Such datasets need to contain both a breadth of tracking data and a range of interactions with the cue being investigated in order to generate enough natural contrasts within the dataset to test for the use of this cue without the manipulation of focal individuals (Demšar et al., 2025). This then introduces the on-going tracking project of Manx shearwaters by the OxNav Research Group. This dataset now contains over 2,000 individual foraging trips from adult breeding Manx shearwaters tracked over the last two decades from sites throughout the British Isles. Unlike the individuals tracked in the Balearic dataset, many of these Manx shearwaters execute foraging trips that span thousands of kilometres, reaching far-off pelagic sites that are truly out of sight of any landmasses, providing a model example to investigate the role of visual landmarks upon their emergence along the homeward trajectory. Not only this, but the extent of this dataset allows for the testing of multiple alternative hypotheses of landmark use under different homing conditions, which could not be investigated in the Balearic dataset.

Manx shearwaters: Methodology

After the processing and track selection discussed in the general methods of this investigation, there were 2,004 Manx shearwater foraging trips available for analysis in this presented case study, originating from 1,110 GPS deployments across 799 individual shearwaters.

First, the modelling procedure described in the Balearic case study above was repeated in this dataset, where the changes in homing deflection in 20 km windows before and after the emergence of landmarks were compared using a mixed-effect beta regression model. This model used foraging trips where the bird began homing out of sight of land along an unobstructed homeward beeline (64 trips). Additionally, the breadth of this dataset allowed for the addition of an interactive factor of landmark familiarity to this model, calculated as the colony-specific encounter rate of each landmark encountered within these free-ranging movements. To calculate an approximation of this colony-level encounter rate with a given landmark, the proportion of tracked birds from each colony that had entered the visible radius of each landmass was calculated. This gives an estimation of the population-level experience with a landmark for each colony, and in turn an expectation to how useful a given landmass may be in position estimations deriving from maps built upon familiarity. This approximation then gave a weighted expectation to the emergence of which landmarks may be expected to yield greater improvements in homing accuracy. This was then factored into the model below testing the change in deflection in windows either side of landmark emergence in unobstructed homing tracks, with the expectation that any reductions in deflection would be stronger in instances where the landmark emerging was highly familiar to the individual:

$$\textit{Homeward deflection} \sim \textit{Presence or absence of visible landmarks} * \textit{Colony-level familiarity of emergent landmark} + (1|\textit{Colony/Ring})$$

In the Manx dataset, there are many instances where the homeward beeline is obstructed by a landmass, and in these, it may be expected that the emergence of landmarks informs birds of this obstacle (see **Chapter 4**). So, rather than

producing a reduction in deflection from the homeward beeline, which is blocked, the bird may turn away from this route, instead orientating towards the route adopted to later circumnavigate this obstacle. These obstructed trips which began homing out of sight of land (n = 28) were modelled in the same way as above, but were modelled twice, first with the response variable as the deflection from the homeward beeline, then second as the deflection from the ultimate circumnavigation route. The familiarity of the emergent landmark was again included, as well as the potential for the emergent landmark to be the landmass that is obstructing the beeline:

*Deflection (homeward / circumnavigation route) ~ Presence or absence of visible landmarks * Colony-level familiarity of emergent landmark + Presence of absence of visible landmarks * Obstacle visibility + (1|Colony/Ring)*

Familiarity changes within trips:

These previous models address how the emergence of visible landmarks in trips that begin homing out of sight of land may mediate homing improvements, but the increasing availability of landmarks throughout these homeward movements may also mediate improvements in their homing accuracy, especially with respects to the familiarity of these landmark arrays. To assess whether changes in landmark availability throughout the return journey influences a shearwater's homing accuracy, every instance of a change in the visible array of landmarks during the homing of all unobstructed homing periods in this Manx dataset (910 trips) was isolated and modelled with respect to characteristics of this change in landmarks.

Here, landmarks were categorised into high familiarity (those encountered by more than 75% of birds from a given colony) and low familiarity (encountered by less than 75%). During homeward flight, each change in landmark count was categorised as an increase or decrease in landmark number with respect to those that were previously available prior to this change (**Figure 6.4**). At each point of change in landmark count, the following deflection in a window of 10 km was averaged to produce an associated deflection value. These deflection values were

then modelled against the number of high and low familiarity landmarks, how this current landmark count had changed compared to previous homing sections, and the distance from home. These values were scaled where appropriate, and modelled using beta regressions as follow:

*Homeward deflection ~ No. of high familiarity landmarks * change in landmark count +*
No. of low familiarity landmarks +
*No. of high familiarity landmarks * distance from home +*
(1 | Colony / Ring)

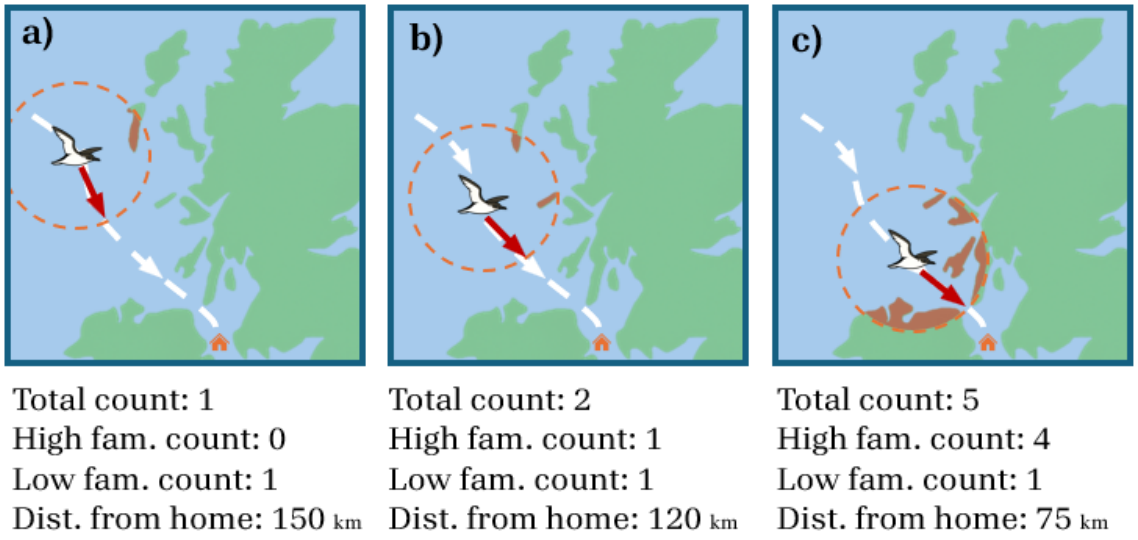


Figure 6.4. A schematic illustrating the changes in the landmark count, count of high and low familiarity landmarks (classified as described above), and distance from home as a shearwater moves through its homing flight. At each point, the deflection of the bird along a 10 km window (red arrow) is taken against the beeline from that point.

Manx shearwaters: Results

Across the dataset, there appeared to be no differences in the initial homeward deflection between birds who began homing in either the presence of absence of landmarks. At the onset of homing, the mean homeward deflection of birds who began homing out of sight of land was 18.06 ° (SD = 15.08 °, n = 92), whilst for birds that began homing in sight of land their mean deflection was 16.26 ° (SD = 13.23 °, n = 846), and despite the marginally lower value for those with visual landmarks, these did not differ significantly ($t_{106.77}$ = –1.102, p = 0.273).

When investigating the changes in homeward orientation in the homing movements of Manx shearwaters which began out of sight of land (irrespective of whether or not their beeline was obstructed) no significant changes in homeward deflection were detected when landmarks first became available. In the model of landmark emergence using birds homing along an unobstructed beeline, the mean deflection in the window before landmark availability was 20.20 ° (SD = 18.70 °, n = 64), and the estimated change after landmarks first became visible was small (-1.47 °, SE = 2.40 °, **Figure 6.5**). The beta mixed-effects model indicated that there were no significant differences in deflection in the periods of homing before and after the first landmark became visible (β = −0.399, SE = 0.452, z = −0.883, p = 0.377). There was a non-significant trend suggesting that emergent landmarks of higher familiarity were associated with lower deflections overall (β = −0.876 ± 0.503, z = −1.743, p = 0.081). However, the interaction between familiarity and the changes in deflection before and after this landmark emergence was not significant (β = 0.364 ± 0.453, z = 0.803, p = 0.422).

Furthermore, in the birds homing from beyond an obstruction to the homeward beeline (such as the example illustrated in **Figure 6.4A**), the emergence of visible landmarks, again, did not have any significant effect on their deflection from this homeward beeline (β = 0.081, SE = 0.179, z = 0.452, p = 0.651, **Figure 6.6A**). Additionally, whether or not the emergent landmark was the obstacle itself (as in many instances birds with ultimately obstructed beelines encounter landmarks before arriving at the obstacle, such as **Figure 6.4A**) did not significantly influence this change (β = 0.285, SE = 0.381, z = 0.749, p = 0.454), nor did the colony-level

familiarity with this first landmark (β = -0.311, SE = 0.418, z = -0.744, p = 0.457). Conversely, the model investigating the deflection to the circumnavigation route reported a significant increase in deflection (β = 0.446, SE = 0.193, z = 2.310, p = 0.021, **Figure 6.6B**). This is to be expected after the reported lack of deviation from the homeward beeline, as these directions are often at odds and so by maintaining their homeward orientation, the deflection towards alternate route options increases. This deflection was stronger when the visible landmass was the obstacle itself, as their proximity to the obstruction for it to be visible meant that the angle towards the circumnavigation route was much larger (β = 0.827, SE = 0.369, z = 2.242, p = 0.025). This suggests that obstacle recognition does not occur immediately, and perhaps that it is only when closer that birds recognise that their beeline is obstructed.

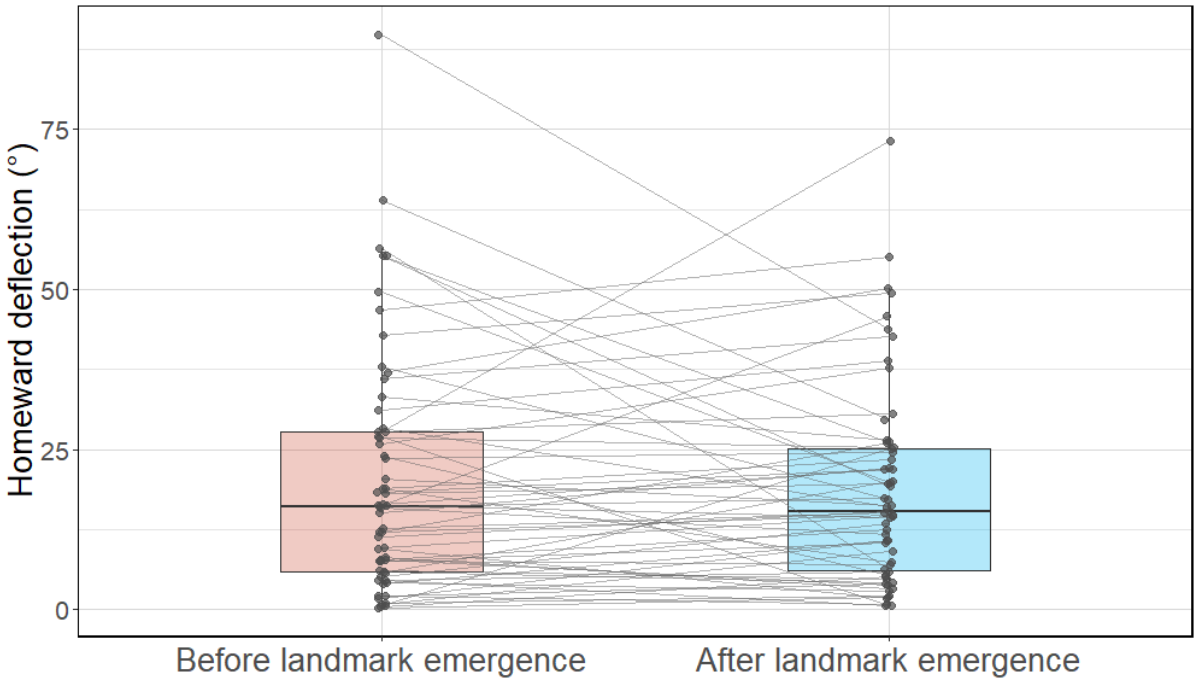


Figure 6.5. A boxplot showing the average homeward deflection in 20 km windows both before (left, red) and after (right, blue) the emergence of landmarks along the homing trajectory of Manx shearwaters. The overlaid points with connecting slopes show the individual paired values within the dataset from each homing trip.

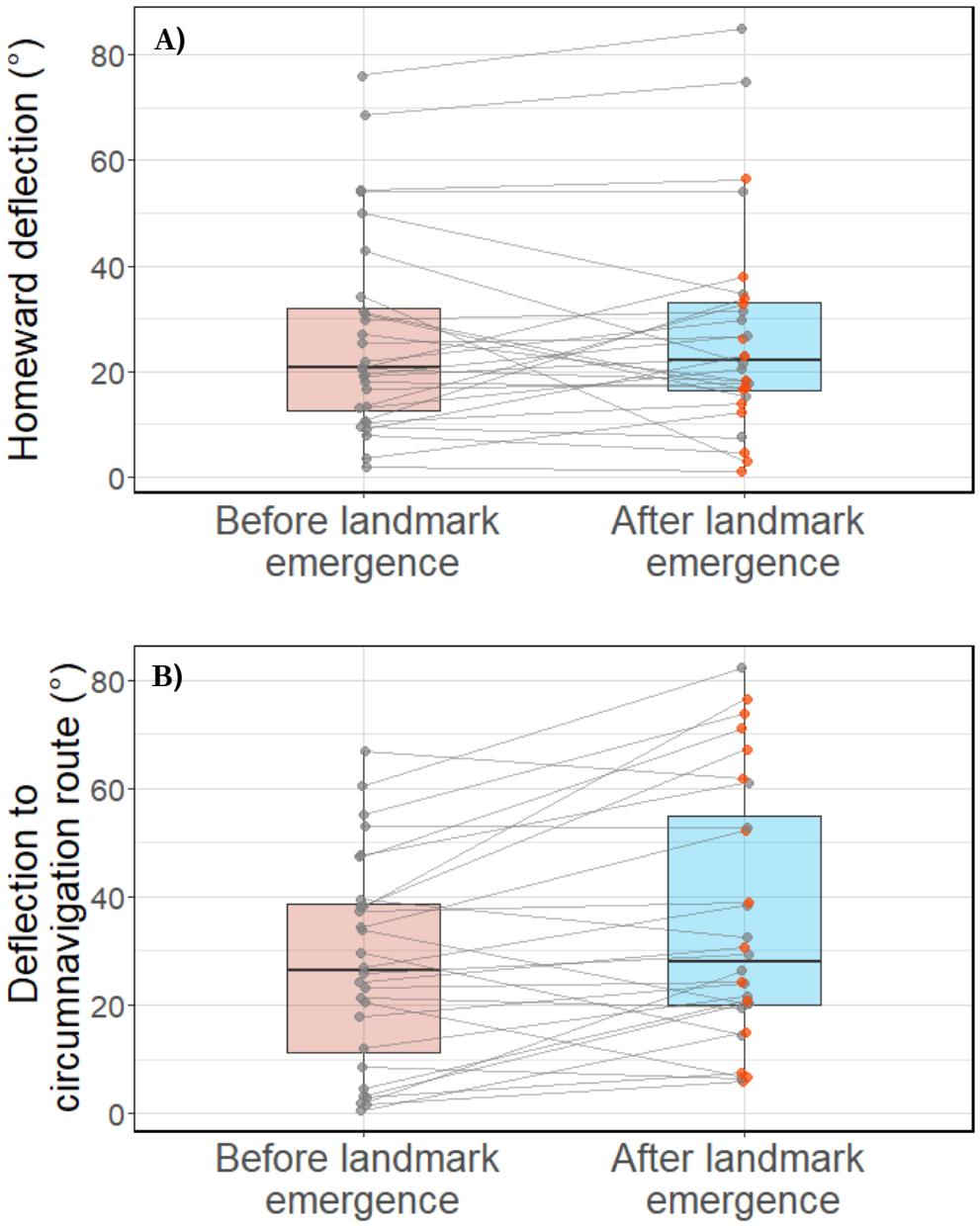


***Figure* 6.6.** The deflections towards the **A**) homeward beeline and **B**) direction of circumnavigation route in birds homing along obstructed beelines before and after the emergence of visible landmarks. The Orange points on the right-hand boxplots indicate the instances in which in the first emergent landmark was also the landmass obstructing the beeline.

Neither changes in the number of high-familiarity (β = -0.001 ± 0.033, z = -0.032, p = 0.974) nor low-familiarity (β = 0.006 ± 0.018, z = 0.337, p = 0.736) landmarks available during homing influenced the deflection from the homeward beeline. Similarly, whether the current landmark count experienced was greater or fewer than those previously experienced did not predict any changes in deflection (β = 0.010 ± 0.036, z = 0.279, p = 0.780). As a fixed term, the distance from home also had no influence on homing deflection (β = 0.036 ± 0.026, z = 1.389, p = 0.165), however, there was an interactive effect between this distance from home and the number of high-familiarity landmarks (β = 0.037 ± 0.016, z = 2.339, p = 0.019, **Figure 6.7**). This showed that as birds approached home their accuracy increased more when many high-familiarity landmarks were visible. Therefore, familiar landmarks seem to mediate improvements in homeward directedness only when near to the colony. It should be noted, however, that whilst using different streams of the central dataset, this analysis includes three related tests that were performed on the same response variable (deflection form the homeward beeline). Therefore, implementing a family-wise Bonferroni correction to this result in light of this family model structure (adjusted p = 3 x 0.019) would yield an adjusted p-value of 0.057; and under this correction the interaction above is marginally non-significant.

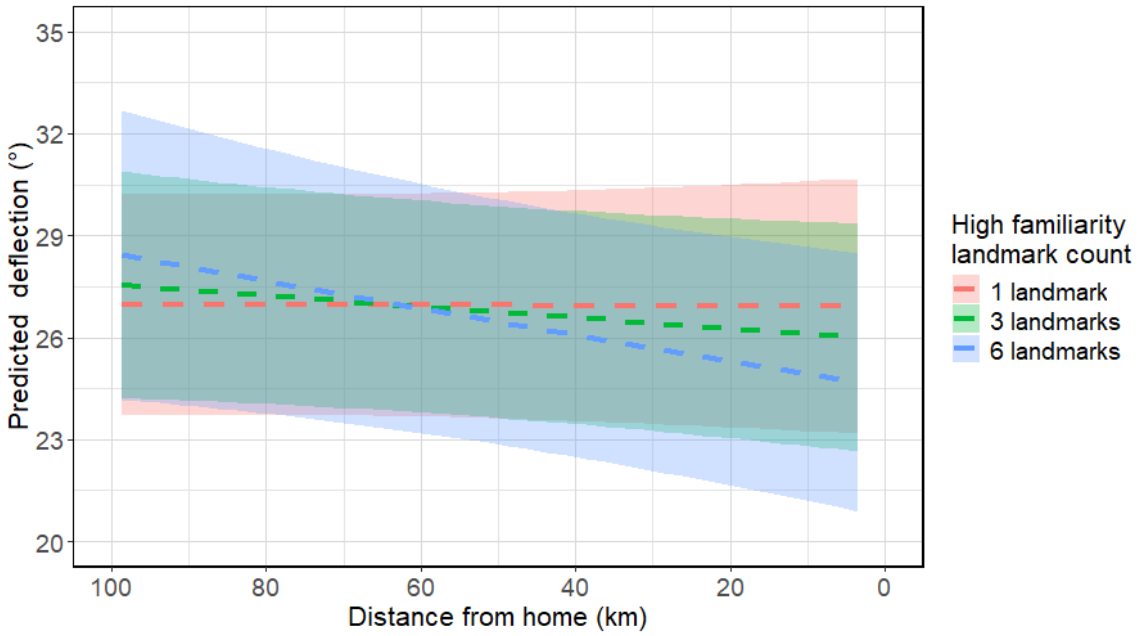


Figure 6.7. The predicted changes in deflection from the homeward beeline as a bird approaches the colony through proximal distances (100-0 km). Each relationship represents an increasing number of landmarks visible during these proximal movements, ranging from 1 (red) to 6 (blue). These modelled relationships were extracted from the beta regression reported above, with 95% confidence intervals plotted in corresponding colours. Reductions in deflection are gradually steeper as the number of landmarks increases (from red, through green, to blue).

Manx shearwaters: Discussion

This chapter investigated the potential influence of landmark availability on the homing performance of free-ranging pelagic shearwaters. Whilst the Balearic dataset presented in the first case study likely lacks the natural contrasts needed to detect the integration of topographical cues in homing decisions, the breadth of the Manx shearwater tracking dataset used in this expanded case study has made it possible to conduct a more thorough exploration of such hypotheses. With this, it was possible to quantify not only the point at which landmarks became potentially available to individuals, but also an expectation of how familiar an individual may be with a specific landmass and therefore predict how much spatial information it may portray. Despite the range of data and landmark variation captured within the Manx shearwater dataset, there was no robust evidence found for the influence of topographical landmark availability on homing performance. The conclusion of this however is not that these shearwater species do not retrieve spatial information from visual landmarks, but that the availability of such information is not apparently pertinent to the accuracy of their homeward movements. This supports the likely hierarchical organisation of natural navigational processes, as demonstrated in experiments which deny access to central processes such as the olfactory map (and discussed in **Chapter 5**; Dell'Ariccia & Bonadonna, 2013; Gagliardo et al., 2013; Padget et al., 2017; Pollonara et al., 2015).

The use of visual landmarks has been demonstrated in the homing behaviour of a range of related shearwater species, but this reliance on topographical features has only been detected once they are denied access to either olfactory or solar cues prior to release. In Scopoli's shearwaters, anosmic individuals showed significantly poorer homeward orientation in pelagic movements, with performance improving only after the topographic cues of surrounding coastline were reached (Pollonara et al., 2015). This was further demonstrated in the successful homing of anosmic shearwaters in Padget et al. (2017), where the coastal homing behaviour of olfactorily-deprived birds was indistinguishable from that of controls. In anosmic Cory's shearwaters (*Calonectris borealis*), who

were displaced to far-off pelagic sites, with no access to topographical information for hundreds of kilometres, almost all individuals failed to home (Gagliardo et al., 2013). Similarly, when Cory's shearwaters were displaced close to their colony at night, unmanipulated birds homed immediately, flying through the dark, whilst anosmic individuals were only able to home the following day, owing to their need for visual landmarks in absence of their olfactory sense (Dell'Ariccia & Bonadonna, 2013). Streaked shearwaters (*Calonectris leucomelas*) appear to time their homing to avoid at-sea flight in the absence of diurnal cues, owed to their reliance on the sun as a compass, but will fly through twilight when proximal to a coastline, which presumably provides an alternative source of directional information (Shiomi et al., 2019).

It is widely accepted that animals often have several navigation mechanisms available to them during homing, and it is likely that these are arranged hierarchically, informed by their ecological demands, where few are primarily relied upon whilst others act as auxiliary information sources (Able, 2001; Bingman & Cheng, 2005; Brodbeck, 1994; Freas & Cheng, 2022; Menti et al., 2023; Papi, 1990). Additionally, as discussed in **Chapter 5**, many species have demonstrated the ability to integrate the homeward vectors arising from multiple navigation mechanisms operating in parallel (Biro et al., 2007; Etienne & Jeffery, 2004). The growing evidence from these investigations into shearwater navigation, particularly those that induce anosmia, suggests that access to large-scale olfactory cues is central to their navigation processes, with visual landmarks constituting an alternative source of information available in the absence of access to this olfactory map (Gagliardo et al., 2013; Padget et al., 2017; Pollonara et al., 2015). In light of these results, it seems highly likely that shearwaters, at least those of the *Calonectris* genus, are encoding and recalling spatial information from topographic landmarks during their natural movements and subsequent homing behaviour, but that the use of such information is undetectable until their olfactory sense is denied.

Given this evidence from the field, it is potentially unsurprising that the detection of landmark use in unmanipulated, free-ranging *Puffinus* shearwaters was not

possible in this chapter. There are several potential explanations for this that I will discuss. Firstly, it is plausible that, as in the *Calonectris* species, these *Puffinus* shearwaters are attentive to topographic cues, but that these landmarks do not act as their primary strategy for at-sea navigation (Pollonara et al., 2015). Instead, these shearwaters are presumably calculating an accurate homeward course from alternative processes, such as large-scale gradient maps (Gagliardo, 2013). Without experimentally denying alternative information sources, such as olfactory cues (as in: Dell'Ariccia & Bonadonna, 2013; Padget et al., 2017; Pollonara et al., 2015), it is unlikely that changes in deflection arising from landmark availability will be detectable. In an early study of olfactory-inhibition in a *Puffinus* species, wedge-tailed shearwaters (*P. pacificus*) were denied their olfactory sense through the severing of their olfactory nerve (Shallenberger, 1975). It was reported that, despite a significant reduction in the number of anosmic birds that successfully homed, 30% of lesioned individuals were still able to return following a short-distance displacement, suggesting that the olfactory sense may not be critical to homing, and that their visually rich landscape may have facilitated their return. The closest example of olfactory deprivation in the species investigated in this chapter comes from a recent investigation by Morford et al. (2023). In this study Manx shearwaters were displaced from Skomer Island, Wales, to a coastal release site along the Bristol channel, Wales, using charcoal filters to prevent the detection of any olfactants during transport. Morford's team then varied the window with which shearwaters were allowed to sample local air prior to release, predicting that those with minimal time to sample such cues would be poorly orientated in their initial movements post-release. Irrespective of the amount of time birds were given in this sampling window, all birds were well orientated towards home in their initial movements. Given the reported ability of lesioned birds to home in Shallenberger (1975), and the well-oriented homing of the anosmic group in Padget et al. (2017) when moving along coastlines, perhaps the Manx shearwaters in Morford et al. were able to recognise familiar visual features around the release site given its proximity to their colony (~120 km), which facilitated accurate homeward orientation and prohibited a detection of the olfactory deprivation

treatments. An alternative explanation is that olfactory recognition was able to occur very rapidly once local air was smelled at release.

Whilst it does not appear that topographical features are critical for the successful homewards orientation of Manx shearwaters, it is potentially surprising that this visual information is not immediately employed to inform them of obstructions to their homeward beeline. It is established that this species does not anticipate such obstacles (Padget et al., 2019), but their failure to recognise this obstruction once associated topography becomes visible has interesting implications for how the spatial information of these landmasses may be stored. It appears that, once they recognise that they must circumnavigate such obstacles, they do so with high efficiency (as reported in **Chapter 4** and Padget et al., 2019, 2022) and yet, this recognition does not appear to be linked to the initial visibility of an obstacle. It could be then, that these landmasses are only recognised from more proximal distances, mediated by the recognition of specific coastlines or features, as seen in Pollonara et al. (2015). Further evidence of this is seen in pigeons, where the recognition of familiar landmarks and sites is mediated by viewing them from perspectives that recapitulate previously experienced views (Biro et al., 2003; Guilford & Biro, 2014; Meade et al., 2006). Alternatively, taking an insect-inspired approach to shearwater navigation (Pritchard & Healy, 2018), perhaps the recognition of such obstruction is tied to a view-matching process, as reported in insect models (Baddeley et al., 2011; Philippides et al., 2011) and sporadically in pigeons (Schwarz et al., 2024; Pecchia et al., 2011; Pecchia & Vallortigara, 2010). If landmark recognition in the shearwaters investigated here is tied to proximal or specific views of topographic features, then perhaps the methods used in this chapter to quantify the availability of visual topography to the shearwaters does not align with the processes within which this information is employed. Here, I assume that landmarks are recognisable from the maximum trigonometric distance that they could be visible from given their elevation above sea level. This was chosen under the assumption that visible topography would be recognisable and, with regards to its egocentric position, could be used to infer the allocentric position of the

goal. These assumptions also imply that landmarks are treated as discrete objects in space. However, if multiple landmarks are encoded in relation to one another (as in insects; Collett et al., 2007), then the emergence of any one of these may not suffice to relay positional information. Furthermore, in those homing beyond an obstacle, it was assumed that a shearwater does not need to recognise a landmass to realise its beeline is obstructed, although this recognition is probably crucial in the later efficient choice of circumnavigation routes (as shown in **Chapter 4**). Ultimately, if the birds are not capable of this distant landmark recognition, and use more proximal cues, then detecting the use of landmarks in the proposed methods of this investigation may not be possible.

The only potential role of topographical features reported here was that the number of highly familiar landmarks yields a greater improvement in homing accuracy when the bird is closer to home, albeit through a marginally non-significant effect when corrected for the model structure in this case study. At these proximal distances, the recognition of landmarks is more plausible, perhaps explaining why this was the only evidence of their use found (Pollonara et al., 2015).

The role of familiar landmarks has been widely demonstrated in the homing pigeon (Biro et al., 2003, 2004; Braithwaite & Guilford, 1991; Burt de Perera et al., 1997), albeit through repeated releases within individuals, and explicit to this landmark use is that these cues are most useful in areas proximal to the loft (Braithwaite, 1993; Guilford & Biro, 2014; Holland, 2003). Furthermore, the landmark use seen in the anosmic shearwaters of the various *Calonectris* studies were, whilst operating at an ecologically different scale of movements, also attributed to being locally mediated (within their familiar area; Gagliardo et al., 2013; Pollonara et al., 2015). It is therefore in line with our expectations from the field that here I found high-familiar landmarks to be associated with better accuracy at proximal distances. If large-scale olfactory maps operate with limited spatial resolution (Wallraff, 2004, 2005), then successful homing at fine scales may become increasingly dependent on alterative cues, such as landmarks (Guilford & Biro, 2014; Holland, 2003; Wiltschko & Wiltschko, 2009). Moreover, if

learnt landmarks become increasing useful at proximal scales, then encoding a greater number of landmarks within a familiar area could facilitate more effective homing within that region (Holland, 2003). It is then plausible to see how, through the potential necessity of landmarks at this spatial scale, proximal landmarks could be readily embedded into a familiar area map, mediating improvements in homing accuracy when close to home as reported, albeit non-significantly, in this analysis (Holland, 2003; Wallraff, 2005). Furthermore, with the expected frequency with which landmarks would be encountered at this proximal scale, it is likely that they would be highly familiar to the birds, reinforcing their use during navigation (Guilford & Burt de Perera, 2017).

Whilst this marginal result aligns with broader expectations of landmark use in the literature, more robust evidence should be obtained to identify the mechanisms with which topographic landmarks are both recognised and integrated into the navigation of this shearwater species.

Case Study synthesis: General conclusions

In this chapter I investigated the role of topographical landmarks in the homing performance of two *Puffinus* shearwaters using natural contrasts present in their free-ranging movements. The first case study exploring these hypotheses in Balearic shearwaters demonstrated the need for a breadth of data in investigating such questions without experimental intervention, in order to capture a range of natural contrasts that could be used to reveal nuances in the factors affecting observed homing performance. These limitations motivated the second case study, which employed an expansive dataset of foraging trips from adult Manx shearwaters that encompassed a wider range of navigational contexts with respect to landmark availability. Despite this more comprehensive analysis, there was little evidence for the availability of topographical landmarks mediating the homing accuracy of either species.

This suggests that the role of topographical landmarks in *Puffinus* shearwater navigation may operate as an auxiliary information source to other sensory cues, particularly demonstrated by the ability of Manx shearwaters to efficiently orientate home out of sight of land. Potentially, then, as demonstrated in related species, the experimental restriction of other senses could help isolate the contribution of visual information to homing. However, the potential consequences of such manipulations on the successful return of these birds to their colony and subsequent breeding success should be carefully considered. Given the endangered status of the Balearic shearwater, it is suggested here that any such investigations are focussed on the Manx shearwater, whose populations are robust enough to tolerate such investigation.

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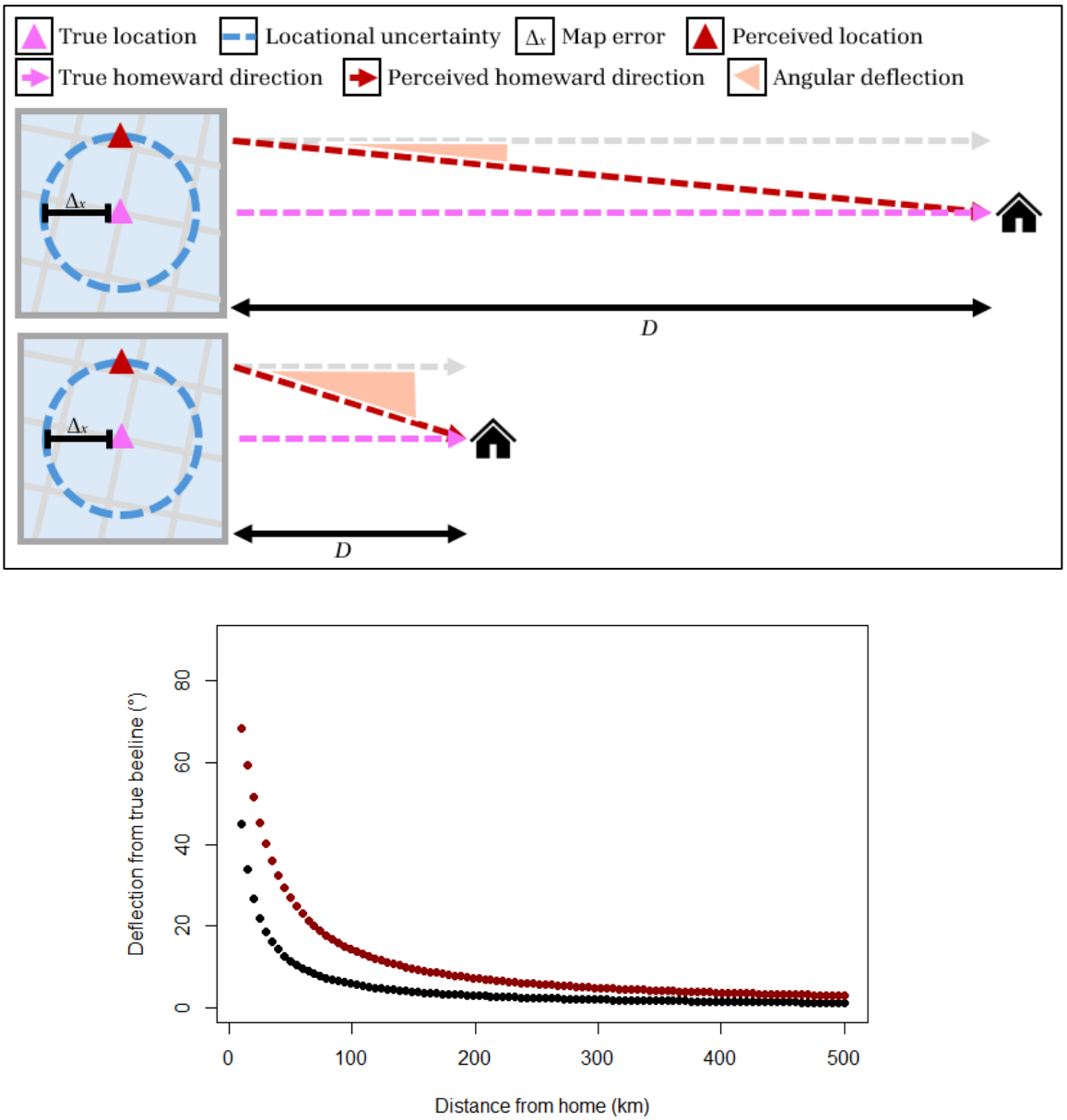
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Supplementary materials

S6.1. A schematic illustrating map error and beeline deflection



S6.1. A schematic illustrating how, under map-like representations with uniform map error, increasing beeline distance (D) reduces the angular deflection between the beeline from the true location and perceived location gith a given error value (Δx). The graph illustrates this relationship for given values of map error (Δx), the black points indicate 10 km error and red 25 km, the take home being that, under uniform map-error, reliance only on true navigation processes to home would produce increasingly lower homeward accuracy as distance from home decreases.

Chapter 7

General Discussion



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Since the formalisation of concepts such as the map and compass model and the cognitive map, biologists' understanding of animal navigation across different scales has made considerable advances. However, we still have much to learn about how these mechanisms interplay in wild, ecologically relevant, systems – beyond those investigated in true navigation. Through this thesis I have aimed to contribute towards a more holistic understanding of wild animal navigation by examining previously neglected processes that are likely to be an important aspect of navigation by organisms in free-ranging contexts. I have also evidenced the role of learning within these processes, discussing the potential cognitive mechanisms that could underly these impressive navigational feats.

In **Chapter 3** I began by investigating local navigation, in particular, whether shearwaters would be able to distinguish route efficiencies at very fine scales. By displacing shearwaters to local release sites around their home island, I found that they minimise homing time and distance by distinguishing between the two available round-island routes and choosing the shorter route following release. With further insights from natural tracking data, I suggested that this must be underpinned by route learning mediated through extensive experience within this familiar area. From this, I then explored how different frameworks of learning could have facilitated such route efficiencies, where the route dichotomies presented to them in this displacement appeared perhaps indistinguishable in their costs.

I then expanded on these ideas in **Chapter 4**, examining instances of obstacle circumnavigation in a large pool of free-ranging Manx shearwater tracking data to detect what drives route choice in natural contexts. I modelled route choices under several learning frameworks and found that shearwaters made more efficient route decisions when the route dichotomies presented were more distinct in their absolute flight distances. Furthermore, I found that proxies for familiarity with the task predicted improved efficiency, and that outward journey information was likely factored into these route decisions. These results were consistent with wider literature on avian route learning (Bonadonna et al., 1997; Guilford & Biro, 2014; Guilford & Burt de Perera, 2017; Wiltschko & Wiltschko, 2023a), and demonstrated that, whilst these obstacles are not represented in their calculation of a homeward

beeline (Padget et al., 2019), shearwaters are able to make well informed route choices when they encounter them.

In **Chapter 5** I examined the influence of outward journey movement properties on the resultant homing of free-ranging Manx shearwaters. Despite the proposed limitations of path-tracking processes at these spatial scales (Biegler, 2000), I found that increasing trip complexity, seen in metrics such as tortuosity, significantly predicted reductions in homeward accuracy, as would be expected under path integration models. However, the rate at which increasingly tortuous movements appear to accrue homing error suggested that any integration of outward movements was not the only process facilitating homing behaviour. I suggested that this outward journey information may act as auxiliary guidance to that gained from alternative navigation mechanisms, such as large-scale maps.

Lastly, in **Chapter 6** I investigated how the availability, and presumed familiarity, of topographic landmarks influenced the homing performance of free-ranging Balearic, *Puffinus mauretanicus*, and Manx, *Puffinus puffinus*, shearwaters. Despite a breadth of available data, I only found marginal evidence for the improvement of homeward accuracy through landmark availability. As in **Chapter 5**, I attributed this to the plausibly hierarchical organisation of navigational processes, and suggested that, without the experimental impairments of alternative processes (as in: Padget et al., 2017) the detection of landmark use in free-ranging homing behaviour may prove challenging.

In this final chapter, I will integrate the results from each of these four data chapters and discuss the wider implications of this thesis as a whole. In light of my findings, I will discuss the future of avian navigation research, questioning the utility of investigations into true navigation. I will then discuss the often-overlooked aspects of animal cognition in navigational investigations, such as the role of learning as highlighted in this thesis, as well as briefly addressing the limitations of correlative studies in the examinations of free-ranging data. I will then propose the future directions that this thesis points to, outlining avenues for the quantifications of experience in free-ranging data, and detailing experiments that could further illuminate some of the findings of this thesis.

Synthesis

1. Beyond true navigation: insights into alternative processes

"An adaptive mechanism for homing without outward journey information and goal emanating cues, that probably makes use of large-scale gradients with which an animal can compare currently perceived values to those learnt close to home, allowing them to chart a course between the two." – **True navigation as defined mechanistically in Chapter 1.**

The ability of an animal to true navigate has become a benchmark in the study of animal navigation (Putman, 2021). Inherent to the detection of this ability is the employment of passive displacements to far-off sites, which have become a ubiquitous tool in our field (Wynn & Liedvogel, 2023). In the pursuit of evidence of this true navigation capacity, such research has often excluded the operation of many other navigational processes (**Figure 7.1**). However, each of the data chapters presented in this thesis investigates an aspect of navigation that appears to not be explainable through the mechanisms of true navigation. Each offering exciting insights into alternative mechanistic and ontogenetic processes that underpin natural, ecologically relevant, navigation.

Through the findings of this thesis, I believe that Manx shearwaters (and, from wider evidence, shearwaters more broadly; Pollonara et al., 2013) have a suite of navigation processes available to them that allow them to achieve well-orientated and efficient homeward movements at a range of spatial scales. There is little doubt that shearwaters have access to some kind of large-scale map, as evidence by previous displacement experiments, and that this process must be able to accurately deduce a homeward course in absence of any other cues (true navigation; Padget et al., 2019; Pollonara et al., 2013). I believe that, if organised hierarchically, this navigation process is heavily weighted, as I found that the emergence of visual landmarks during homing does not appear to mediate improvements across broad spatial scales

(**Chapter 6**). Whilst landmarks can convey reliable spatial information, I believe that, as demonstrated in other shearwater species, they likely relay information that has already been deduced from this large-scale map, and it is only at spatial scales too fine to be reliably resolved from such maps alone (or in the absence of such maps) that landmarks are weighed into the homing decision (**Chapter 6**). However, this true navigation cannot solve all navigational tasks (**Chapters 3** and **4**), and we see that when displaced beyond obstacles shearwaters can make costly route choices (Padget et al., 2022), that are not adopted in free-ranging movements (**Chapter 4**). It is in this that, I believe, we find support to the integration of these auxiliary navigational processes alongside true navigation. As this thesis demonstrates, information gathered on the outward journey can indeed facilitate effective route decisions in natural contexts (**Chapter 4**) and appears to factor into the resolution of a homeward direction during free-ranging movements (**Chapter 5**). These auxiliary processes are actively denied in experimental studies, but it is the investigation of these mechanisms, and their underlying ontogeny, that I believe will be most important in the advancement of our field.

Central to our pursuits as ethologists should be the contextualisation of behaviour within natural systems, where selection drives the expression of behaviours best suited for an animal to survive in its environment (Demšar et al., 2025; Flack et al., 2022). Whilst examples of such contextualisation are well-established (Healy & Hurly, 2013), the mechanistic perspective of navigation that is perpetuated through the displacement paradigm of true navigation has led us towards the investigation of increasingly proximal components of this ability, often without the behaviour's function being considered explicitly (Guilford & Burt de Perera, 2017; Warrant, 2021; Wiltschko & Wiltschko, 2023b; Wynn & Liedvogel, 2023). Once more, as a field we should question whether this perceived ability to orientate from such a far-off site always indicates a biologically adaptive understanding of one's position relative to the goal, or alternatively, an approximation of a correct homeward direction from processes that have evolved for use in other navigational contexts (Guilford & Burt de Perera, 2017; Putman, 2021; Wynn & Liedvogel, 2023). Perhaps, then, by taking a step back in our perspective of navigation and readdressing *why* an animal is

performing this behaviour, as opposed to *how*, we may gain new insights into the avenues of avian navigation that are most pressing to investigate (Wynn & Liedvogel, 2023).

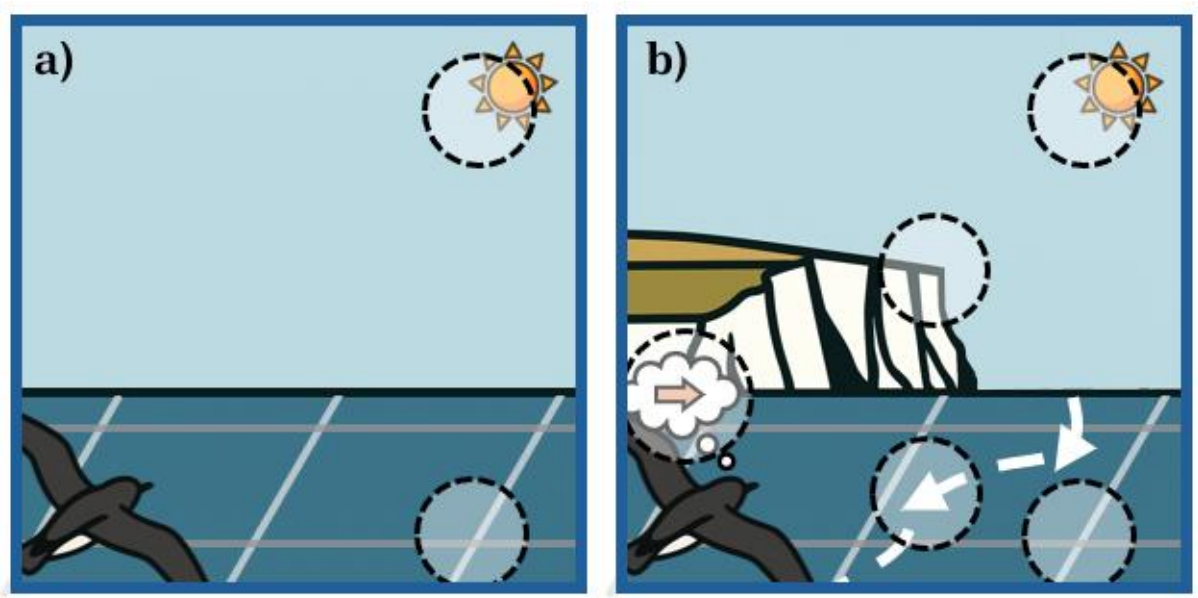


Figure 7.1. A schematic illustrating the navigational mechanisms investigated in **a**) classical displacement experiments of shearwaters compared to the **b**) diversity available of processes for examination in their natural movements, including details of the outward route, available landmarks, and auxiliary outward information (such as the direction taken around obstacles previously).

For example, shearwaters are reluctant to fly over land, owing to their extremely long wings, and legs positioned far back on the body; morphological adaptations for the exploitation of at-sea wind gradients during flight (Kempton et al., 2022) and diving at sea (Brooke, 1990). This means that a beeline computed from large-scale gradients (true navigation) is not executable if a landmass lies between itself and its goal (Padget et al., 2019). This nuance in its homing behaviour, shaped by its ecological constraints and the archipelagic environment within which it moves, allows us to shape our mechanistic questions of this behaviour through the natural contexts in which they have emerged (Wynn & Liedvogel, 2023). Therefore, in both **Chapters 3** and **4** I investigated the navigational decisions of shearwaters when arriving at such

obstacles and demonstrate that these birds likely (whilst largely failing to detect their use in **Chapter 6**), possess allocentric representations of landmasses, seen in their familiarity-mediated route choices when circumnavigating such obstacles (**Chapter 4**). Similarly, the current focus on true navigation within our field may limit both the exploration of, and receptiveness to, alternative theories (Wallraff, 1999). It has long been presumed that path-tracking processes could not operate over vast spatial scales as those seen in the pelagic movements of shearwaters. Moreover, their ability to home following displacement via true navigation, which precludes the use of outward journey information (OJI), suggested that the investigation of such OJI during the homing of wide-ranging avian species was not warranted. Yet, through nuanced natural experimentation Padget et al. (2022) found that outward journey information appeared to mediate efficient route choices when homing from beyond an obstacle, a finding that was further evidenced in **Chapter 4**, along with the additional use of outward journey information demonstrated in the results of **Chapter 5**.

Perhaps the most remarkable aspect of the results presented in this thesis is that, with the exclusion of the displacement in **Chapter 3**, all navigational processes could be investigated, and with various strengths detected, within the same pool of free ranging foraging trips (Demšar et al., 2025). This alludes to, as discussed in the wider field of avian navigation, the likely hierarchical structure, and inherent redundancy, in navigational processes (Demšar et al., 2025; Flack et al., 2022). In nature, it is implausible to presume that one such process would be able to provide ubiquitous guidance across all navigational contexts (Wallraff, 2004). Therefore, this contextualisation of studies of navigation in wild systems, as demonstrated in this thesis, may be inherent to unveiling the organisation of such processes. Without observing the operation of these behaviours within the contexts of which they have evolved, their interplay in these wider navigational systems may not be fully realised.

Research into the mechanisms of avian navigation in the 21st century has become increasingly centred on not only the phenomenon of true navigation, but the possible sensory modalities that underly it, with an arguably disproportionate level of attention currently being directed towards solving the molecular and physiological

basis of magnetoreception in birds (Wallraff, 1999; Warrant, 2021; Wiltschko et al., 2021; Wiltschko & Wiltschko, 2023b; Wong et al., 2021; Wynn & Liedvogel, 2023). The demonstrations of auxiliary navigational processes in this thesis highlight that true navigation is unlikely to be the only mechanism by which natural navigators find their way. As such, the pursuit of such granular understandings of specific sensory modalities as those observed in contemporary works, whilst indeed forming interesting parts of the puzzle, cannot aid in resolving the broader questions of animal navigation that still remain unanswered (Flack et al., 2022; Wynn & Liedvogel, 2023).

This thesis therefore acts as a compelling case to continue the investigation of navigation in wild avian models, looking beyond true navigation into alternative and complementary processes that guide a bird home. Central to this, is to examine the ecological context of a wild navigator and ask *how* navigation strategies may be expressed in that species (**Figure 7.1**; Demšar et al., 2025; Flack et al., 2022). Variation in cue availability and signal strength may favour the use of alternative cues (Boström et al., 2012) or mechanisms across species, even in those that are highly related (as discussed with regards to shearwaters and olfactory map cues in Morford, 2023). By first asking what navigational tasks an animal needs to solve, and what environmental information is available to guide such decisions, we can frame subsequent hypotheses in natural behaviour. Inspiration from the wider field can, and should, be used to inform such hypotheses, but preconceptions into the plausible navigational strategies of wild models should be driven by intra-species observations, not inter-species extrapolations (Flack et al., 2022; Pritchard & Healy, 2018).

2. Understanding learning and cognition in navigation

The enhancement of navigation through learning is not a new concept (Baldaccini et al., 1975; Clayton & Krebs, 1995; Guilford & Biro, 2014; Healy & Hurly, 2013; Holland, 2003; Kashetsky et al., 2021; Morford, Wynn, et al., 2025; Wallraff, 2005; Wynn et al., 2020). The use of spatial memory in locating profitable foraging sites and cached food

has been demonstrated in several wild models (Brea et al., 2023; Male & Smulders, 2007; Pritchard, Scott, et al., 2016), and advances in computational power have been invoked to simulate how grid maps may form through learning (Morford, Lewin, et al., 2025; Morford, Wynn, et al., 2025). However, whilst the necessity of learning is often acknowledged in the construction of cognitive representations of space, the underlying mechanisms with which this learning operates in wild contexts remains largely unknown (Flack et al., 2022; Guilford & Burt de Perera, 2017; Pritchard, Hurly, et al., 2016). In this thesis I explored questions regarding the frameworks and resolutions of learning in free-ranging shearwater movements. I found evidence to suggest that learning is involved in their route choices of obstacle circumnavigation (**Chapter 4**) and fine-scale movements (**Chapter 3**) facilitated through their experience (or at least proxies for this) with such navigational tasks. This, however, still leaves interesting questions about the underlying mechanisms with which learning may operate, and how stimuli within a shearwater's ranges may be detected and represented cognitively. The results of this thesis suggest that evidencing the ontogeny of a shearwater's navigational processes as it explores its home ranges should be one of the next pursuits of this field, which will likely pose its own challenges.

Evidencing learning is inherently challenging in wild systems as not only are inferences made indirectly through changes in behaviour, but it is also not possible to systematically rule out non-learning alternatives such as changes in state and motivation, or inter-individual differences in experience levels (Kashetsky et al., 2021; Morand-Ferron et al., 2016). The findings of **Chapter 3** that shearwaters are not only able to make efficient route decisions, but that this can occur at very fine spatial scales, prompted much internal discussion of the underlying mechanisms that could facilitate such efficiencies, with **Chapter 4** then serving to test some of these decision-making frameworks. The detection, and adoption, of efficient routes at these proximal spatial scales initially led to the proposal of latent learning, and the involvement of some cognitive map, due to an assumed lack of salience in the small cost differences needed to facilitate associative learning (Farina et al., 2015; Guilford & Burt de Perera, 2017; Wang & Hayden, 2021). On the contrary, it is entirely plausible

that shearwater's may remain sensitive to such small differences, allowing for small-scale route efficiencies to be learnt associatively, as we do not yet know their sensitivity to such stimuli (Guilford & Burt de Perera, 2017; Pearce, 2008). Furthermore, as examined in **Chapter 4**, alternative representations of reward dichotomies, such as those discussed in Weber's Law, could make such route differences highly salient, irrespective of the spatial scale at which these decisions are made (Brus et al., 2019; Kacelnik et al., 2023). Herein lies the crux, and indeed excitement, of exploring such navigational, and cognitive, hypotheses in wild models – in order to test and detect such nuances in their cognitive capacities, we must develop innovative investigations into wild movements beyond controlled experimental paradigms (Pritchard, Hurly, et al., 2016).

For example, in **Chapters 3** and **4** I discuss potential learning frameworks through different models of the comparison between the 'values' of alternative circumnavigation routes; but what is this 'value'? How does a shearwater recognise the landmass in front of it, and how does this recognition elicit the recall of subsequent route knowledge? Are route values extracted from allocentric representations of these obstacles, or are they formed through experience, where idiothetic measures of route distance are then associated to specific routes, which are in turn associated with specific obstacles? These questions remain a matter of conjecture but should be prioritised in the advancement of our understanding of shearwater navigation. In Chapter 4 I explored such questions, modelling potential representations of route value in route dichotomies that occurred naturally within free-ranging shearwater foraging trips. Examples where such models have been demonstrated in other avian taxa (Kacelnik et al., 2023; Kacelnik & Bateson, 1997) were evidenced using precisely controlled experiments, using stimuli entirely novel to the birds. Therefore, such comparative quantifications may prove challenging in wild models, where such factors cannot be as readily controlled (Pritchard, Hurly, et al., 2016; Sulikowski & Burke, 2015). This calls for the integration of natural experimentation to further address these underlying learning frameworks, maintaining an ecological context whilst exposing birds to a novel, repeatable, task which can be manipulated to address specific cognitive hypotheses, such as those

applied in hummingbirds systems (Healy & Hurly, 2013; Pritchard, Hurly, et al., 2016; Sulikowski & Burke, 2015; Tello-Ramos et al., 2022).

One target for such investigation highlighted in this thesis is the representation of landmarks in shearwater navigation. Landmark recognition has been shown to not necessarily be tied simply to their visibility (Fukushi & Wehner, 2004; Healy & Hurly, 1998; Meade et al., 2006; Pollonara et al., 2015; Pritchard, Scott, et al., 2016), potentially explaining the inability to detect their use in the methods employed in **Chapter 6**. However, without knowing the full extent of experience with a given landmark, or landmass, or even *how* landmarks are used to inform position, it may be hard to deduce how such recognition is mediated or acquired. This learning is likely to occur during exploratory movements, which is perhaps why experimentation may be required in inducing novelty into such investigations of adult shearwaters. Alternatively, the comparison between age classes may also reveal this link between experience and landmark attendance. Stark differences in the navigation of naïve shearwaters have already been demonstrated, as in passerines, in their inability to deviate from an inherited compass orientation during migration compared to the flexible routes adopted by adults (Yoda et al., 2017). The quantification of experience throughout subsequent movements though, particularly those made within the home range during exploratory pre-breeding stages where rapid-onset learning may occur, appears to remain extremely difficult with the current constraints on tracking technologies (Wynn et al., 2020, 2025).

Since individual age was not known throughout the data used in this thesis, and individuals were rarely tracked repeatedly, I approximated experience through colony-level movements, as seen in **Chapters 3** and **4**, as intra-colony fidelity in foraging sites has been previously shown to be high (Dean et al., 2015). Whilst I do believe this broadly captured an expectation of space use for any one individual shearwater, and in turn an expectation of its familiarity with a navigational task, the goal for addressing ontogenetic questions in such navigation should be observations of refinement in intra-individual performance, such as that demonstrated in experimental contexts (Guilford & Biro, 2014; Pritchard, Hurly, et al., 2016).

Herein lies the challenge. It is plausible that in shearwaters, as suggested in common terns, *Sterna Hirundo*, navigational learning may be limited to pre-breeding stages (Wynn et al., 2025). Manx shearwaters spend several years moving through the areas surrounding their natal colony as non-breeders, or immatures, and it is plausible that it is during these movements, which are difficult to track, that this learning could be occurring (Brooke, 1990; Perrins et al., 1973). Furthermore, as discussed in **Chapter 4**, route learning efficiency appears to asymptote after relatively little experience in pigeons and hummingbirds (Bonadonna et al., 1997; Meade et al., 2005; Pritchard, Scott, et al., 2016; Tello-Ramos et al., 2022), which in combination with the results in terns (Wynn et al., 2025), suggests that it may be hard to detect route refinement in the natural movements of adult shearwaters.

Admittedly then, this suggestion to further explore ontogeny in navigation is potentially at odds with the simultaneous call for the investigation of navigation in natural contexts. This may be especially true in shearwaters, as the quantification of experience in the early life stages of this wild, wide-ranging bird may prove challenging. Nevertheless, their high site fidelity across colonies (Dean et al., 2015), and indeed within individuals where studied (Jaggers, 2023), sets up a strong ecological foundation for the learning and encoding of salient environmental information through routine and exploratory movements (Guilford & Biro, 2014; O'Keefe & Nadel, 1978). Furthermore, recent advances in tracking technologies (as discussed in **Chapter 2**) have now facilitated the integration of remote download tags into the tracking fleet within this dataset. Whilst their utility is not fully represented in this thesis, future tracking will deploy these tags to track the movements of immatures (see **Future Directions**), and perhaps in the comparison of these with adult movements lies the answers to some questions posed by this thesis regarding the ontogeny of navigation in these free-ranging movements.

3. The capacity of correlative study

This thesis has demonstrated that free-ranging tracking data can be used to investigate a range of navigational hypotheses.

This highlights the contribution that 'data-driven' studies can make to the study of navigation, in which long-term data are co-opted for analyses to uncover new aspects of behaviour (Demšar et al., 2025; Lewin et al., 2024; Wynn et al., 2020). However, this does not come without its drawbacks (Gelman & Loken, 2016). Much of the hypothesis generation for this thesis, and indeed for works both prior to and after this, were products of exploratory analyses. Once hypotheses were generated, there were then several iterations and comparisons of suitable metrics (e.g. tortuosity in **Chapter 5**), before the implementation and comparison of several model structures (such as those seen in **Chapter 4**). Whilst there are statistical measures that can account for this (such as those applied in **Chapter 6**), given the multiple analytical decisions available at each step of data processing, researcher degrees of freedom can inadvertently bias outcomes towards significance (Forstmeier & Schielzeth, 2011; Fraser et al., 2018; Simmons et al., 2011). More fundamentally, correlative analyses of free-ranging movements are limited in the strength of inference they can provide regarding underlying navigational mechanisms. Similar observations in navigational performance may arise from multiple competing processes, making it difficult to distinguish causal mechanisms from free-ranging data alone. Hence, much of the work done to date have employed experimental manipulations to eliminate competing processes.

I do not think that this exploratory correlative approach undermines the results of this thesis, however, for several reasons. Many of the analytical approaches within this thesis are sufficiently novel and nuanced to justify their reporting, but this transparency with regards to correlative studies is an important component of the investigation into such systems (Gelman & Loken, 2016). If anything, the results from these correlative analyses into free-ranging data give us the foundations of some exciting experimental avenues (see **Future Directions**), such as that seen in the correlative findings of Padget et al. (2019) leading to the experimental paradigm of Padget et al. (2022).

Future Directions

This thesis, whilst providing insights into several avenues of auxiliary navigational processes, leaves many questions on such processes unanswered. Such questions, however, could be addressed with innovative experimental designs framed through natural contexts as highlighted in these chapters. Furthermore, some methods presented within this thesis may also warrant future refinement. Specifically, refining the methods used to quantify landmark availability in **Chapter 6** could prove insightful in further investigations into hypotheses regarding landmark use during free-ranging movements. Below, I will highlight several themes from this thesis that could be expanded upon in coming years, employing both correlative analysis of free-ranging data alongside ecologically relevant displacements.

The role of experience in navigational decision making

At several points in this thesis, I have discussed how quantifying the age of individuals may clarify their orientation in several contexts (such as in the route-choices following displacement in **Chapter 3**). In this, I propose age as a proxy for experience, since we cannot quantify the extent of individual experience in such a long-lived, wide-ranging, seabird. It is plausible that, for example, the birds who made inefficient route choices in **Chapter 3** were younger, less experienced, birds, and so being able to include age as a predictive variable in subsequent investigations could help further contextualise individual variation.

However, age was in fact known in all displaced birds in Padget et al. (2022), and no detectable effect was found on subsequent route choice around the Isle of Ireland (although they noted that the small sample size may have impeded this). It is therefore plausible, as discussed previously, that such route learning could occur early on in life (Wynn et al., 2025). If this is the case, then quantifying comparative route decisions in immature birds would allow us to further parse out the role of experience in these navigational decisions. Indeed, future projects plan to do just this, incorporating immature tracking into the long-term data of Manx shearwater

movements, opening up various avenues to investigate natural navigation across age classes.

Quantification of behavioural decision points

As discussed, the failure to largely detect the influence of topographical landmarks in **Chapter 6** may be a product of insufficient methods in the calculation of when landmarks are available. Alternative approaches could be applied to this dataset, such as the identification of decision points using backward path analysis (as in Pollonara et al., 2015), which are similar in their function to those used in this thesis to identify the onset of homing behaviour (see **Chapter 2**). Similarly, line simplification algorithms, such as the Douglas-Peucker algorithm (Douglas & Peucker, 1973), have also been applied to seabird movement tracks, correctly distinguishing between behavioural states during free-ranging movements at sea (Thiebault & Tremblay, 2013). Indeed, these were used in an exploratory analysis in **Chapter 3** and were able to correctly identify the points at which birds significantly switched orientation. The inevitable challenge in applying such algorithms to free-ranging homing behaviour, however, would be identifying potentially very nuanced changes in orientation. As discussed in **Chapter 6**, these birds are already well orientated towards home in the absence of landmarks and so it is plausible that landmarks confer a homeward direction already known to the bird, meaning that landmark detection may not manifest as a detectable 'decision point' in the GPS track. Nevertheless, these algorithms have the potential to be finely tuned in their sensitivity to changes, and in unobstructed directed homing where we would expect movements to follow a beeline, detectable changes in orientation may flag up interesting points along the track worth investigating, be that the appearance of landmarks or other cues. These algorithms too have applicability in the recognition and ultimate circumnavigation of at-sea obstacles (**Chapters 4** and **6**).

Further Investigations of outward journey information

This thesis adds to a growing body of evidence suggesting that outward journey information, in several potential forms, aids the homing accuracy of Manx shearwaters. It appears that auxiliary outward journey information, such as recalling the egocentric position of landmasses, mediates route choice when circumnavigating obstacles during homing (as reported in **Chapter 4** and in Padget et al., 2022). **Chapter 5** then suggests that the translations and distances of the outward journey are integrated in path tracking processes, and used to inform, at least in part, the homeward direction. I believe that nuanced experimental verification of this could further reveal the role of such processes in free-ranging movements. Here I will summarise an experiment that was planned to be conducted during this thesis but could not be due to fieldwork constraints (**Figure 7.2**):

Firstly, a large pool of adult Manx shearwaters is fitted with GPS devices, such that an appropriate sample is achieved in the following steps. These shearwaters are allowed to embark on a free-ranging foraging trip, for simplicity of explanation, let's assume they can go to one of two foraging sites (A or B**; Figure 7.2A**). These shearwaters then return to the colony, again for simplicity let's assume this occurs on the same night (hence the need for a large sample; **Figure 7.2B**). We then displace these returned birds to either the location that they just returned from, or the alternative foraging location (**Figure 7.2C**), and observe their homing (**Figure 7.2D**). There is now a two-fold comparison with can help parse out to the role of outward journey information. First, between birds displaced to the same site but having previously foraged at different sites (**Figure 7.2**, 'C1'). In this, we can assess whether a bird's recent natural trip to the site has biased its homing against a bird that has not been there, accounting for and recency biases. Second, we can compare a bird's homing performance between its free-ranging homing from a site and when displaced to that site (**Figure 2**, 'C2'). Presumably, if there are no detectable differences in the homing performance of birds displaced to the same site (C1), then any differences between a bird's natural and displaced homing (C2) could be taken as a product of the availability of outward journey information.

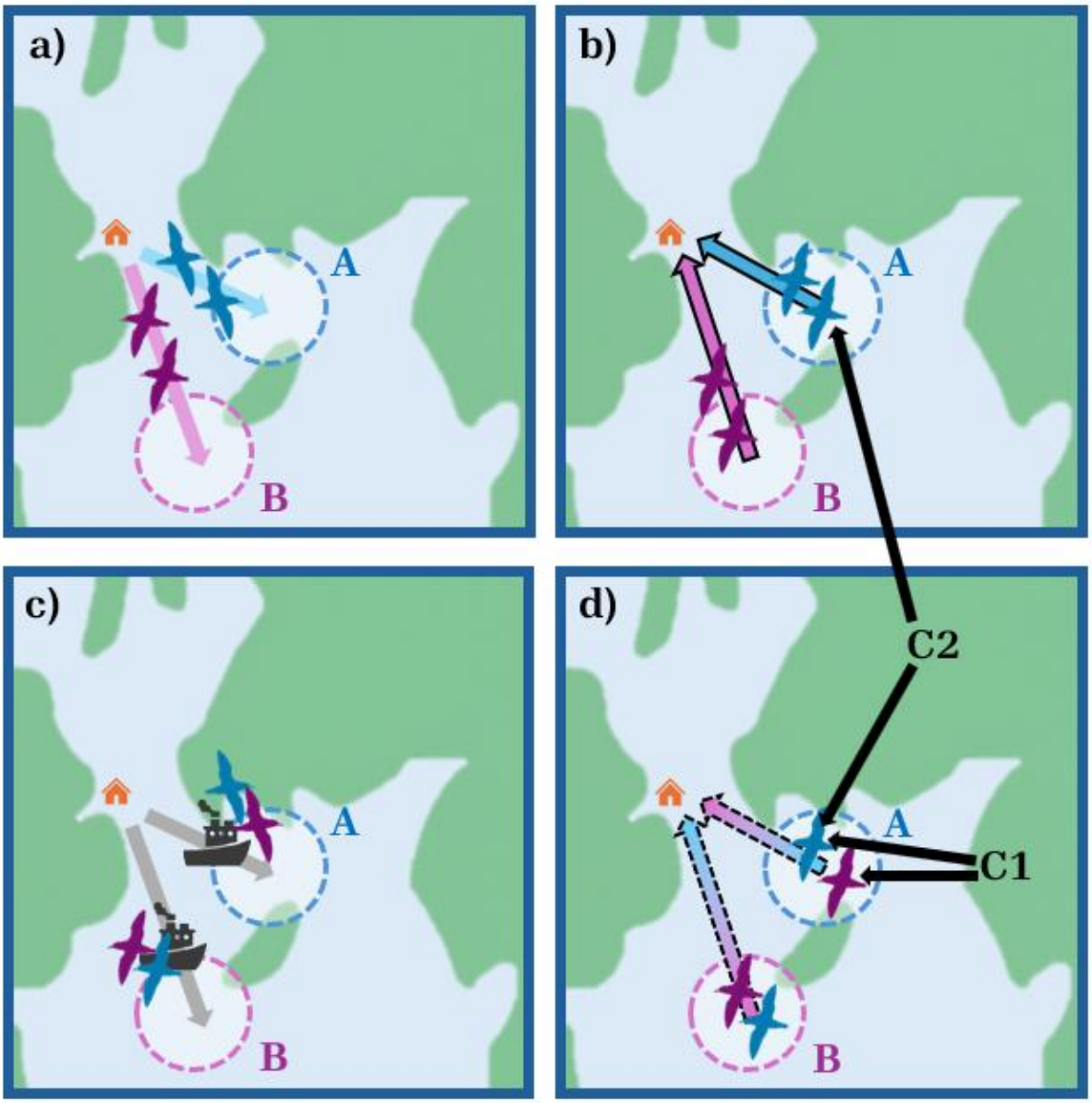


Figure 7.2. A schematic detailing a displacement procedure to investigate outward journey information. Details given in text.

Concluding remarks

This thesis has demonstrated the use, and suitability, of free-ranging tracking data to examine the navigational processes of birds in a wild model. Throughout this thesis I have investigated the auxiliary processes that are involved in the impressive navigation of the Manx shearwater, beyond those usually considered in studies of true navigation.

I have shown in **Chapter 4** that shearwaters are able to make efficient route decisions when faced with obstacles during their free-ranging movements, despite such obstacles apparently not being encoded in the extrapolated map that facilitates true navigation (Padget et al., 2019). Furthermore, through a short distance displacement in **Chapter 3** I found that these efficient route choices persist at very fine scales, likely beyond the resolution of such gradient-based maps. I therefore suggest, through both of these findings, that learning must underpin such route efficiencies, and that these are likely learnt through repeated experience during natural movements through the detection and subsequent encoding of optimal routes with their associated rewards. Whilst I discussed the plausible frameworks of learning that may underpin these observed route efficiencies, evidencing learning in free-ranging data is inherently challenging (Wynn et al., 2025). This poses exciting avenues for future analyses, and I suggest that incorporating known-age and immature shearwaters into this tracking dataset, and indeed into experimental studies, could illuminate these cognitive processes further. Technological advancements, such as those discussed in **Chapter 2**, will surely be at the forefront of these investigations.

In **Chapter 6** I explored the role of topographical landmarks in the homing accuracy of free-ranging shearwaters, following their observed utility in experimental studies (Padget et al., 2017; Pollonara et al., 2015). However, I found limited evidence to show that the availability of such landmarks improves orientation during homing behaviour, likely owing to the accurate orientation that can seemingly be derived in their absence through alternative processes (such as extrapolated maps). I suggested that this, in combination with the observed experimental results in anosmic shearwaters (Padget et al., 2017; Pollonara et al., 2015), likely conveys the

hierarchical structure of navigational processes, and the need for redundancy in systems mediating such an important behaviour for wide-ranging species. Equally, methodological limitations in the approaches of **Chapter 6** may have limited the detection of landmark use. Nevertheless, the findings of **Chapter 4** suggest that these shearwaters still recognise topographical obstacles, and as such plausibly have an allocentric representation of these landmasses through space, and that familiarity may underpin the formation of this map, particularly in highly familiar areas (such as near the colony; **Chapter 6**) as seen in pigeons (Guilford & Biro, 2014). Despite presumed constraints imposed by their wide-ranging movements, in **Chapter 5** I report that outward journey information appears to influence the homing accuracy of Manx shearwaters, in line with path tracking processes. Furthermore, 'auxiliary outward journey information' appears to aid in the decision-making processes seen in **Chapter 4**, as in Padget et al. (2022). Future works could engineer nuanced displacement experiments (such as that proposed above) to further examine the role of outward journey information in natural movements.

Outward journey information is actively denied in traditional displacements pursuing true navigation, as are landmarks, and yet in this thesis I have demonstrated the use of both in the navigation of free-ranging shearwaters. Furthermore, the exposure to novel sites in such displacements is something that does not naturally occur in their movements, and I have shown that within familiar areas, learning can facilitate high efficiency in route decisions during homing. This thesis therefore demonstrates the range of navigational processes, and indeed unanswered questions within such, that occur in the free-ranging movements of shearwaters. By investigating navigation through free-ranging movement data, we are able to frame our analyses, and subsequent experiments, within ecologically relevant hypotheses – examining the naturally occurring processes that facilitate this remarkable behaviour in the wild.

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Softly onward we go,

gently homeward we row

to the bonnie, bonnie isle of our home.

Leave the sadness behind,

and the tears that are cried

aye, you'll see me no more in this life.

I'm on the crest of the wave,

in the deepest dark cave,

everywhere and always at once

In the wind touching you

and the sea's turquoise blue,

I'm the bird who flew safely away.

– **Iona Boat Song** (altered), Simon de Voil
Sang by Eve at Skomer Farmfest 2022