Drivers of ocean movement patterns in Round Island petrels

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I dedicate this PhD thesis to my mum, Jacqueline Franklin.

Thank you for sharing your love of the seaside with me, and for making me believe anything was possible. I just wish you were here to see this – me, a Dr?!

Rest in peace, Mum.

4th January 1971 – 14th March 2016

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Abstract

Among migratory bird species, shifts in phenology and distribution in response to changing environmental conditions are occurring across the world. Understanding the mechanisms through which these shifts occur, and thus the consequences for species conservation, relies on knowing the extent of within- and between-individual variation in migratory strategies, and their consequences for the conditions experienced by individuals. In this thesis, I use a global, multi-species, meta-analytical approach of published studies, a long-term (2009-2019) geolocator tracking dataset from a well-studied population of *Pterodroma* petrels on Round Island, Mauritius, in the tropical western Indian Ocean, and a field study of remote monitoring of petrel breeding ecology to explore these issues. These approaches revealed that repeatability in migratory timings is a common feature of avian migratory systems, yet is poorly studied in tropical systems, where resources are often patchy and unpredictable. Round Island petrel tracking helps to fill this knowledge gap, and their unusual hybrid status, year-round breeding, and monsoon-driven seasonal environment make them a model species for such questions. Repeat tracking of individual petrels revealed low levels of within-individual variation in migratory behaviour, but very high levels of between-individual variation, with petrels occurring across the Indian Ocean. Despite the huge area over which non-breeding petrels occur, petrel night-time activity patterns closely tracked the lunar cycle in all cases, including in migratory strategies used by very few tracked individuals. Deployment of remote cameras was successful at capturing individual petrel breeding events and citizen science processing of images produced only slightly lower estimates of breeding activity. Overall, the work in this thesis contributes to the understanding of migratory systems and how they can change, and of the conditions experienced by tropical seabirds.

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Contents

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Author contributions

The following manuscripts have arisen from this thesis, and are presented in chapters 2, 3, 4, 5 and 6. These are collaborative efforts, although in each case the majority of work is my own. Below I provide a full author list and highlight author contributions for each chapter.

Chapter 2: Individual repeatability of avian migration phenology: A systematic review and meta-analysis.

> Authors: Kirsty A. Franklin, Malcolm A.C. Nicoll, Simon J. Butler, Ken Norris, Norman Ratcliffe, Shinichi Nakagawa and Jennifer A. Gill.
>
> K.A.F, J.A.G., M.A.C.N., K.N., N.R. and S.J.B. conceived the idea of the study; K.A.F. collected the data, conducted the statistical analyses, and wrote the manuscript; S.N. provided statistical advice and support. All authors critically revised the manuscript, contributed to interpreting results, and gave final approval for publication.

Chapter 3: Individual consistency in migration strategies of a tropical seabird, the Round Island petrel.

> Authors: Kirsty A. Franklin, Ken Norris, Jennifer A. Gill, Norman Ratcliffe, Anne-Sophie Bonnet-Lebrun, Simon J. Butler, Nik C. Cole, Carl G. Jones, Simeon Lisovski, Kevin Ruhomaun, Vikash Tatayah and Malcolm A.C. Nicoll.
>
> M.A.C.N., K.N., C.G.J. and V.T. conceived and initiated the petrel migration study; M.A.C.N., K.N., N.C.C. and K.R. deployed and recovered geolocators; C.G.J., V.T., N.C.C. and K.R. facilitated access to Round Island and provided logistical support through the Mauritian Wildlife Foundation and National Parks and Conservation Service; K.A.F. analysed the data with support from N.R., A.S.B.L., J.A.G., S.J.B., M.A.C.N. and S.L.; K.A.F. wrote the manuscript; all authors contributed critically to the drafts and gave final approval for publication.

Chapter 4: Drivers of ocean movement patterns in Round Island petrels

Authors: Kirsty A. Franklin, Ken Norris, Jennifer A. Gill, Norman Ratcliffe, Simon J. Butler, Katherine A. Booth Jones, Nik C. Cole, Carl G. Jones, Garth Holloway, Simeon Lisovski, Kevin Ruhomaun, Vikash Tatyah and Malcolm A.C. Nicoll.

M.A.C.N., K.N., C.G.J. and V.T. conceived and initiated the petrel migration study; M.A.C.N., K.A.B.J., K.N., N.C.C. and K.R. deployed and recovered geolocators; C.G.J., V.T., N.C.C. and K.R. facilitated access to Round Island and provided logistical support through the Mauritian Wildlife Foundation and National Parks and Conservation Service; K.A.B.J. conducted molecular analysis; G.H. and M.A.C.N. performed the Bayesian Mixtures Analysis; K.A.F. analysed the data with support from N.R., J.A.G., S.J.B., M.A.C.N. and S.L.; K.A.F. wrote the chapter; K.A.F., J.A.G., M.A.C.N., N.R., K.N., and S.J.B. contributed critically to the chapter.

Chapter 5: Variation in night-time activity of tropical gadfly petrels with lunar cycles and at-sea locations

Authors: Kirsty A. Franklin, Ken Norris, Jennifer A. Gill, Norman Ratcliffe, Simon J. Butler, Nik C. Cole, Carl G. Jones, Kevin Ruhomaun, Vikash Tatayah and Malcolm A.C. Nicoll.

M.A.C.N., K.N., C.G.J. and V.T. conceived and initiated the petrel migration study; M.A.C.N., K.N., N.C.C. and K.R. deployed and recovered geolocators; C.G.J., V.T., N.C.C. and K.R. facilitated access to Round Island and provided logistical support through the Mauritian Wildlife Foundation and National Parks and Conservation Service; K.A.F. analysed the data with support from N.R.; K.A.F. wrote the manuscript; K.A.F. and J.A.G. contributed critically to the chapter.

Chapter 6: Utility of automated time-lapse cameras to monitor breeding phenology and nest success of tropical ground-nesting seabirds

Authors: Kirsty A. Franklin, Jennifer A. Gill, Max Hellicar, Ken Norris, Norman Ratcliffe, Simon J. Butler, Alice Edney, Tom Hart, Mark Jessopp, Johannes Chambon, Nik C. Cole, Carl G. Jones, Kevin Ruhomaun, Vikash Tatayah and Malcolm A.C. Nicoll.

K.A.F, J.A.G., M.A.C.N., K.N., N.R. and S.J.B. conceived the idea of the study; C.G.J., V.T., N.C.C. and K.R. facilitated access to Round Island and provided logistical support through the Mauritian Wildlife Foundation and National Parks and Conservation Service; K.A.F. and J.C. designed and installed cameras; K.A.F. and M.H. manually processed images; A.E., T.H., and M.J. provided access and support with the citizen science element of the chapter; K.A.F. analysed the data with support from J.A.G.; K.A.F. wrote the chapter; K.A.F., J.A.G., M.A.C.N., N.R., K.N., and S.J.B. contributed critically to the chapter.

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Chapter 1

General Introduction

Photo: Johannes Chambon

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General Introduction

Migratory species and environmental change

Environmental conditions are changing across the world at unprecedented rates. Driven by climate change and other anthropogenic threats, we are experiencing rising temperatures, an increasing frequency of flood and drought events, as well as an increasing frequency of storms, all of which are projected to continue unless drastic changes in human activities are made (IPCC, 2022). It is therefore of no surprise that these changes in climate are having strong impacts on biodiversity and ecosystems. However, the observed effects of environmental change often vary among species, with shifts in phenology and range expansions reported in numerous species, while others are in severe decline, or have even become extinct (Díaz et al., 2019). As such, understanding and predicting species' responses to environmental change is going to be critical for the conservation and management of wildlife as we know it.

Migratory species, which rely on a range of sites and conditions across the annual cycle, may represent something of a paradox (Robinson et al., 2009). Changes in environmental conditions may occur anywhere across the migratory range, and in one or multiple locations, greatly increasing the potential for deleterious, and potentially additive, impacts at some point in the annual cycle (Knudsen et al., 2011). Alternatively, it has been argued that the highly mobile nature of migratory species may mean they can move vast distances to find different locations of suitable environments (Knudsen et al., 2011). This, however, would rely on either high levels of within-individual plasticity in order to cope with dynamic environmental conditions, allowing individuals to continually adapt their temporal and spatial routines (Åkesson & Helm, 2020), or large levels of (spatiotemporal) between-individual variation within populations, such that individuals are unlikely to experience the same environmental changes. For example, European bird species with higher diversity in migratory movements and destinations have been shown to be less likely to be declining at present than those with less diverse ranges and strategies (Gilroy et al., 2016), but the contributions of within-individual plasticity and between-individual variation to this diversity in movements are rarely known.

The ability to design effective conservation plans for migratory species will require researchers to understand where and how individuals move through their environments, and the different conditions and threats they experience at different stages of their migratory journeys (Runge et al., 2015). Conservation often operates through the creation and management of protected areas, and these areas are often designated due to the large numbers of individuals and/or species of conservation concern which they support. Shifts in distribution in response to environmental changes may also impact the effectiveness of protected areas and may require the establishment of new protected areas. Understanding how much individuals can change their distribution in response to changing environmental conditions, and what influences those changes, will be required to predict the situations in which protected area networks may become less effective. Additionally, an understanding of potential rates and directions of change in species' distributions will be needed to identify where protected areas may need to be established. For species that range across multiple international borders, successful conservation can be particularly challenging, as conservation will require coordinated international action (Yong et al., 2018).

The importance of individuals

In migratory systems, there are multiple processes that could lead to shifts in migratory timings and distributions. These could result from behavioural changes, such that individuals do different things in different years. For example, individuals may respond flexibly to environmental conditions by moving to locate more suitable conditions (home range change), or by individuals changing migratory timings and/or durations (phenological change). Alternatively, these changes could arise from generational change, whereby the proportion of new recruits using particular locations or schedules differs from previous generations, as a result of changes in the conditions influencing those behaviours (Gill et al., 2014; Gill et al., 2019; Verhoeven et al., 2018). Similarly, change could happen through selective mortality of certain parts of the population that do different things. For example, if survival rates change for certain migratory routes/schedules, this could alter the frequency of individuals on those migratory journeys within a population (Gill et al., 2019).

The rate and direction of shifts in migratory routes and/or timings could vary greatly with each mechanism. Behavioural flexibility, when there is high variation within individuals, could result in relatively rapid and directional change (Gill et al., 2019). By contrast, shifts arising through generational change would be much slower, especially for long-lived species, as the direction and magnitude of change depends on the number of annual recruits in a population, the proportion of those experiencing different conditions that influence individual routes and phenologies, and their subsequent survival rates (Gill et al., 2019). To date, there is little evidence of population-level migratory shifts due to behavioural changes (but see Conklin et al., 2021; Fraser et al., 2019), and it is increasingly being recognised that consistent individual differences are common across the majority of animal behaviours (Bolnick et al., 2003; Dall et al., 2012), with studies reporting high levels of repeatability in many different aspects of migratory journeys (Both et al., 2016; Hasselquist et al., 2017).

Understanding the different levels of within- and between-individual variation in different migratory traits will therefore be key to predicting likely rates and directionality of population responses to environmental change (Fig. 1.1). For example, quadrant one (Fig. 1.1) is likely to capture irruptive species such as waxwings and redpolls. The distribution of individuals in these populations often varies greatly from year to year, but individuals often move together in large flocks (Newton, 2006). Species such as the Atlantic puffin *Fratercula arctica* have a dispersive migration with individuals showing large variation in non-breeding distances and directions, yet individuals show remarkable consistency between years (Guilford et al., 2011), meaning they would sit in quadrant four. Quadrant two (individuals across a population varying annually and idiosyncratically) appears to be relatively rare, whereas quadrants three and four likely capture the most commonly reported systems, with species captured by quadrant three potentially more constrained spatially by landmasses and environmental conditions. However, it is important to note that these quadrants are probably best regarded, not as distinct categories, but representing extremes of a continuum of migratory behaviour found among birds. Understanding these levels of within- and between-individual variation in migratory behaviour relies on being able to track individuals repeatedly across the full annual cycle.

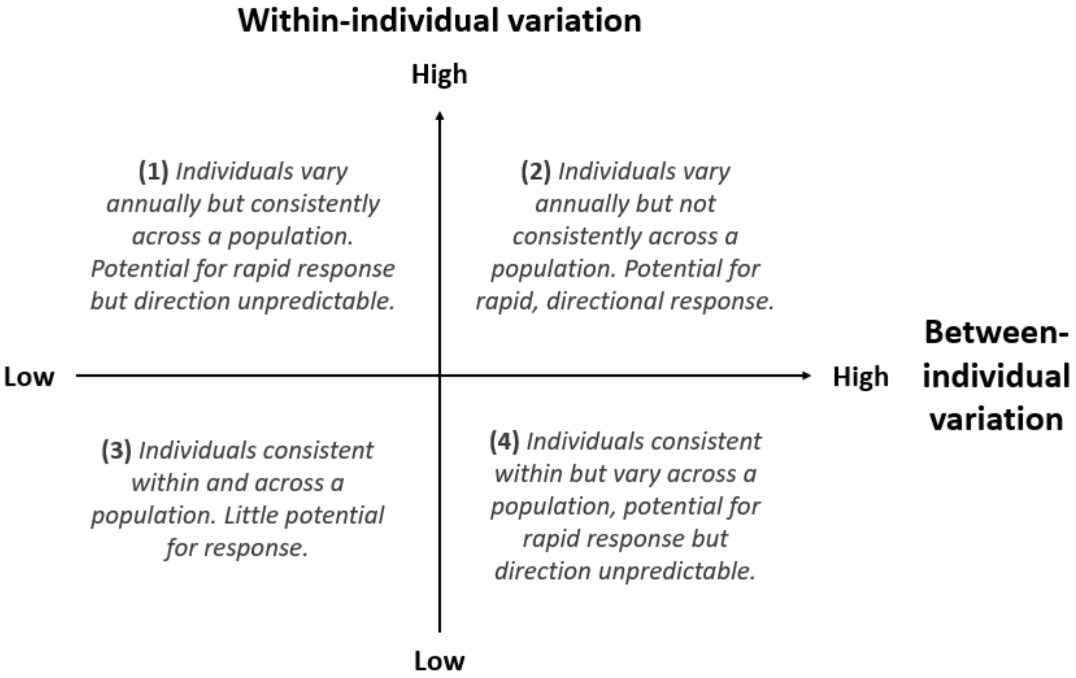

Figure 1.1. Conceptual diagram of the potential rates and directionality of shifts in space and time in response to changing environmental conditions that might be expected when species vary in the extent of within-and between-individual variation in migratory behaviour (where and when they travel).

Tracking individual movements

Over the last century, migration research has advanced together with technological advances in our ability to track individuals at increasing spatiotemporal resolutions. Historically, long-term observations of the numbers of individuals at key times of year at migration hotspots (e.g., coastlines, straits, mountain valleys) have been used to monitor phenological patterns (e.g., Panuccio et al., 2016; Wehermann et al., 2019). In the marine realm, ship-based surveys have been, and are still, commonly used to count and estimate the distributions of animals at sea (Camphuysen et al., 2012; Gjerdrum & Bolduc, 2016; Ryan & Cooper, 1989). However, these methods provide little detail on movement at the individual level. Instead, this requires the marking of individuals, which has been a long tradition in ornithology, principally in the form of bird ringing. The attachment of unique metal and colour rings to individual birds has provided information on individual movements (at a range of scales), survival rates, behaviour, and much more (Anderson & Green, 2009). Rings have the advantage that they can last for most or all of a marked individual's lifetime, and are typically cheap, allowing samples of hundreds and even thousands of individuals. However, these conventional ringing methods rely on recapturing or re-sighting the marked birds, thus analyses using these data can be prone to spatiotemporal biases arising from variation in detectability (Thorup et al., 2014). Also, these methods typically provide little information on the actual routes taken by individuals between marking and relocation sites.

The rapid development of tracking devices, including light-level geolocators, radio, satellite, and GPS transmitters, have allowed scientists to overcome some of the limitations involved with conventional tracking methods and have transformed our understanding of bird movements. For example, studies have revealed impressive migration feats with Arctic terns *Sterna artica* annually travelling >80,000 km pole to pole (Egevang et al., 2010), and great snipes *Gallinago media* reaching altitudes of > 6,000 m (Lindström et al., 2021). Ongoing reductions in size and price, and improvements in battery capacity, have led to the widespread use of tracking devices on even very small species (e.g., Burgess et al., 2022; Jahn et al., 2019; Militão et al., 2022). The different tracking devices can be classified in two ways: either by the way they derive location data or whether devices transmit or store the data (Bridge et al., 2011). Devices might derive positions via satellite triangulation, satellite-derived Doppler acceleration, or ambient light-levels. Transmitter devices send data on radio or sound waves via satellites, local relay and receiver stations, or the mobile phone network, ultimately arriving at the researcher's desk. In contrast, archival devices store location data locally meaning devices must be retrieved in the field, but this in turn reduces power consumption and thus device size. The general trade-offs between devices therefore include temporal and spatial resolution, lifespan, and the mass and cost of each unit (Wakefield et al., 2009). Satellite and GPS loggers have high temporal (e.g., on a minute or hourly basis) and spatial accuracy (within ~150 m and 10 m, respectively) but until recently their mass restricted their use to species of larger body size (Hobson et al., 2019). By contrast, geolocators have low power requirements, allowing the devices to be considerably lighter (<1 g; Bridge et al., 2011), and are relatively cheap. Consequently, large numbers of individuals can often be tracked with geolocators, but they provide only two locations per day with varying but generally low accuracy (Halpin et al., 2021; Phillips et al., 2004) and need to be retrieved after deployment.

Due to the above-mentioned trade-offs, light-level geolocators are one of the most commonly-used devices to study the migratory behaviour of birds (and are used in this thesis). These devices, at a minimum, measure and record ambient light levels at regular intervals, and some are integrated with immersion, temperature, depth, and/or barometric sensors. Once retrieved, raw light data are downloaded and used to define twilight events (i.e., sunrise and sunset times), and then used to estimate and refine spatial locations in combination with sophisticated modelling approaches (Lisovski et al., 2020). These methods provide only one or two positions per day, with latitude estimated from day length, and longitude estimated by the timing of local midday or midnight relative to Greenwich Mean Time and day of the year (Hill, 1994). It is therefore of no surprise that positions from geolocators are inherently less accurate than those derived from other devices (e.g., GPS; see Halpin et al., 2021), but geolocators are well-suited to tackling questions related to large-scale movements of individual animals which travel distances that are far larger than the estimated spatial inaccuracies. Geolocators have therefore been a particularly attractive year-round option for tracking migratory birds and, with the inclusion of immersion and temperature sensors, they are commonly used on seabirds to investigate individual space use and behaviour (e.g., Carreiro et al., 2020; Pinet et al., 2011).

Seabirds as a model system

Many seabird species are wide-ranging, traveling thousands of kilometres to locate patchily distributed prey. They depend on land to breed but are also reliant on marine environments throughout the year (for foraging). This means that seabirds can be exposed to anthropogenic threats in both the terrestrial and marine realms, including impacts of invasive species, overfishing, bycatch, and contaminants (Dias et al., 2019; Lewison et al., 2012). In addition, climate change is altering marine conditions at unprecedented rates (Harley et al., 2006), resulting in seabirds being more threatened than other comparable taxonomic groups (Croxall et al., 2012).

Seabirds offer an ideal system in which to study individual variation in non-breeding movements. The majority of seabird species are large enough to carry biologging devices, facilitating the tracking of individuals' year-round movements and behaviours. As such, there are currently > 7,600 non-breeding tracks for > 100 species on the Seabird Tracking Database (www.seabirdtracking.org; BirdLife International, 2022). Consequently, we now know that, during the non-breeding period, seabirds can undertake a high diversity of migratory strategies. For example, some species, such as whiskered auklets *Aethia pygmaea*, remain close to the breeding colony throughout the annual cycle (Schacter & Jones, 2018). Contrastingly, other species of seabird are known to undertake some of the longest migratory journeys recorded, with well-known examples including the Arctic tern and the grey-headed albatross

Thalassarche chrysostoma, which use exceptionally long-distance migration strategies that stretch from pole to pole or circumnavigate the globe, respectively (Croxall et al., 2005; Egevang et al., 2010). Yet within species, there is also often a wide range of migratory strategies, with individuals breeding at the same colonies migrating to very different places, and these migratory journeys are often repeated year after year (Fayet et al., 2016; Kopp et al., 2011).

Environmental and oceanographic conditions are often hypothesised to be key drivers of seabird migratory strategies. This may be particularly evident in temperate and polar systems, where environmental conditions undergo strong seasonal changes, making availability of prey resources more predictable (Weimerskirch, 2007). Individual birds in these systems tend to have predictable migrations to one or more of these high-productivity ocean areas and show high levels of migration fidelity between years (e.g., Orben et al., 2015; Phillips et al., 2005). By contrast, large areas of tropical oceans are often considered low in productivity and prey abundance, and have less marked seasonal variation in temperature, potentially making prey aggregations unpredictable (Weimerskirch., 2007; but see Kumar et al., 2009). In response to this, tropical seabirds often have extended and/or asynchronous breeding seasons (Carr et al., 2020) and are often described as more wide-ranging (Oppel et al., 2018). Seabirds in these less predictable systems may therefore be expected to show higher levels of spatial and temporal variation within- and between-individuals. However, due to the often-inaccessible locations of tropical seabird colonies, they are frequently overlooked and remain understudied in comparison to their temperate and polar counterparts (Bernard et al., 2021; Ceia & Ramos, 2015). Yet, the broad range of individual migratory timings and distributions in tropical seabirds make them ideal systems in which to explore the factors influencing within- and between-individual variation in movement patterns.

Study site: Round Island

Situated 22.5 km off the north-east coast of mainland Mauritius, in the tropical western Indian Ocean, Round Island (19.85° S, 57.78° E) is the second largest (219 ha) of Mauritius' offshore islets (Fig. 1.2). The island is a basaltic and tuff volcanic cone, probably dating between 25,000-100,000 years, and rises steeply from sea level to reach a maximum altitude of 280 m (Tatayah, 2010). The climate of Round Island, and the surrounding ocean, is strongly seasonal because of the monsoon circulation of the Indian Ocean. From October to April is the warm and wet north-east monsoon (i.e., austral summer), and from May to September is the cooler, drier south-west monsoon (i.e., austral winter; Schott & McCreary, 2001).

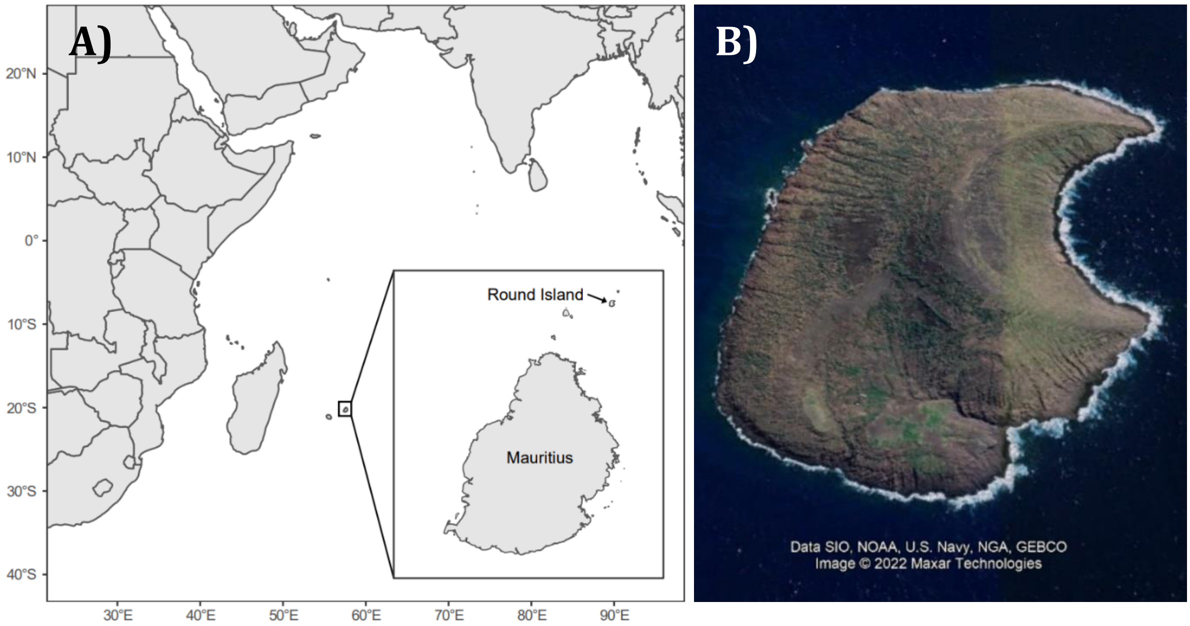

Figure 1.2. Location of Round Island in relation to Mauritius and the surrounding western Indian Ocean (a), and satellite image of Round Island (b). Map data: Google, Maxar Technologies.

Round Island is one of Mauritius' most important islands for conservation, with unique or significantly large remnant populations of endemic plants, reptiles and native seabirds. As such, the island was designated a nature reserve in 1957 and is the flagship conservation project of the Mauritian Wildlife Foundation (MWF), managed in partnership with the Mauritian Government National Parks and Conservation Service (NPCS). Unlike many small tropical oceanic islands around the world, the island has never been colonised by non-native invasive predatory mammals; however, goats and rabbits were introduced in the early 19th century that caused severe loss of soil and vegetation (Tatayah, 2010). By 1979, the goats were removed, followed by the rabbits and, since 1970, the damage they caused to the vegetation is being restored by MWF and NPCS through the Round Island habitat restoration project.

The island is home to large numbers of several species of seabird. Population estimates from over a decade ago (Tatayah, 2010) showed the most commonly breeding seabird on the island (approximately 40,000-80,000 pairs, and notably one of the largest colonies in the Indian Ocean), to be the wedge-tailed shearwater *Ardenna pacifica*. Approximately 3,000-4,000 pairs of red-tailed tropicbirds *Phaethon rubricauda*, 750-1500 pairs of white-tailed tropicbirds *Phaethon lepturus*, three pairs of Bulwer's petrels *Bulweria bulwerii*, as well as several other non-breeding seabird visitors were also recorded on Round Island (Tatayah, 2010). Recent surveys have also shown that the populations of the most common species of seabird have recovered markedly post-restoration and continue to increase. For example, the population of red-tailed tropicbirds has increased dramatically and, in 2018, was estimated at 17,000 pairs (Mauritian Wildlife Foundation Round Island Restoration Annual Report, 2018). But perhaps the most interesting species is the Round Island petrel (*Pterodroma* sp.).

Study species: The Round Island petrel

Despite naturalists visiting and documenting the flora and fauna on Round Island regularly since 1844, it wasn't until the mid-1940s that breeding *Pterodroma* petrels were first reported (Brown et al., 2010; Brown et al., 2011; Tatayah, 2010), suggesting that extensive breeding only became established within the last century. These birds, known locally as the Round Island petrel (Fig. 1.3), are surface nesters, breeding year-round with a peak in egg laying in the austral spring/early summer (Nicoll et al., 2017). They breed mainly under rock ledges and in clusters of boulders, but also in and under the native tussock grass (*Vetiveria arguta*) and Scaevola bushes. They use generally little or no nesting material, with a single white egg laid directly on bare rock or shallow silt. It is therefore likely that the loss of plant life on Round Island, and thus the extensive erosion of the island's topsoil, by introduced goats and rabbits, resulted in more available nest sites for the petrels (Brown et al., 2011). In addition, it is hypothesised that poaching of the larger, and more aggressive, red-tailed tropicbirds in the 19th and early 20th centuries may have reduced competition between these species, again increasing the number of available nesting sites for the Round Island petrel (Cheke & Hume, 2008; Tatayah, 2010). The number of petrels on Round Island has continued to increase since they were first discovered, with capture-mark-recapture analyses estimating ~ 1900 individuals visiting the island in the 2018 season (Nicoll, unpublished data).

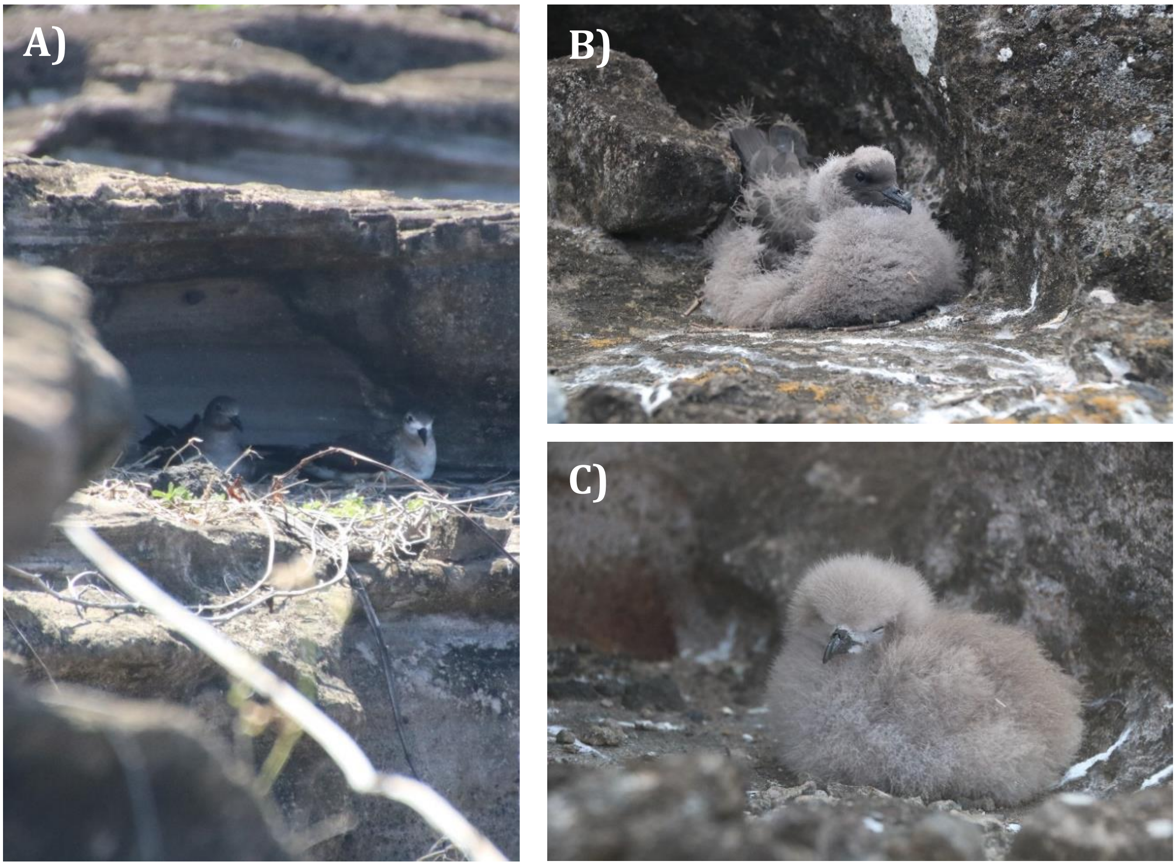

Figure 1.3. Images of a) light- and dark- morph adult Round Island petrels, b) a well-developed but downy chick, and c) a recently hatched chick. All photos taken by Kirsty Franklin.

Since their discovery, the classification of petrels on Round Island has caused a great deal of confusion and debate. Initially, Round Island petrels were identified as a single species, the Trindade petrel *Pterodroma arminjoniana*. The native range of this species is in the Atlantic Ocean (Fig 1.4; population estimate ~1130 individuals; Luigi et al., 2009), where they were previously thought to breed only at Trindade Island. The two islands (Round Island and Trindade Island) are separated by a distance of roughly 9000 km and by the landmass of continental Africa.

In the mid-1980s, a second petrel species, the Kermadec petrel *P. neglecta*, was also discovered to be breeding on Round Island, though in much smaller numbers (Brooke et al., 1999). Kermadec petrels are widely distributed throughout the Pacific Ocean (Fig 1.4), breeding on many islands (Brooke, 2004), although there has also been debate over whether the species has been seen in the Atlantic Ocean (Imber, 2004; Imber, 2005; Imber, 2008; Tove, 2005). This species was first suspected on Round Island by Don Merton in 1986, who identified petrel calls belonging to the Kermadec petrel (Brooke et al., 1999). Physically, Trindade and Kermadec petrels are very similar, and both display plumage polymorphism, with colour morphs ranging from dark brown to a pale grey with white underparts, and intermediate colour phases (Murphy & Pennoyer, 1952; Tatayah, 2010). But the main diagnostic trait of Kermadec petrels is the characteristic, white-shafted primary feathers, compared to dark brown or black in Trindade petrels (and several other congeners). In later years, dark-shafted and white-shafted birds on Round Island were observed forming pairs, and a small proportion were found to have intermediate-coloured shafts and intermediate calls, resulting in the first suggestions that some of the petrels on Round Island were hybrids.

The taxonomy of petrels on Round Island was far from being resolved, however. Since the mid-1990s, small, very pale petrels were observed on Round Island, presumed to be the Herald petrel *P. heraldica*. Two lines of evidence supported this observation. First, a single species of feather louse *Halipeurus heraldicus* found previously only on Herald petrels in the Pacific was found in the Round

Island petrel population. Whereas the Trindade and Kermadec petrels hosted a different species (*H. kermadecensis*; Brown et al., 2011). Second, one of these pale birds on Round Island was caught wearing a metal ring after being originally ringed as a breeding adult on Raine Island, on the outer edges of the Great Barrier Reef off north-eastern Australia. This bird was ringed in 1984 and was recorded to be at Raine Island until at least 1987, until it was subsequently caught on Round Island with an egg in 2008, and again in 2012. This provided the first concrete evidence of petrels switching colonies between oceans, despite petrels often displaying a very high level of natal philopatry (Warham, 1990). Before this, Herald petrels were found only in the tropical South Pacific, their range overlapping, and birds sometimes breeding sympatrically, with Kermadec petrels (Fig 1.4; Brooke, 2004).

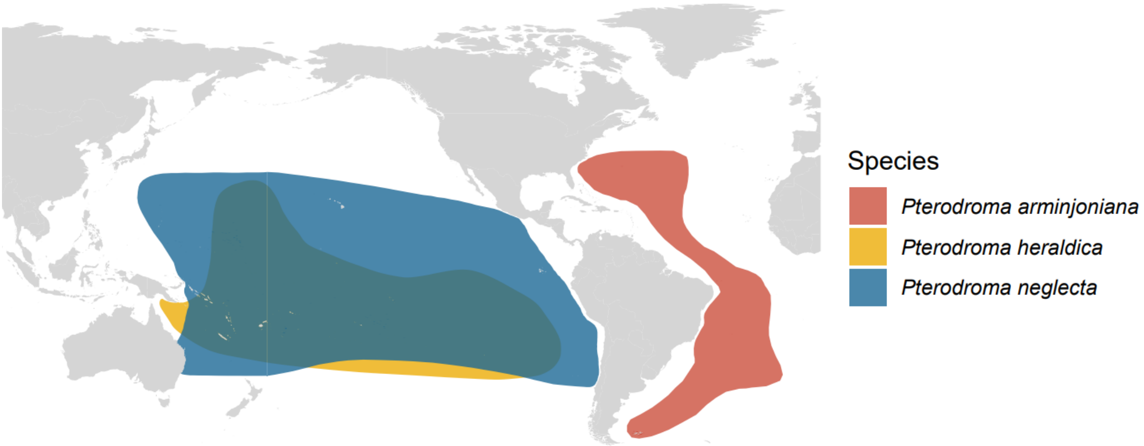

Figure 1.4. Current distributions in the Pacific and Atlantic Oceans for each of the three Round Island petrel parental species (Trindade petrel *Pterodroma arminjoniana*, Herald petrel *P. heraldica*, and Kermadec petrel *P. neglecta*). Data from BirdLife International and Handbook of the Birds of the World (2022).

Molecular phylogenetic analysis of *Pterodroma* petrels from Round Island, Trindade, and the Pacific Islands by Brown et al. (2011) described for the first time the extensive hybridization between the three species that breed on Round Island. This analysis also proposed that there could be an additional *Pterodroma* parental species present on Round Island, as haplotypes were found in the Round Island petrel population that were not seen in the sampled populations of Trindade, Kermadec or Herald petrels. The proposed species is the Phoenix petrel *P. alba*, and individuals on Round Island have been observed to bear a strong resemblance to this species (Tatayah, 2010). They are morphologically similar to Herald petrels but are more uniform in colour. However, it has so far not been possible to distinguish between Herald and Phoenix petrels on Round Island through genetic analyses (Booth Jones et al., 2017).

Until recently, it was not clear whether Round Island was unique for its hybrid population of *Pterodroma* petrels, with Round Island acting as a point of secondary contact between the Pacific and Atlantic Oceans, or whether gene-flow was much more widespread with hybrids occurring outside the Indian Ocean. Microsatellite genotyping data by Booth Jones et al. (2017) found that inter-ocean migrants and hybrids were not unique to Round Island, however the island does have the highest proportion of hybrids and is therefore likely acting as an intermediate population for gene flow between the Atlantic and Pacific populations. The Round Island population is, however, the best-studied example of a naturally occurring three-way hybrid seabird population, being a major focus of the work on Round Island for decades, resulting in one of the most comprehensive data sets relating to the ecology of a tropical seabird in the world.

The Round Island petrel project

The Round Island petrel has been the focus of an intensive nest monitoring and ringing programme since the early 1990s. Before this, only very small numbers of petrels had been ringed. For example, only 61 individuals are known to have been ringed between 1970 and 1993 (Tatayah, 2010), compared to 3497 petrels between 1993 and 2019 (Nicoll et al., 2022). The ringed birds are believed to cover a high percentage (~95 %) of the petrel population (Tatayah, 2010). The increased frequency and intensity of petrel monitoring and ringing coincided with the initiation of regular management trips each year, and the establishment of a permanently staffed field station in 2001. The permanent presence of staff on Round Island has allowed routine petrel surveys to be conducted every month (or more recently, every two months). These surveys involve regular visits to the five petrel colonies (Fig. 1.5) to monitor breeding activity, ringing of adults and chicks, and their subsequent recapture.

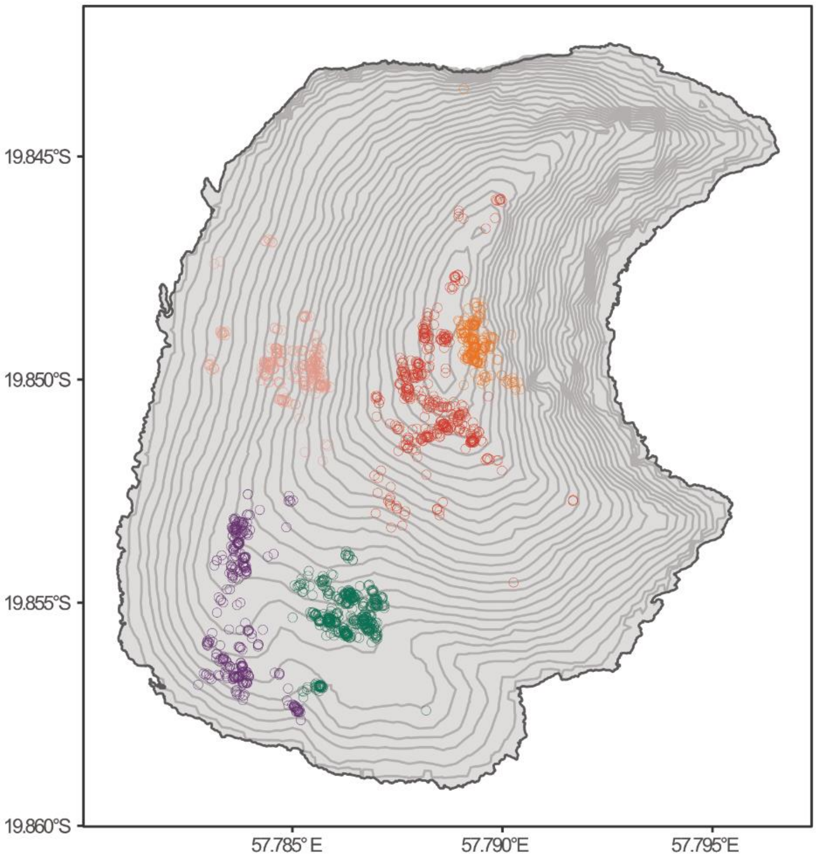

Figure 1.5. Round Island petrel nest sites (open circles; as of 29th November 2019) are clustered into five main colonies: purple = 'south-west coast' (SWC), green = 'above camp' (ABC), pink = 'big slab' (BSL), red = 'summit' (SUM), and orange = 'crater' (CRA). Elevation contours are at 10 m intervals.

Additionally, there has been a programme of tagging petrels to explore their movement patterns when away from the colony, with particular focus on the non-breeding period. This extended time scale, together with the size of the petrels (300–600 g), renders devices such as GPS of limited use, as the storage capacity and battery life would not be sufficient to capture data over the period of interest. Light-level geolocators with saltwater immersion switches have therefore been used for this project, and 421 devices were deployed on adult petrels between 2009 and 2016. Retrievals of these devices are still ongoing, but the focus of the tracking project since 2016 has shifted to juveniles, with geolocators now being deployed on petrels pre-fledging, although most of these have yet to be retrieved.

This thesis makes use of the geolocator data from adult petrels collected as part of the tracking project, which has been conducted by the Institute of Zoology (Zoological Society of London), in collaboration with MWF and NPCS. These tracking data have revealed extraordinary levels of individual variation in ocean movements (Fig. 1.6), yet the levels of within- and between-individual variation, and the factors influencing ocean movement patterns, are not clear. The unusual hybrid status of the Round Island petrel population, and their asynchronous breeding cycle, make them a unique system in which to explore these questions.

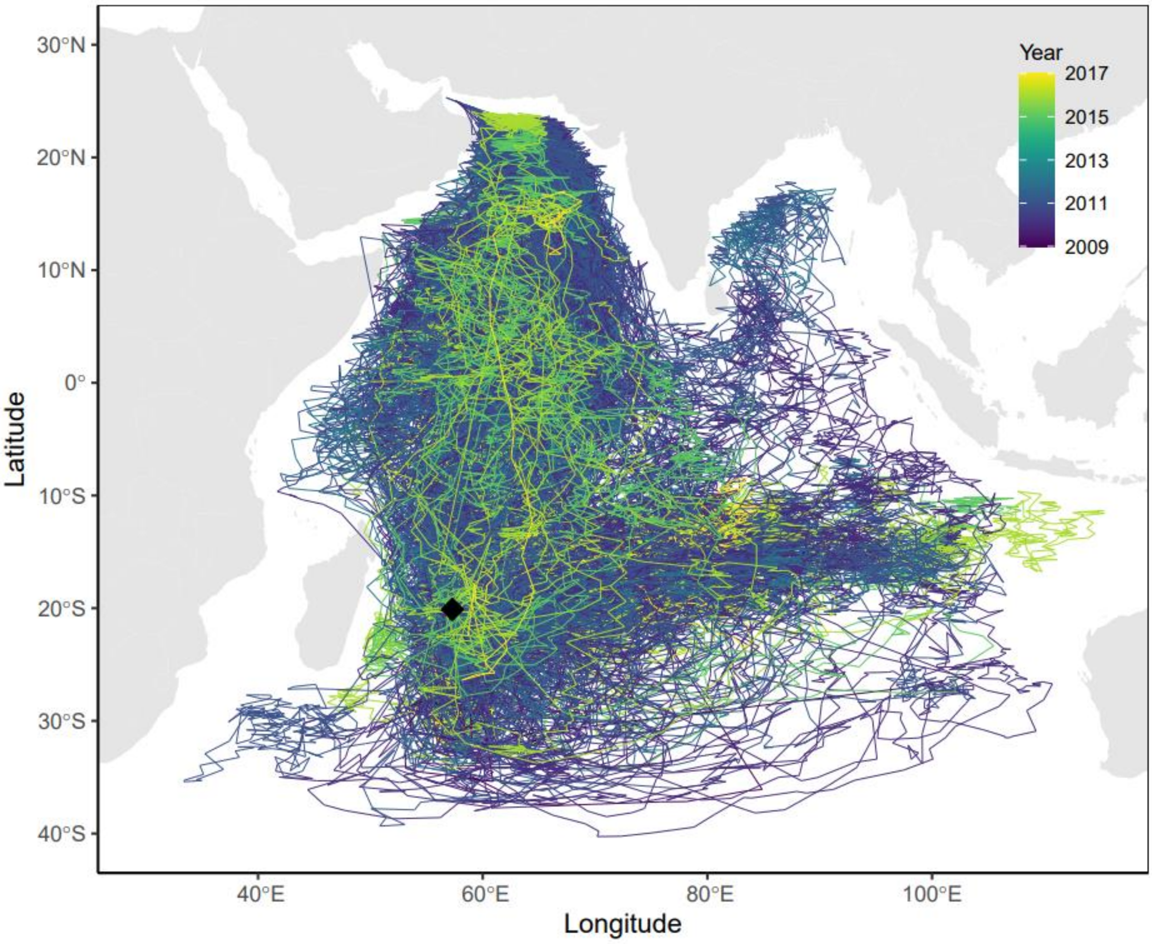

Figure 1.6. Non-breeding migration tracks (n=267) from all Round Island petrels (n=198) that feature within this thesis. All individuals were tracked between 2009 and 2018 (coloured by tracking year) during the non-breeding period using geolocator loggers. Black diamond indicates the location of Round Island Mauritius.

Thesis aims and outline

The overarching aim of this thesis is to explore the factors influencing the within- and between-individual variation in at-sea movement patterns of a tropical, pelagic seabird, and the resulting conservation implications. Whilst focused on Round Island petrels, the results presented here extend beyond seabirds to contribute to a broader understanding of the drivers of movement behaviour. Note, each chapter has been written as a stand-alone paper for submission to peer-reviewed journals. At the time of writing, Chapter 2 is published in *Journal of Animal Ecology*, and Chapter 3 is published in *Movement Ecology*. Only minor alterations have been made to already published chapters to improve the readability and cohesiveness of this thesis, and therefore some information is repeated across chapters.

Understanding variation in migratory behaviour, and the likelihood of migratory species responding to environmental change, relies on knowing both within- and between-individual variation in migratory behaviours. These estimates are commonly combined to provide a measure known as the 'repeatability index'. In **Chapter 2**, I conducted a meta-analysis of avian migratory timing repeatability estimates to understand if repeatability varies a) across the annual cycle, b) with tracking method, c) across ecological groups, d) between male and females, and e) with sampling design. I use data from 54 studies of 47 different species and illustrate consistent individual differences to be a common feature across seabirds, landbirds, and waterbirds, and thus migratory systems.

Chapter 2 highlighted a lack of studies investigating repeatability of migratory timings in tropical species. Unlike temperate and polar zones, tropical oceans are often considered low in productivity and prey abundance, and have less seasonal variation in temperatures, making prey aggregations unpredictable. Flexibility in migration behaviour may therefore be more beneficial in these environments. In **Chapter 3**, I address this knowledge gap by investigating the spatial and temporal repeatability of migratory behaviours of a tropical, pelagic seabird, the Round Island petrel. Using a multi-year geolocator tracking dataset, I quantify the levels of within- and between-individual variation in non-breeding distributions and timings. I developed a new method to calculate the start and end dates of petrel migration, and use multiple analytical approaches to quantify migratory variation, including repeatability analysis and a similarity index to measure spatial consistency.

Chapter 3 revealed striking levels of between-individual variation in at-sea movements and timings, with non-breeding migrations covering much of the Indian Ocean. However, individuals were remarkably consistent, suggesting they repeatedly follow the same migration strategy. **Chapter 4** therefore builds on these findings by describing the range of migratory strategies the Round Island petrel population undertakes and attempts to identify the factors that drive and maintain the large levels of between-individual variation. The unusual compound-hybrid status of the Round Island petrel population, and their asynchronous breeding cycle, made them a unique system in which to explore the influence of genotype and seasonal variation in environmental conditions on migratory distributions.

Round Island, and the surrounding ocean, is a strongly seasonal environment. This means that different petrels may potentially be exposed to very different environmental conditions, both when on migration and when attending the colony, depending on the migratory strategy that they undertake. After identifying the range of migratory strategies undertaken by the petrel population in Chapter 4, I then, in **Chapter 5**, examine Round Island petrel non-breeding activity patterns and how they vary spatially across different areas of the Indian Ocean. I pay particular focus to the night-time behaviour of petrels and investigate the influence of the lunar cycle on petrel activity.

As previously mentioned, environmental conditions at the colony vary year-round, meaning as well as understanding when and where individual petrels go on migration and the fitness consequences, it is important to understand variation in reproductive success at different times of year. Consequently, in **Chapter 6**, my focus shifts from the non-breeding period to the breeding period.

Previously, due to their aseasonal breeding cycle and the indeterminate nature of nests, it has not been possible to follow individual petrel breeding attempts, and only population-level metrics of breeding effort and success have been quantifiable. So, in this chapter, I established a field study on Round Island to test the utility of automated time-lapse photography as a tool for monitoring petrel breeding phenology and nest success. By hosting images on a citizen science website, I also assess the consistency of image processing by researchers and citizen scientists.

Finally, in **Chapter 7**, I summarise and discuss the key findings of the above chapters in the broader context of animal movement and seabird ecology. I discuss implications of these findings, and outline ideas for future directions.

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Chapter 2

Individual repeatability of avian migration phenology: A systematic review and meta-analysis

Photo: Kirsty Franklin

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Individual repeatability of avian migration phenology: A systematic review and meta-analysis

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Abstract

1. Changes in phenology and distribution are being widely reported for many migratory species in response to shifting environmental conditions. Understanding these changes and the situations in which they occur can be aided by understanding consistent individual differences in phenology and distribution and the situations in which consistency varies in strength or detectability.

2. Studies tracking the same individuals over consecutive years are increasingly reporting migratory timings to be a repeatable trait, suggesting that flexible individual responses to environmental conditions may contribute little to population-level changes in phenology and distribution. However, how this varies across species and sexes, across the annual cycle and in relation to study (tracking method, study design) and/or ecosystem characteristics is not yet clear.

3. Here, we take advantage of the growing number of publications in movement ecology to perform a phylogenetic multilevel meta-analysis of repeatability estimates for avian migratory timings to investigate these questions. Of 2,433 reviewed studies, 54 contained suitable information for meta-analysis, resulting in 177 effect sizes from 47 species.

4. Individual repeatability of avian migratory timings averaged 0.414 (95% confidence interval: 0.3–0.5) across landbirds, waterbirds and seabirds, suggesting consistent individual differences in migratory timings is a common feature of migratory systems. Timing of departure from the non-breeding grounds was more repeatable than timings of arrival at or departure from breeding grounds, suggesting that conditions encountered on migratory journeys and outcome of breeding attempts can influence individual variation.

5. Population-level shifts in phenology could arise through individual timings changing with environmental conditions and/or through shifts in the numbers of individuals with different timings. Our findings suggest that, in addition to identifying the conditions associated with individual variation in

phenology, exploring the causes of between-individual variation will be key in predicting future rates and directions of changes in migratory timings. We therefore encourage researchers to report the within- and between-individual variance components underpinning the reported repeatability estimates to aid interpretation of migration behaviour. In addition, the lack of studies in the tropics means that levels of repeatability in less strongly seasonal environments are not yet clear.

Keywords: annual cycle; bird migration; consistent individual differences; individual variation; intraclass correlation coefficient; timing.

Introduction

Rapid environmental change is having profound impacts on the distribution, abundance, behaviour and interactions of species (Walther et al., 2002). For migratory species, identifying and ultimately tackling the problems caused by environmental change are particularly difficult because of the range of sites and conditions experienced by individuals across the annual cycle (Alves et al., 2013; Gilroy et al., 2016; Knudsen et al., 2011). Therefore, changes in conditions across all or part of migratory ranges could have strong implications in terms of survival rates and population dynamics at local and global scales (Newton, 2004), raising concerns regarding the effectiveness of existing protected area networks (Hanson et al., 2020; Méndez et al., 2017). The complexity and unpredictability of how migratory systems respond to environmental change represents a major challenge for conservation planners.

Changes in migratory behaviour in response to climate change have been documented in many species (Ambrosini et al., 2019). The most frequent responses are shifts in phenology in parallel with climate warming, for example migrant arrival dates at the breeding grounds in spring are getting earlier in many species (Gordo, 2007; Gunnarsson & Tómasson, 2011; Lawrence et al., 2022). In some species, shifts in migratory routes and wintering destinations (Dias et al., 2011; Sutherland, 1998) or reduced propensity for migration have been recorded, such that part or all of a population has become resident (Chapman et al., 2011; van Vliet et al., 2009). Migratory species currently showing little or no phenological change are more likely to be those experiencing population declines (Gilroy et al., 2016; Møller et al., 2008; Newton, 2008), possibly arising from a reduction in synchrony with the phenology of prey abundance (known as trophic mismatch; Thackery et al., 2010). Therefore, identifying the mechanisms through which shifts in migratory routes and/or timings occur may be key to mitigating the effects of rapid environmental change on declining migratory species (Knudsen et al., 2011; Gill et al., 2019).

In migratory systems, there are two processes that could lead to shifts in migration routes and/or timings; 1) behavioural flexibility, whereby individuals adjust their migratory behaviour according to the environmental conditions they experience (Charmantier & Gienapp, 2014), and 2) generational change, whereby the proportion of new recruits using particular locations or schedules differs from previous generations, as a result of changes in the conditions influencing those behaviours and/or the associated survival rates (Gill et al., 2014; Gill et al., 2019; Verhoeven et al., 2018). The rate and direction of shifts in migratory routes and/or timings could vary greatly with each mechanism, with behavioural flexibility facilitating relatively rapid and, potentially, directional change. By contrast, generational change would likely result in slower changes, especially for long-lived species, as the direction and magnitude of change depends on the number of annual recruits in a population, the proportion of those experiencing different conditions that influence individual routes and phenologies, and their subsequent survival rates (Gill et al., 2019).

A key first step towards assessing the likelihood of migratory routes and timings altering in response to environmental changes is therefore quantifying when individuals show consistent differences in these behaviours. This requires repeated measurements from individuals across years to assess the amount of variation in behaviour attributable to differences among individuals. In animal movement studies, this individual-based approach has become increasingly possible due to recent advances in remote-tracking technology (Geen et al., 2019; López-López, 2016), primarily satellite telemetry, and more recently through light-level geolocators (GLS). Before this, most studies of migratory behaviour have been conducted by means of visual observations or, more specifically for birds, through ringing studies (e.g., Møller, 2001; Potti, 1998; Rees, 1989). Repeated tracking of multiple individuals over multiple years can allow estimation of the variation in migratory behaviours that is explained by between-individual variation relative to both between- and within-individual variation (and measurement error; termed 'repeatability' (R) or the 'intra-class correlation coefficient' (ICC; Nakagawa & Schielzeth, 2010)). High repeatability estimates could indicate a consistent behaviour within individuals relative to high variation between individuals (Lessells & Boag, 1987; Nakagawa & Schielzeth, 2010; but see Cleasby et al., 2015; Sánchez-Tójar et al., 2022). For example, changes in phenology have long been assumed to be caused by within-individual effects, but between-individual effects could also contribute to changes, making it key that we understand the contributions of within- and between-individual variation to repeatability estimates and interpretation.

Repeatability in migratory behaviour has been explored across taxa, including amphibians (Semlitsch et al., 1993), insects (Kent & Rankin, 2001) fishes (Brodersen et al., 2012; Thorsteinsson et al., 2012; Villegas-Ríos et al., 2017), bats (Lehnurt et al., 2018), ungulates (Laforge et al., 2021), sea turtles (Schofield et al., 2010) and birds (see Results). Previous meta-analyses of behavioural repeatability have extracted repeatability estimates for migratory behaviours (Bell et al., 2009; Holtmann et al., 2017) but many possible sources of variation in levels of repeatability have not yet been explored. For example, in addition to variation as a result of different sampling designs and/or between sexes (Bell et al., 2009; Holtmann et al., 2017), repeatability may vary with tracking method, species and/or among different stages of the annual cycle. Differences in sampling strategies (e.g., number of individuals tracked, number of observations per individual) can influence estimates of repeatability (Dingemanse & Dochtermann, 2013; Wolak et al., 2012). An increase in both individual- and population-level variation in migratory behaviours might be expected if individuals are tracked for longer (e.g., Berthold et al., 2004; Catry et al., 1999), and variability may be underestimated if sample sizes are small, as estimates will be less likely to capture the total population variation (Conklin et al., 2013).

Repeatability may also be affected by the methods used to track individuals. The earliest estimates of repeatability in avian migration used conventional ringing methods such as ring recaptures, and colour ring re-sightings, which have the advantages that they last for most or all of marked individuals' lifetime, and are much cheaper, allowing samples of hundreds and even thousands of individuals. These Eulerian sampling methods (i.e., fixed in space) rely on re-capturing the marked birds (and recovery rates are generally low) or depend highly on the spatiotemporal distribution of observers. Detection of individuals with this method may be incomplete, which may introduce variable lags in observation of the timing of migratory arrivals and/or departures. Lagrangian tracking of individuals through time and space (i.e., animal-borne tracking devices) may therefore be more suited to studies of the timing of individual movements (Phillips et al., 2019). For example, the accuracy of estimates of timing of arrival at the breeding grounds as observed through conventional studies may be low in comparison to more recent methods, such as satellite telemetry, GPS, and GLS (Korner-Nievergelt et al., 2012). The general trade-offs between these methods therefore include temporal and spatial resolution, lifespan, and the mass and cost of each unit (Wakefield et al., 2009). Satellite and GPS loggers have good temporal (e.g., on a minute or hourly basis) and spatial accuracy (within ~150 m and 10 m, respectively) but until recently their mass restricted them to species of larger body size (Hobson et al., 2019). In contrast, GLS have low power requirements, allowing the devices to be considerably lighter (<1 g; Bridge et al., 2011), and are relatively cheap but provide only two locations per day with varying levels of spatial inaccuracy (Halpin et al., 2021; Phillips et al., 2004).

Repeatability values of migration parameters may also vary across the annual cycle. For example, we might expect the pre-breeding stages of migratory species to be more time-sensitive than post-breeding stages (Alerstam et al., 2003; McNamara et al., 1998). Repeatability in timing of arrival at breeding grounds has been demonstrated for several species (e.g., Conklin et al., 2013; Krietsch et al., 2017; Stanley et al., 2012), and may be related to the benefits of synchronous arrival times with mates (Gunnarsson et al., 2004; Morrison et al., 2019), and/or to exploiting consistently-timed local resource peaks (Alerstam et al., 2003). Familiarity with conditions at a certain location and time may improve chances of survival and breeding success compared to using a different site, or the same site at a different time (McNamara & Dall, 2010; Shimada et al., 2019). By contrast, timing of other stages (e.g., departure from breeding ground) may be less time-sensitive, but constraints may still exist if carry-over effects influence performance later in the annual cycle (Stutchbury et al., 2011).

In bird migration studies, repeatability has become standard for describing consistent individual differences in migratory behaviour. These studies are increasingly reporting high repeatability in migratory timings, but how repeatability varies across the annual cycle and in relation to study and/or ecosystem characteristics is not yet clear. To address these issues, we performed a systematic review and phylogenetic multilevel meta-analysis to synthesise the current literature and quantitatively assess the repeatability of avian migratory timings and possible sources of variation in repeatability estimates. We focus on the following five questions: Does repeatability vary 1) across the annual cycle, 2) with tracking method, 3) across ecological groups (seabirds, landbirds and waterbirds; Geen et al., 2019), 4) between males and females, and 5) with the number of observations per individual?

Methods

Literature search

We aimed to conduct a comprehensive search for studies estimating repeatability of temporal parameters of avian migration using a combination of approaches. We focused on arrival at, and departure from, breeding and non-breeding grounds. First, we performed a systematic search for published studies using the Web of Science and Scopus online databases on 1st June 2021. Second, we consulted a recently published meta-analysis of hormonal, metabolic and behavioural repeatability in birds (Holtmann et al., 2017), which included repeatability estimates of migration. We manually checked each entry from those sources to confirm suitability for our purposes and extracted additional moderator variables to be used in our analyses (see below). Finally, in order to add to – and validate the accuracy of – the results of the literature search, we searched the reference lists of papers already in our accepted reference library. The details of these search strategies and the Boolean search strings used are presented in the Supplementary Material, along with a flow diagram (often referred to as a PRISMA flow chart – the Preferred Reporting Items in Systematic Reviews and Meta-Analyses; Moher et al., 2009; O'Dea et al., 2021; Fig. S2.1) which shows the stages at which studies were disqualified or eventually used in the current study.

Inclusion and exclusion criteria

To be included in our analyses, observational studies needed to adhere to five main criteria. First, studies had to report repeatability estimates in the form of intraclass correlation coefficients (ICC) using an ANOVA based (Lessells & Boag, 1987) or Linear Mixed Model (LMM) based approach (Nakagawa & Schielzeth, 2010), or a Spearman/Pearson correlation coefficient (*r;* cf. Barbosa & Morrissey, 2021). If both ICC and *r* estimates were reported using the same data, we only included the ICC estimates in our data as this was the most commonly reported (>90%) repeatability metric in our data set. Second, studies which calculated repeatability using dates when certain latitudes were crossed were excluded unless they were explicitly stated as the arrival or departure dates for the species. We relied on authors' descriptions as to what determines arrival at/departure from the breeding and non-breeding grounds. Third, we restricted all data sets to breeding adults only. We used this criterion because the refinement of migratory behaviour has shown to be a progressive process mediated by age and experience, particularly for long-lived species (Campioni et al., 2019). Fourth, only English-language studies were included. Finally, in addition to repeatability estimates, studies also needed to report sample sizes, and moderator variables were extracted where reported and included in our analyses (see below). Where any of the repeatability estimates or sample size data were missing, we attempted to contact authors (n = 2 studies) for this information. One author replied but was unable to provide the requested data, and so neither of these studies was included.

Study selection

The exact number of screened and included studies are shown in Fig. S2.1, and a list of all studies included in the analyses can be found in the Supplementary Material Data sources section. We used Rayyan software to screen titles and abstracts (Ouzanni et al., 2016). One person (KAF) screened the abstracts, using a decision tree (Fig. S2.2). Approximately 93% of the 2433 abstracts were excluded after screening. We performed full-text screening for the remaining 160 papers included after abstract screening, from which 47 were included for data extraction. After searching the reference lists of these papers accepted for data extraction, we found an additional six suitable for our analyses, and included two repeatability estimates from our own paper (Chapter 3), providing a total of 54 papers.

Data collection

Data were extracted from text, tables or figures. To extract data from figures, we used WebPlotDigitizer software (Rohatgi, 2015). All data were extracted by one author (KAF). In addition to the repeatability estimates (r or ICC) from each study, we also extracted the following moderator variables: the annual event for which repeatability was estimated (arrival at, or departure from, breeding or non-breeding grounds), the method used to track individuals, the coordinates of tagging, and whether this was on the breeding or non-breeding grounds, study species, sex (male, female, mixed/unknown), the number of individuals (n), the mean number of observations per individual (k), and year of publication. For studies that did not state k but reported the total number of observations, we calculated *k* by dividing the number of observations by the number of individuals. The methods used to track individuals were grouped into three categories, which represent the type of sampling method (Eulerian or Lagrangian) and the spatial and temporal accuracy of the method: (a) conventional (bird ringing, colour-ringing); (b) geolocation (geolocators); and (c) GPS (GPS, satellite, PTTs, radio-telemetry). If studies used > 1 type of tracking method on different groups of individuals, we included both repeatability estimates. Finally, we recorded the statistic that was used to report repeatability (ICC or *r*), whether any fixed or random effects (in addition to individual as random effect) were included when calculating repeatability (i.e., agreement vs. adjusted repeatability; Nakagawa & Schielzeth, 2010), and whether those calculating (ANOVA- or L MM-based) repeatability reported the unstandardized variance components.

Data analysis

Studies included in our dataset varied in sample size, number of samples per individual, and in how repeatability was estimated. Thus, it was important to weight studies appropriately and to convert reported repeatabilities to a comparable statistic. We therefore converted all repeatability estimates (ICC and *r*) to the standardised effect size Fisher's Z (*Zr*) along with the corresponding sampling variance for each study (as described in Holtmann et al., 2017 and McGraw & Wong, 1996). As correlation- and ANOVA-based repeatabilities can produce negative values, often reflecting noise around a statistical zero (Nakagawa & Schielzeth, 2010), we set the negative repeatability estimates/*Zr* values in our dataset (n = 13) to zero for our analyses. We used these *Zr* values and sampling variances (see below) in all meta-analytical models, but when plotting and reporting parameter estimates we back-transformed effect sizes to ICC to aid interpretation. The results of all the meta-analytic and meta-regression models when including the negative repeatability estimates are reported in the Supplementary Materials (Tables S2.11-S2.18).

Meta-analysis

We fit meta-analytic and meta-regression multilevel linear mixed-effects models, using the rma.mv function in the metafor package (v. 3.0.2; Viechtbauer, 2010) in R (v. 3.6.2; R Core Team, 2019). Our data contained multiple levels and different types of non-independence (Noble et al., 2017). We partially accounted for this non-independence with random-effects, and sampling variance-covariance matrices.

All models included the following random effects: (a) paper ID, which encompasses multiple effect sizes extracted from the same paper, (b) cohort ID, which encompasses multiple effect sizes obtained from the same group of birds within the same paper, (c) species ID, which encompasses multiple effect sizes from the same species across papers, and (d) effect ID, which is a unit-level random effect representing residual/within-study variance. In addition to species ID (a non-phylogenetic measure), we also included (e) phylogeny (modelled with a phylogenetic relatedness correlation matrix), to account for species similarities due to evolutionary history (Cinar et al., 2022). To generate the phylogeny, we used a phylogenetic tree from Jetz et al. (2012), provided by Holtmann et al. (2017) and prepared on the basis of Hackett backbone (Hackett tree; Hackett et al., 2008). After trimming the tree using the species names in our data set, we computed branch lengths using Grafen's method (Grafen, 1989) in the compute.brlen function in the R package ape (v. 5.5; Paradis & Schliep, 2019). For the final phylogenetic tree see Fig. S2.3.

Multiple repeatability estimates were measured on the same animals within a paper (cohort ID) which induces a correlation between sampling error variances (Noble et al., 2017). Thus, we constructed variance-covariance matrices to model shared sampling error for effect sizes from the same cohort, assuming a 0.5 correlation (Noble et al., 2017). We also ran the phylogenetic meta-analytic model assuming a 0.25 and 0.75 correlation between estimates from the same cohort. All three correlations yielded qualitatively similar results, thus we assume a 0.5 correlation throughout, and present the results for the other correlation values in Table S2.10.

A multilevel intercept-only meta-analytic model was fitted to estimate the overall mean of the effect sizes with the random effects listed above. To evaluate the effects of moderators, we ran a univariate multilevel meta-regression model for each of the following: (1) tracking method, (2) ecological group, (3) sex, (4) annual event, and (5) k, the number of observations per individual. Interaction terms were not included between ecological group and a) method or b) annual event, due to insufficient sample sizes of certain levels of categorical variables.

For meta-analytic models, we quantified a multilevel version of the 'heterogeneity' measures (I^2), which indicate the amount of variance unexplained after controlling for sampling variance (Higgins & Thompson, 2002; Nakagawa & Santos, 2012) while, for meta-regression, we estimated the percentage of heterogeneity explained by the moderators using marginal R^2 (Nakagawa & Schielzeth, 2013) using the function 'r2_ml' in the R package orchaRd v.0.0.0.9000 (Nakagawa et al., 2021). Missing and unreported data were not included in the meta-regressions (i.e., we ran complete-case analyses). Results of the main effect model and meta-regressions with categorical moderators were graphically represented as orchard plots using code adapted from the R package orchaRd.

All model specifications, model selection procedures and associated coding are provided in our online Supporting Information. We followed reporting guidelines outlined in the PRISMA-EcoEvo checklist for this study (O'Dea et al., 2021).

Sensitivity analysis and publication bias

To test for small-study bias, we fitted a multilevel meta-regression with sampling standard error (i.e., the square root of sampling variance) as a moderator (a modification of Egger's regression). Likewise, to test for time-lag bias (i.e., a decline effect), we fitted a multilevel meta-regression with the year of publication (mean-centred, to help with interpretation) as a continuous moderator. Finally, we fitted an ‘all-in’ publication bias test, which included the sampling standard error and year of publication to test for small-study bias and time-lag bias, as well as the moderators (above) to account for heterogeneity in our data (Nakagawa et al., 2022).

Results

A total of 177 effect sizes covering dates of arrival at and departure from breeding and non-breeding grounds were obtained from 54 papers, including 87 cohorts of birds (Table 2.1). These effect sizes represent 47 species, comprising 18 landbird, 15 seabird, and 14 waterbird species. For most species, estimates were only reported by one study and only a few species had estimates from several studies (five studies estimated repeatability for black-tailed godwit *Limosa limosa*, three for bar-tailed godwit *Limosa lapponica*, three for pied flycatcher *Ficedula hypoleuca*, and two for barn swallow *Hirundo rustica*).

The median and mean sample sizes (number of individuals tracked) per effect size were 12 and 39.5, respectively (range: 3-1232; Table 2.1). Conventional methods (ringing and colour-ringing) allowed for a larger number of individuals to be tracked across all three ecological groups compared to GLS and satellite methods and over a longer period (Table 2.1). Most studies tracked individuals over two, three, or four years, although one study tracked some individuals for up to 20 years (k of study = 12.4 years). The majority of the extracted repeatability values originated from temperate latitudes in Europe and North America (77.9%; Fig. 2.1). Of the articles calculating ANOVA- or LMM-based repeatability, only 26% reported the unstandardized estimates for both within- and among-individual variances.

Overall repeatability and heterogeneity

The phylogenetic multilevel meta-analysis (intercept-only) model revealed a mean repeatability estimate (ICC) for all avian migratory timings across the whole annual cycle of 0.414 (95% confidence interval, hereafter, CI = [0.313 to 0.508]; Fig. 2.2a; Table S2.2). A similar model, but without controlling for phylogeny, also showed a statistically significant overall repeatability (multilevel meta-analysis: $ICC_{[all]}$ = 0.421, CI = [0.348:0.490]; Table S2.2). The total heterogeneity in the data set was high ($I^2_{[total]}$ = 84.2%), which is common across ecological meta-analyses (Senior et al., 2016). When I^2 was partitioned, 49.7% was attributed to effect ID, 0% to paper ID, 0% to cohort ID, 27.3% to species ID, and 7.2% to phylogeny.

Table 2.1. Number of effect sizes, cohorts, studies, the median (range) sample size of individuals, and the median (range) repeated measures per individual (*k*) analysed in the meta-analyses. The total dataset is summarised separately for the overall meta-analysis, followed by a summary that illustrates the distribution of data based on ecological group and tracking method of individuals included in the analyses.

Meta-analysis		**Effect sizes**	**Cohort**	**Studies**	**Median *n* (range)**	**Median *k* (range)**
All data		177	87	54*	12 (3-1232)	2.3 (1.1-12.4)
Ecological group	**Tracking method**					
Landbird	Conventional	19	19	11	39 (12-480)	2.3 (2.0-5.2)
	GLS	19	6	6	9 (3-33)	2 (2.0-2.3)
	Satellite	16	4	3	6 (3-25)	3.55 (2.6-5.0)
Waterbird	Conventional	21	18	12	44 (11-180)	2.7 (2.0-12.4)
	GLS	18	6	4	16 (6-36)	2.5 (2.0-2.9)
	Satellite	16	5	5	12 (5-35)	3 (2.0-4.5)
Seabird	Conventional	2	2	1	940 (648-1232)	4.35 (4.3-4.4)
	GLS	54	24	10	7 (3-76)	2 (1.1-4.3)
	Satellite	12	3	3	4 (4-82)	2.93 (2.5-3.5)

*Note that the total number of studies is one less than the sum of the number of studies when divided by ecological group and tracking method as one study tracked the same species using two different methods.

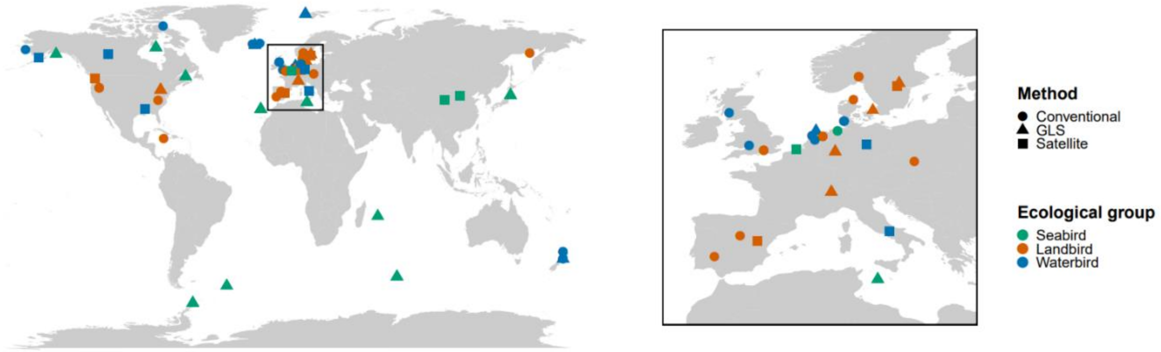

Figure 2.1. The marking locations of birds for all studies with repeatability estimates collated from the literature and included in analyses, coloured by ecological group (waterbird, seabird, or landbird), and shaped by tracking method (conventional, satellite, or GLS).

Variation in repeatability estimates

Repeatability values vary across the annual cycle, with departure from the non-breeding grounds being the most repeatable, and departure from the breeding grounds being the least repeatable ($\text{ICC}_{[\text{depart non-breeding}]}$ = 0.522, CI = [0.391:0.636]; $\text{ICC}_{[\text{arrival breeding}]}$ = 0.381, CI = [0.250:0.503]; $\text{ICC}_{[\text{arrival non-breeding}]}$ = 0.416, CI = [0.274:0.547]; $\text{ICC}_{[\text{depart breeding}]}$ = 0.326, CI = [0.172:0.469]; Fig. 2.2b; Table S2.3). However, there were only statistically significant differences between departure from the breeding grounds and a) arrival at and b) departure from, the non-breeding grounds, and between arrival at the breeding grounds and departure from the non-breeding grounds (Table S2.3).

There was no statistically significant difference in repeatability between males and females, but there was between males and the 'mixed' (both/unknown) group ($\text{ICC}_{[\text{male}]}$ = 0.287, CI = [0.152:0.419]; $\text{ICC}_{[\text{female}]}$ = 0.397, CI = [0.229:0.545]; $\text{ICC}_{[\text{mixed}]}$ = 0.499, CI = [0.417:0.573]; Fig. 2.2e; Table S2.5). However, this effect seemed to be due to the fact that the majority of repeatability estimates measured for males only were represented by the two least repeatable annual events (arrival at breeding grounds, n = 22; departure from the breeding grounds, n = 7; out of 31), and sample sizes for males and females only were small. None of the other moderators (tracking method ($ICC_{[conventional]}$ = 0.306, CI = [0.202:0.409]; $ICC_{[GLS]}$ = 0.512, CI = [0.404:0.608]; $ICC_{[satellite]}$ = 0.440, CI = [0.292:0.575]; Fig. 2.2c; Table S5), ecological group ($ICC_{[seabird]}$ = 0.520, CI = [0.398:0.626]; $ICC_{[waterbird]}$ = 0.404, CI = [0.289:0.513]; $ICC_{[landbird]}$ = 0.333, CI = [0.205:0.454]; Fig. 2.2d; Table S2.6) or number of samples per individual (slope = -0.011, CI = [-0.062:0.041]; Fig. S2.4; Table S2.7)) showed statistically significant influences on repeatability.

Model selection and multi-model inference

We found five candidate models within two units of AICc from the best-fitting model. All five moderators tested in our univariate models were included in the top five models, with annual event being the most important predictor (Table S2.8). Our model-averaging approach highlighted the most repeatable period of the annual cycle to be departure from the non-breeding grounds, with statistically significant differences in repeatability between that period and a) arrival at, and b) departure from, the breeding grounds. Arrival at the non-breeding grounds was also statistically significantly more repeatable than departure from the breeding grounds (Table S2.9). The importance of this moderator is consistent with our univariate models. However, the association we observed in our univariate meta-regression with sex included as a moderator was not robust to the model averaging. Finally, in our top model, we found repeatability of avian migratory behaviours to be statistically significantly influenced by annual event and ecological group (Table S2.8).

Sensitivity analysis and publication bias

In the univariate meta-regression models to test for bias, our results revealed little statistical sign of small-study or time-lag bias. The slope of sampling standard error was not statistically significant (slope = 0.213, CI = [-0.326:0.752]), indicating that effect sizes with larger SEs (i.e., more uncertain effect sizes) do not tend to be larger (Table S2.19), and the estimated effect of publication year was very close to zero (slope = 0.008, CI = [-0.002:0.019]), suggesting there has been no linear change in effect sizes over time since the first effect size was published (Table S2.20). These results were consistent with those from the multi-moderator meta-regression which explained a sizeable amount of the heterogeneity in our data (R^2 = ~21%; Figs S2.5-S2.6; Table S2.21).

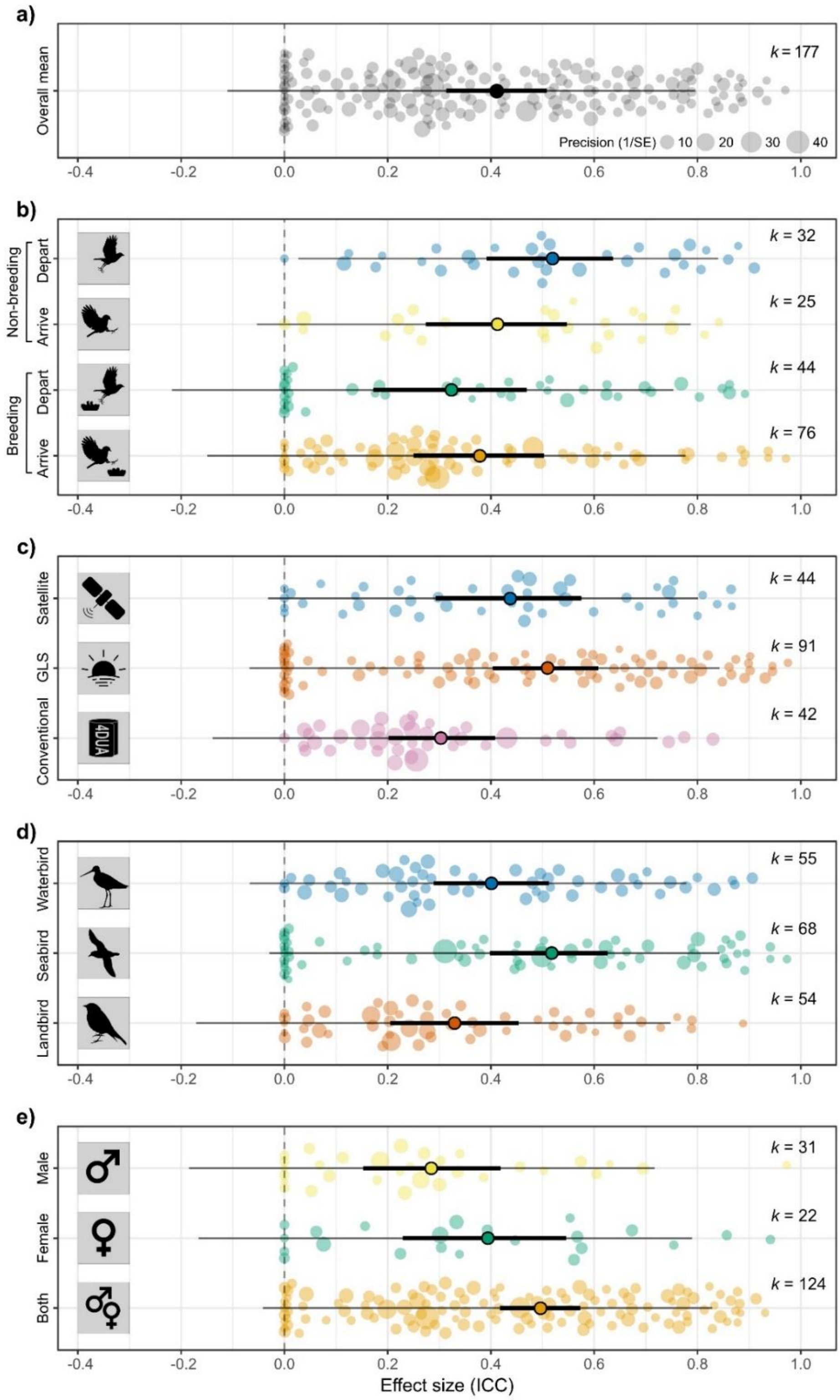

Figure 2.2. Repeatability of avian migration timing for a) all estimates together; b) annual migration events; c) tracking methods; d) ecological groups; and e) sex. Plots show mean(s) with 95% confidence intervals (thick lines, indicating uncertainty around the overall estimate) and 95% prediction intervals (thin lines, indicating the possible range for a new effect size (without sampling errors)), observed effect sizes (back-transformed to ICC) scaled by precision (circles) and k = number of effect sizes.

Discussion

Advances in tracking technology have allowed the movements of individual birds on repeated journeys to be recorded, which has fuelled interest in the scale of individual variation in migratory journeys. Our meta-analysis of avian studies tracking the repeat journeys of individuals reveals that repeatability estimates (ICC) of avian migration timing averaged 0.414 (95% CI = 0.3 to 0.5) although there existed a high heterogeneity ($I^2_{[\text{total}]} > 84\%$). Repeatability estimates of the four annual events (arrival at, and departure from, breeding and non-breeding grounds) focused on in this study were found to vary, with departure from the non-breeding grounds being the most repeatable. However, there was no statistically significant difference in repeatability across ecological groups, the tracking method used to calculate repeatability, between sexes, or with the number of measurements per individual.

Our overall ICC of 0.414 was similar to the migration repeatability estimate from an earlier meta-analysis (ICC = ~0.46; Holtmann et al., 2017). Given the spread of migratory timings that is typical for migratory bird populations (Kikuchi & Reinhold, 2021), our findings suggest that consistent individual differences in arrival at, and departure from, breeding and non-breeding grounds is a common feature of avian migration. Population-level shifts in phenology of many migratory species are common at present (Gordo, 2007; Gunnarsson & Tómasson, 2011), and these could arise from individuals responding directionally to changing environmental conditions and/or by generational changes in the frequency of individuals with different timings within populations. For example, Gill et al. (2014) showed individual Icelandic black-tailed godwits *L. l. islandica* to be consistent in spring arrival dates, and that advancing spring arrival dates were driven by new recruits to the population with differing phenology distributions than their predecessors. Changes in the distribution of phenologies within a population could reflect changes in the conditions influencing the development of individual phenologies and/or their subsequent survival rates (Gill et al., 2019), and could be influenced by heritable components of migratory behaviours (see Dochtermann et al., 2019).

Consequently, a focus on understanding (a) the environmental and/or demographic factors influencing between-individual phenological variation and (b) the extent to which individual variation in phenology is directional with respect to changing environmental conditions is likely to be needed in order to understand how phenological change happens, and thus how rapidly species may adapt to changing environmental conditions.

Repeatability values were found to vary significantly across the annual cycle and, contrary to our predictions, departure from the non-breeding grounds was found to be the most repeatable. This suggests that the other annual events likely have higher within-individual variation relative to between-individual variation. The significantly higher repeatability of departure from the non-breeding grounds than arrival at the breeding grounds might suggest that the environmental conditions experienced on migration can influence timing of arrival, which may be especially true for long-distance migrants (Carneiro et al., 2019; Drake et al., 2014; but see Brown et al., 2021). Departure from the breeding grounds and hence arrival at the non-breeding grounds may also be constrained by events during the breeding season. For example, the timing of departure from the breeding grounds is likely to vary with the timing and outcome of breeding attempts, which can vary across years and individuals. For example, in many seabirds, successful breeders tend to leave later than failed breeders (Catry et al., 2013), while many migratory passerines and waders may lay replacement clutches following nest loss (Morrison et al., 2019), with knock-on effects for departure dates. This may therefore increase within-individual variation in these timings and thereby decrease repeatability. However, relatively few studies have considered the effect of breeding outcome on individual repeatability in migratory timing (Catry et al., 2013; Phillips et al., 2005; Yamamoto et al., 2014).

Across the three ecological groups (waterbird, seabird and landbird), there was no statistically significant variation in repeatability values, suggesting consistent individual differences in migratory timings is a common feature of migratory systems (Gill et al., 2014). However, most studies that have investigated repeatability in migration have focused on species breeding at temperate and polar latitudes. The locations extracted for studies in this review represent where individuals were tagged (which were the breeding grounds for 89% of studies), but many species spend their non-breeding period in the tropics. Our review has highlighted a lack of studies exploring repeatability of species breeding in the tropics (but see Jaeger et al., 2017; Chapter 3), where seasonality is less marked and, particularly for seabirds, resources are often less predictable than at higher latitudes (Weimerskirch, 2007). We therefore propose this should be a priority for future research. For some tropical species, at least for most tropical seabirds, the timing of breeding tends to be more variable at the population level compared to higher latitudes with some species breeding year-round, while others show flattened peaks that extend over several months. Consequently, repeatability may be naturally inflated when a large number of viable phenologies exist in a population. However, many tropical species do not make long-distance migrations, which may make finding information on arrival and departure timings difficult. A recent study on a population of blue tits *Cyanistes caeruleus* showed there to be substantial individual variation and high repeatability in the timing of arrival at the breeding grounds (Gilsenan et al., 2019), suggesting that repeatability in timings may be a common feature even in species that are generally considered non-migratory.

Despite the different temporal and spatial resolutions of the three tracking methods considered in this study, there was no statistically significant effect of tracking method on repeatability estimates. Considering that conventional methods rely on the spatiotemporal distribution of colour-ring observers and/or the activity of ringing stations, whereas geolocators and GPS/satellite tags are more likely to be tracking individuals in real-time, it is perhaps surprising that repeatability is captured equally well by all three methods. However, it is likely that there will be lower confidence in repeatability estimates measured using methods with lower resolution (see Korner-Nievergelt et al., 2012; Strandberg et al., 2009). Very few studies have used two or more different methods to estimate repeatability of a single species, but those that did reported no variation with type of device (Senner et al., 2019). This may be different, however, when estimating spatial repeatability due to the different spatial resolutions and measurement errors of each method (see Dingemanse et al., 2022). For example, geolocators can have large errors around location estimates (Halpin et al., 2021; Phillips et al., 2004), which may underestimate repeatability due to uncertainty when a bird reaches an exact location. Nonetheless, it is important to note the costs and limitations associated with each tracking method that is likely to be a constraint of the study system.

The number of studies tracking repeated individual migratory journeys has increased greatly over the past decade, but the number that actually report repeatability of key elements of these journeys is much lower. Reasons as to why these estimates have not been reported, if given, have included the number of individuals with repeat tracks being too small (e.g., n = 9, van Bemmelen et al., 2019). However, we have identified studies calculating repeatability with as few as three individuals (Vardanis et al., 2016; Wellbrock et al., 2017; but see Wolak et al., 2012). Regardless of the method used, our study showed no effect of the number of measurements per individual on repeatability suggesting that calculating repeatability is always worthwhile, although it is important to note that the power of those estimates with small samples may be low (Dingemanse & Dochtermann, 2013).

The repeatability estimates used in this study were all for breeding adults, and it is possible that migratory timings could vary with age, especially if they are refined with age and experience (e.g., Campioni et al., 2019). This age-related variation may be especially true for long-lived individuals; however, shifts in migratory timings with age would need to be directional in order for ontogeny to drive phenological change. In addition, a potential caveat which may affect repeatability estimates and thus comparisons across studies, is the different definitions and calculations of breeding and non-breeding locations across studies. For example, arrival at the breeding grounds can range from entry into the nest/burrow (Yamamoto et al., 2014), entry to breeding territory (Kentie et al., 2017), and entry into region/area (Carneiro et al., 2019), which may cause noise and, potentially, systematic bias in repeatability estimates across studies. For example, arrival into a breeding territory could be more repeatable than arrival into the breeding region. This again, may be down to the tracking method used and its resolution, and the species in question.

Repeatability represents the proportion of the total phenotypic variation (sum of between-individual variance, within-individual variance, and measurement error) in the sampled population that can be attributed to variation between groups (usually individuals). Therefore, it is important to note that the same repeatability estimates can arise from different patterns of these variance components (see Dochtermann & Royauté, 2019). Interpreting repeatability would therefore be aided greatly by knowing the spread of variation that exists in the sampled population and estimations of measurement error. Only 26% of studies included in our meta-analysis provided unstandardized estimates for both within- and among-individual variances, which is slightly lower than that found by Sánchez-Tójar et al. (2022) (30.7%, 95% CI = 22.0 to 41.0), and none formally quantified measurement error. While we included tracking method in our meta-analysis to investigate how repeatability varies with devices with varying measurement errors, this component can also vary with environmental conditions (Dingemanse et al., 2022) and thus is likely to add noise to comparative patterns in repeatability. We therefore support the recommendation that authors report the variance components and measurement errors underpinning the reported repeatability estimates where possible, as well as the coefficients of variation for each hierarchical level (Dingemanse & Wright, 2020; Sánchez-Tójar et al., 2022), and the specific details of model structure (error structures, transformations and structure of random and fixed effects) to aid evaluation of differences in specific variance components (Pick et al., 2019; Royauté & Dochtermann, 2021; Sánchez-Tójar et al., 2022). Very few of the studies in our literature search reported these elements, which may have reduced the power of our models.

In addition to repeatability in migratory timing, it is also important to consider repeatability in migratory routes and locations. This aspect of migration was not touched upon in this study, but many studies also report high levels of fidelity to breeding and wintering locations (e.g., Delord et al., 2019; Grist et al., 2014; Ramírez et al., 2016), and migratory routes (López-López et al., 2014; but see also Dias et al., 2011; Dias et al., 2013). Throughout the literature, a variety of methods have been used to investigate spatial repeatability (e.g., Dias et al., 2013; Fayet et al., 2016; Ramírez et al., 2016), making comparisons across studies difficult. However, understanding repeatability of migration in both space and time will be crucial for understanding how species will adapt to environmental change.

In conclusion, the similar repeatability estimates of avian migration timing reported by studies of many different species suggests that consistent individual differences in migratory timings is likely to be a common feature of migratory systems. In many cases, repeated collection of individual migration data is not intentional, but rather a by-product of retrieving a tracking device two or more years post-deployment. There is also a current gap in the literature with limited information on tropical species, which may limit our understanding of how these species may respond to environmental change in less strongly seasonal environments. As phenological responses to environmental change will depend on the processes that drive within- and between-individual variation and change in migratory timings, methods to disentangle within- and between-individual variation should be incorporated into study designs, for example through structured sampling of individuals across phenological ranges. As migration phenologies are often associated with variation in demographic rates, understanding the consequences of phenological variation will be important for future conservation management strategies and understanding population change.

Acknowledgments

We thank the editor, associate editor, Alfredo Sánchez-Tójar, and two anonymous reviewers who provided valuable feedback that greatly improved the manuscript. The work was supported by NERC (NE/P002986/1) and K.A.F was funded by a John and Pat Warham PhD studentship from the British Ornithologists' Union (BOU).

Data accessibility

Data, code and lists of screened studies are available from the Dryad Digital Repository https://doi.org/10.5061/dryad.n02v6wx09 (Franklin, Nicoll, et al., 2022).

Supplementary materials to Chapter 2: Individual repeatability of avian migration phenology: a systematic review and meta-analysis

Supplementary Methods

The search strategies and the Boolean search strings we used are presented below, along with a flow diagram (often referred to as a PRISMA flow chart – the Preferred Reporting Items in Systematic Reviews and Meta-Analyses; Figure S2.1) which shows the stages at which studies were disqualified or eventually used in the current study.

Web of Science Core Collection:

(TS=("repeat*" OR "intraclass correlation" OR "ICC" OR "individual variation" OR "intra-individual variation" OR "between-individual variation" OR "consisten*" OR "flexib*") AND TS=("migration" OR "migratory") AND TS=("*bird*" OR "aves" OR "avian")) AND (SU=(Behavioral Sciences OR Biodiversity & Conservation OR Environmental Sciences & Ecology OR Evolutionary Biology OR Genetics & Heredity OR Marine & Freshwater Biology OR Oceanography OR Veterinary Sciences OR Zoology))

Scopus:

TITLE-ABS-KEY ("repeat*" OR "intraclass correlation" OR "ICC" OR "individual variation" OR "intra-individual variation" OR "between-individual variation" OR "consisten*" OR "flexib*") AND TITLE-ABS-KEY ("migration" OR "migratory") AND TITLE-ABS-KEY ("*bird*" OR "aves" OR "avian") AND (LIMIT-TO (SUBJAREA , "AGRI") OR LIMIT-TO (SUBJAREA , "ENVI") OR LIMIT-TO (SUBJAREA , "VETE"))

Supplementary Figures

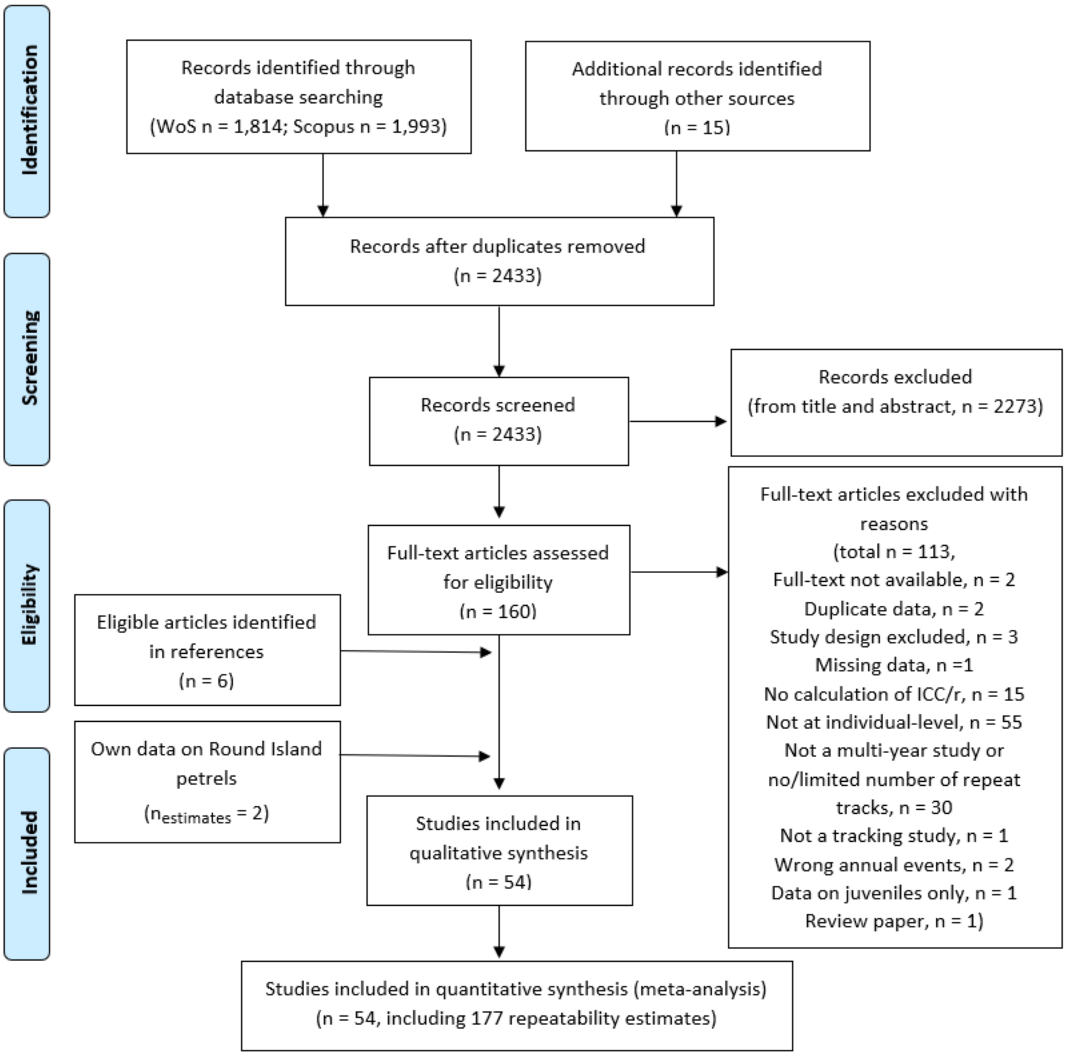

Figure S2.1. PRISMA flow chart summarising search methods and screening for studies included in analyses, and reasons for excluding studies.

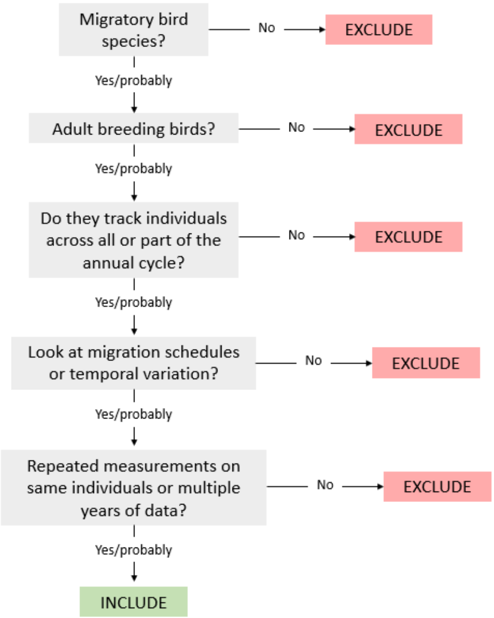

Figure S2.2. Decision tree used to evaluate studies for inclusion and exclusion at the stage of title and abstract screening.

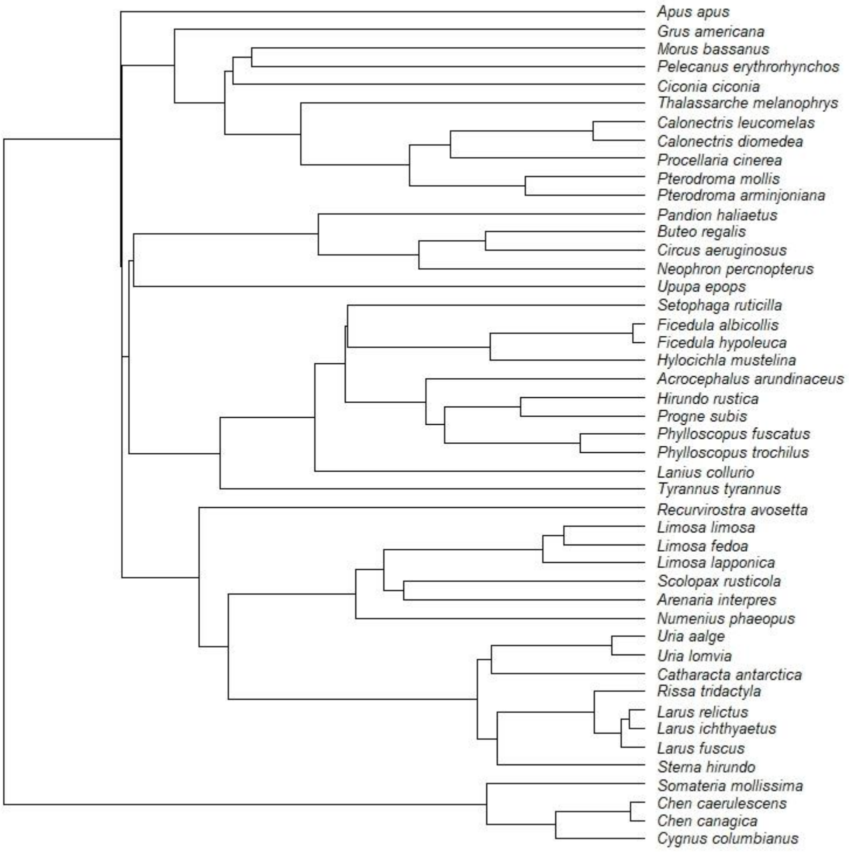

Figure S2.3. Phylogenetic tree (with Hackett backbone) used for phylogenetic meta-analysis and meta-regression on repeatability in avian migratory timings.

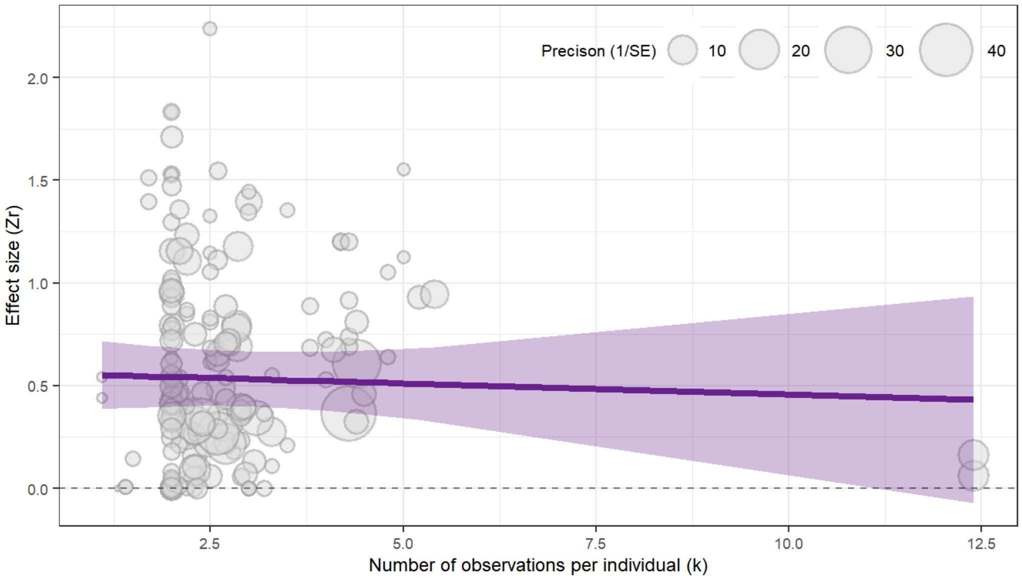

Figure S2.4. Repeatability of avian migration timing for the continuous variable *k*, where the solid line represents the model estimate and the shading shows the 95% confidence intervals, with individual data points scaled by precision (1/SE).

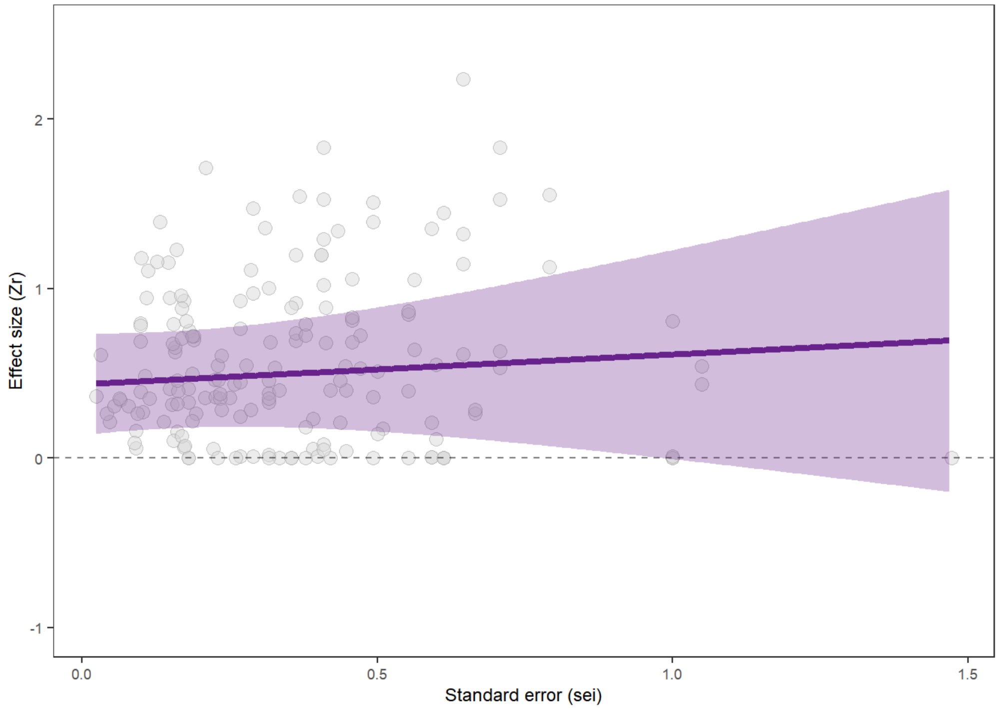

Figure S2.5. A bubble plot showing that effect sizes with larger standard errors do not tend to be larger, providing no evidence of small-study effects in the meta-analytic dataset. The solid line represents the model estimate and the shading shows its 95% confidence intervals.

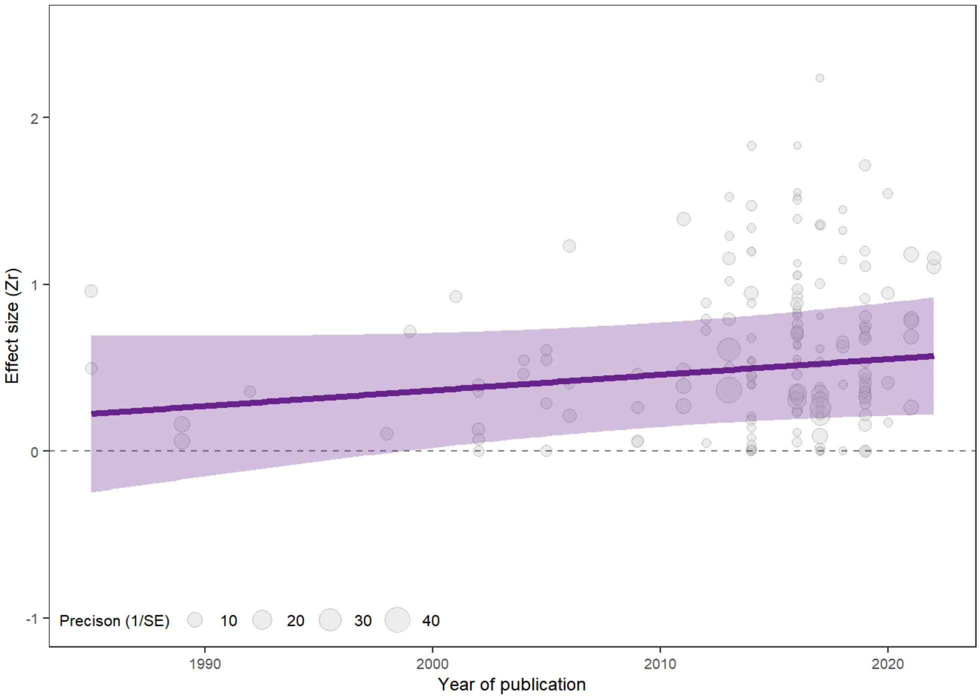

Figure S2.6. A bubble plot showing that the overall effect size has not changed over time, where the solid line represents the model estimate and the shading shows its 95% confidence intervals, with individual data points scaled by precision (1/SE).

Supplementary Tables

Table S2.1. Sample sizes for our data set in terms of effect sizes, cohorts, studies, species, and the number of effect sizes in the different levels of categorical variables (factors), split by ecological group (seabird, waterbird and landbird), and overall.

Number of	**Landbird**	**Seabird**	**Waterbird**	**All**
All data				
Effect sizes (analyses)	54	68	55	177
Cohort	29	29	29	87
Studies	20	14	20	54
Annual event				
Arrival at breeding grounds	27	29	20	76
Departure from breeding grounds	10	27	7	44
Arrival at non-breeding grounds	8	6	11	25
Departure from non-breeding grounds	9	6	17	32
Tracking method				
Conventional method	19	2	21	42
GLS method	19	54	18	91
Satellite method	16	12	16	44
Sex				
Female	4	8	10	22
Male	20	8	3	31
Mixed sex	30	52	42	124

Table S2.2. Overall effects (meta-analytic means) and 95% confidence intervals (CIs) both in *Zr* and back-transformed to ICC, and heterogeneity (I^2), for the multilevel intercept-only meta-analysis models including and excluding phenology.

Model	Overall mean	CI.lb	CI.ub	I^2_{total}	I^2_{es}	I^2_{paper}	I^2_{cohort}	$I^2_{species}$	I^2_{phylo}
Meta-analysis (*Zr*)	0.541	0.445	0.637	84.0	50.6	0.0	0.0	33.4	NA
Meta-analysis (ICC)	0.421	0.348	0.490	NA	NA	NA	NA	NA	NA
Meta-analysis phylo (*Zr*)	0.532	0.400	0.664	84.2	49.7	0.0	0.0	27.3	7.2
Meta-analysis phylo (ICC)	0.414	0.313	0.508	NA	NA	NA	NA	NA	NA

Table S2.3. Regression coefficients (estimates) and 95% confidence intervals (CIs) both in *Zr* and back-transformed to ICC from the meta-regression with annual event fitted as fixed effect. Note that mu means the group mean while beta represents the contrast between two groups in the Unit column. $R^2_{[marginal]}$ = 10.5%.

Fixed effect	Unit	Estimate	CI.lb	CI.ub
Arrival_breed	Zr (mu)	0.472	0.308	0.637
Depart_breed	Zr (mu)	0.391	0.206	0.576
Arrival_nonbreed	Zr (mu)	0.593	0.396	0.791
Depart_nonbreed	Zr (mu)	0.719	0.531	0.908
Arrival_breed	ICC (mu)	0.381	0.250	0.503
Depart_breed	ICC (mu)	0.326	0.172	0.469
Arrival_nonbreed	ICC (mu)	0.416	0.274	0.547
Depart_nonbreed	ICC (mu)	0.522	0.391	0.636
Arrival_breed - Depart_breed	Zr (beta)	-0.081	-0.225	0.062
Arrival_breed - Arrival_nonbreed	Zr (beta)	0.121	-0.048	0.290
Arrival_breed - Depart_nonbreed	Zr (beta)	0.247	0.088	0.405
Depart_breed - Arrival_nonbreed	Zr (beta)	0.202	0.023	0.382
Depart_breed - Depart_nonbreed	Zr (beta)	0.328	0.157	0.500
Depart_nonbreed - Arrival_nonbreed	Zr (beta)	-0.126	-0.301	0.049

Table S2.4. Regression coefficients (estimates) and 95% confidence intervals (CIs) both in *Zr* and back-transformed to ICC from the meta-regression with tracking method fitted as fixed effect. Note that mu means the group mean while beta represents the contrast between two groups in the Unit column. $R^2_{[marginal]}$ = 5.1%.

Fixed effect	**Unit**	**Estimate**	**CI.lb**	**CI.ub**
Conventional	Zr (mu)	0.434	0.291	0.576
GLS	Zr (mu)	0.599	0.456	0.742
Satellite	Zr (mu)	0.638	0.428	0.847
Conventional	ICC (mu)	0.306	0.202	0.409
GLS	ICC (mu)	0.512	0.404	0.608
Satellite	ICC (mu)	0.440	0.292	0.575
Conventional - GLS	Zr (beta)	0.165	-0.026	0.356
Conventional - Satellite	Zr (beta)	0.204	-0.049	0.457
GLS - Satellite	Zr (beta)	0.039	-0.215	0.292

Table S2.5. Regression coefficients (estimates) and 95% confidence intervals (CIs) both in *Zr* and back-transformed to ICC from the meta-regression with sex fitted as fixed effect. Note that mu means the group mean while beta represents the contrast between two groups in the Unit column. $R^2_{[marginal]}$ = 6.9%.

Fixed effect	**Unit**	**Estimate**	**CI.lb**	**CI.ub**
Both	Zr (mu)	0.606	0.496	0.715
Female	Zr (mu)	0.471	0.267	0.675
Male	Zr (mu)	0.380	0.205	0.554
Both	ICC (mu)	0.499	0.417	0.573
Female	ICC (mu)	0.397	0.229	0.545
Male	ICC (mu)	0.287	0.152	0.419
Both - Female	Zr (beta)	-0.135	-0.359	0.089
Both - Male	Zr (beta)	-0.226	-0.425	-0.027
Male - Female	Zr (beta)	0.091	-0.144	0.327

Table S2.6. Regression coefficients (estimates) and 95% confidence intervals (CIs) both in *Zr* and back-transformed to ICC from the meta-regression with ecological group fitted as fixed effect. Note that mu means the group mean while beta represents the contrast between two groups in the Unit column. $R^2_{[\text{marginal}]}$ = 6.7%.

Fixed effect	**Unit**	**Estimate**	**CI.lb**	**CI.ub**
Landbird	Zr (mu)	0.424	0.263	0.585
Seabird	Zr (mu)	0.638	0.472	0.804
Waterbird	Zr (mu)	0.564	0.405	0.722
Landbird	ICC (mu)	0.333	0.205	0.454
Seabird	ICC (mu)	0.520	0.398	0.626
Waterbird	ICC (mu)	0.404	0.289	0.513
Landbird - Seabird	Zr (beta)	0.214	-0.017	0.445
Landbird - Waterbird	Zr (beta)	0.140	-0.086	0.366
Seabird - Waterbird	Zr (beta)	0.074	-0.155	0.304

Table S2.7. Regression coefficients (estimates) and 95% confidence intervals (CIs) in *Zr* from the meta-regression with number of observations per individual (*k*) fitted as fixed effect. $R^2_{[\text{marginal}]}$ = 0.2%.

Fixed effect	**Estimate**	**CI.lb**	**CI.ub**
Intercept	0.563	0.358	0.769
k	-0.011	-0.062	0.041

Table S2.8. The top five models within the ΔAICc difference of 2, and which five variables were included (indicated by +), model weights and the sum of weights for each of the variables are included.

Model	**Annual event**	**Ecological group**	**Method**	**k**	**sex**	**ΔAICc**	**weight**
Model1	+	+				0.000	0.288
Model2	+					0.353	0.242
Model3	+		+			0.474	0.227
Model4	+	+		+		1.512	0.135
Model5	+				+	1.978	0.107
(Sum of weights)	1.00	0.424	0.227	0.135	0.107	NA	NA

Table S2.9. The average estimates for regression coefficients (Estimate) and 95% confidence intervals (CIs) from the model averaging procedure using full-averages (assuming zero values for moderators when they do not occur).

Fixed effect	**Estimate**	**CI.lb**	**CI.ub**
Intercept	0.437	0.251	0.624
Depart_breed	-0.090	-0.236	0.056
Arrival_nonbreed	0.110	-0.063	0.282
Depart_nonbreed	0.241	0.081	0.402
Female	0.108	-0.177	0.393
Male	0.039	-0.126	0.204
Seabird	0.044	-0.139	0.227
Waterbird	0.044	-0.155	0.244
GLS	-0.003	-0.026	0.020
Satellite	-0.012	-0.108	0.085
k	-0.019	-0.143	0.105

Table S2.10. Overall effects (meta-analytic means) and 95% confidence intervals (CIs) in *Zr* and heterogeneity (I^2) for the phylogenetic multilevel intercept-only meta-analysis model when testing different levels of correlation (r = 0.25, 0.50, and 0.75) between sampling variances from the same cohort of birds.

Model	**Overall mean**	**CI.lb**	**CI.ub**	I^2_{total}	I^2_{es}	I^2_{paper}	I^2_{cohort}	$I^2_{species}$	I^2_{phylo}
Meta-analysis, r=0.25	0.535	0.405	0.664	82.8	40.6	0.0	0.0	34.3	7.8
Meta-analysis, r=0.50	0.532	0.400	0.664	84.2	49.7	0.0	0.0	27.3	7.2
Meta-analysis, r=0.75	0.530	0.396	0.663	86.2	60.5	0.0	0.0	19.6	6.1

Table S2.11. Overall effects (meta-analytic means) and 95% confidence intervals (CIs) both in *Zr* and back-transformed to ICC, and heterogeneity (I^2) for the multilevel intercept-only meta-analysis models including and excluding phylogeny when negative repeatability values are included.

Fixed effect	**Overall mean**	**CI.lb**	**CI.ub**	I^2_{total}	I^2_{es}	I^2_{paper}	I^2_{cohort}	$I^2_{species}$	I^2_{phylo}
Meta-analysis (Zr)	0.529	0.429	0.629	85.3	51.2	0.0	0.0	34.2	NA
Meta-analysis (ICC)	0.412	0.336	0.484	NA	NA	NA	NA	NA	NA
Meta-analysis phylo (Zr)	0.524	0.397	0.650	85.5	50.6	0.0	0.0	30.2	4.8
Meta-analysis phylo (ICC)	0.408	0.311	0.498	NA	NA	NA	NA	NA	NA

Table S2.12. Regression coefficients (estimates) and 95% confidence intervals (CIs) from the meta-regression with annual event fitted as fixed effect when negative repeatability values are included. Note that mu means the group mean while beta represents the contrast between two groups in the Unit column. $R^2_{[\mathrm{marginal}]}$ = 10.9%.

Fixed effect	**Unit**	**Estimate**	**CI.lb**	**CI.ub**
Arrival_breed	Zr (mu)	0.477	0.314	0.640
Depart_breed	Zr (mu)	0.352	0.168	0.536
Nonbreed_arrival	Zr (mu)	0.592	0.394	0.790
Nonbreed_depart	Zr (mu)	0.712	0.523	0.901
Arrival_breed	ICC (mu)	0.385	0.256	0.505
Depart_breed	ICC (mu)	0.294	0.140	0.440
Nonbreed_arrival	ICC (mu)	0.414	0.272	0.546
Nonbreed_depart	ICC (mu)	0.518	0.386	0.632
Arrival_breed - Depart_breed	Zr (beta)	-0.125	-0.273	0.022
Arrival_breed - Nonbreed_arrival	Zr (beta)	0.114	-0.060	0.289
Arrival_breed - Nonbreed_depart	Zr (beta)	0.235	0.071	0.399
Depart_breed - Nonbreed_arrival	Zr (beta)	0.240	0.055	0.424
Depart_breed - Nonbreed_depart	Zr (beta)	0.360	0.183	0.537
Nonbreed_arrival - Nonbreed_depart	Zr (beta)	-0.120	-0.301	0.060

Table S2.13. Regression coefficients (estimates) and 95% confidence intervals (CIs) both in Zr and back-transformed to ICC from the meta-regression with tracking method fitted as fixed effect when negative repeatability values are included. Note that mu means the group mean while beta represents the contrast between two groups in the Unit column. $R^2_{[\text{marginal}]}$ = 4.2%.

Fixed effect	**Unit**	**Estimate**	**CI.lb**	**CI.ub**
Conventional	Zr (mu)	0.429	0.278	0.579
GLS	Zr (mu)	0.574	0.425	0.723
Satellite	Zr (mu)	0.633	0.415	0.851
Conventional	ICC (mu)	0.302	0.192	0.411
GLS	ICC (mu)	0.494	0.379	0.596
Satellite	ICC (mu)	0.437	0.283	0.577
Conventional - GLS	Zr (beta)	0.145	-0.054	0.345
Conventional - Satellite	Zr (beta)	0.204	-0.060	0.469
GLS - Satellite	Zr (beta)	0.059	-0.205	0.323

Table S2.14. Regression coefficients (estimates) and 95% confidence intervals (CIs) both in *Zr* and back-transformed to ICC from the meta-regression with sex fitted as fixed effect when negative repeatability values are included. Note that mu means the group mean while beta represents the contrast between two groups in the Unit column. $R^2_{[\text{marginal}]}$ = 8%.

Fixed effect	**Unit**	**Estimate**	**CI.lb**	**CI.ub**
Both	Zr (mu)	0.602	0.489	0.715
Female	Zr (mu)	0.450	0.239	0.661
Male	Zr (mu)	0.347	0.166	0.527
Both	ICC (mu)	0.496	0.412	0.573
Female	ICC (mu)	0.380	0.205	0.536
Male	ICC (mu)	0.262	0.122	0.399
Both - Female	Zr (beta)	-0.153	-0.384	0.079
Both - Male	Zr (beta)	-0.256	-0.462	-0.050
Male - Female	Zr (beta)	0.103	-0.141	0.347

Table S2.15. Regression coefficients (estimates) and 95% confidence intervals (CIs) from the meta-regression with ecological group fitted as fixed effect when negative repeatability values are included. Note that mu means the group mean while beta represents the contrast between two groups in the Unit column. R2[marginal] = 5.1%.

Fixed effect	Unit	Estimate	CI.lb	CI.ub
Landbird	Zr (mu)	0.417	0.247	0.587
Seabird	Zr (mu)	0.612	0.438	0.786
Waterbird	Zr (mu)	0.562	0.394	0.729
Landbird	ICC (mu)	0.327	0.193	0.454
Seabird	ICC (mu)	0.502	0.371	0.616
Waterbird	ICC (mu)	0.403	0.280	0.517
Landbird - Seabird	Zr (beta)	0.195	-0.048	0.438
Landbird - Waterbird	Zr (beta)	0.145	-0.094	0.383
Seabird - Waterbird	Zr (beta)	0.050	-0.191	0.292

Table S2.16. Regression coefficients (estimates) and 95% confidence intervals (CIs) in *Zr* from the meta-regression with number of observations per individual (*k*) fitted as fixed effect when negative repeatability values are included. $R^2_{[marginal]}$ = 0.1%.

Fixed effect	Estimate	CI.lb	CI.ub
Intercept	0.563	0.358	0.769
k	-0.006	-0.061	0.048

Table S2.17. The top six models (when negative repeatability values are included) within the ΔAICc difference of 2, and which five variables were included (indicated by +), model weights and the sum of weights for each of the variables are included.

Model	**Annual event**	**Sex**	**Ecological group**	**Method**	***k***	**ΔAICc**	**weight**
Model1	+					0.000	0.241
Model2	+		+			0.428	0.195
Model3	+			+		0.434	0.194
Model4	+	+				0.515	0.186
Model5	+	+			+	1.921	0.092
Model6	+				+	1.955	0.091
(Sum of weights)	1.00	0.279	0.195	0.194	0.183	NA	NA

Table S2.18. The average estimates for regression coefficients (Estimate) and 95% confidence intervals (CIs) from the model averaging procedure using full-averages (assuming zero values for moderators when they do not occur).

Fixed effect	**Estimate**	**CI.lb**	**CI.ub**
Intercept	0.486	0.260	0.713
Depart_breed	-0.134	-0.284	0.017
Arrival_nonbreed	0.098	-0.079	0.276
Depart_nonbreed	0.222	0.055	0.389
Seabird	0.047	-0.167	0.262
Waterbird	0.017	-0.104	0.138
GLS	0.036	-0.133	0.206
Satellite	0.040	-0.156	0.236
k	-0.039	-0.208	0.131
Female	-0.060	-0.279	0.158
Male	-0.004	-0.030	0.023

Table S2.19. Regression coefficients (estimates) and 95% confidence intervals (CIs) from the meta-regression with standard error fitted as fixed effect. $R^2_{[marginal]}$ = 2.1%.

Fixed effect	Estimate	CI.lb	CI.ub
Intercept	0.482	0.303	0.662
sqrt(VZr)	0.213	-0.326	0.752

Table S2.20. Regression coefficients (estimates) and 95% confidence intervals (CIs) from the meta-regression with publication year (mean-centred, to help with interpretation) fitted as fixed effect. $R^2_{[marginal]}$ = 2.5%.

Fixed effect	Estimate	CI.lb	CI.ub
Intercept	0.550	0.428	0.673
Publication year	0.008	-0.002	0.019

Table S2.21. Regression coefficients (estimates) and 95% confidence intervals (CIs) from the meta-regression with publication year, standard error, and the five moderator variables fitted as fixed effects. $R^2_{[marginal]}$ = 20.8%.

Fixed effect	Estimate	CI.lb	CI.ub
Intercept	0.435	0.136	0.734
sqrt(VZr)	0.176	-0.459	0.811
Publication year	0.009	-0.004	0.023
Depart_breed	-0.113	-0.266	-0.040
Arrival_nonbreed	0.100	-0.082	0.282
Depart_nonbreed	0.237	0.067	0.408
GLS	-0.012	-0.299	0.275
Satellite	-0.023	-0.369	0.323
Seabird	0.191	-0.066	0.448
Waterbird	0.108	-0.137	0.352
Female	-0.072	-0.307	0.163
Male	0.094	-0.325	0.137
k	-0.006	-0.061	0.050

Data sources

Arnaud, C.M., Becker, P.H., Dobson, F.S. & Charmantier, A. (2013). Canalization of phenology in common terns: genetic and phenotypic variations in spring arrival date. *Behavioural Ecology*, 24: 683-690.

Battley, P.F. (2006). Consistent annual schedules in a migratory shorebird. *Biology Letters*, 2: 517-520.

Bêty, J., Giroux, J.F. & Gauthier, G. (2004). Individual variation in timing of migration: causes and reproductive consequences in greater snow geese (*Anser caerulescens atlanticus*). *Behavioural Ecology and Sociobiology*, 57: 1-8.

Bjørnlid, N. (2016). Repeatability and flexibility in the migration strategies of an arctic seabird. MSc Thesis, Norwegian University of Science and Technology.

Both, C., Bijlsma, R.G. & Ouwehand, J. (2016). Repeatability in spring arrival dates in Pied flycatchers varies among years and sexes. *Ardea*, 104: 3-21.

Brown, J.M., van Loon, E.E., Bouten, W., Camphuysen, C.J., Lens, L., Müller, W., Thaxter, C.B. & Shamoun-Baranes, J. (2021). Long-distance migrants vary migratory behaviour as much as short-distance migrants: An individual-level comparison from a seabird species with diverse migration strategies. *Journal of Animal Ecology*, 90(5): 1058-1070.

Cadahía, L., Labra, A., Knudsen, E., Nilsson, A., Lampe, H.M., Slagsvold, T. & Stenseth, N.C. (2017). Advancement of spring arrival in a long-term study of a passerine bird: sex, age and environmental effects. *Oecologia*, 184(4): 917-929.

Carneiro, C., Gunnarsson, T.G. & Alves, J.A. (2019). Why are Whimbrels not advancing their arrival dates into Iceland? Exploring seasonal and sex-specific variation in consistency of individual timing during the annual cycle. *Frontiers in Ecology and Evolution*, 7: 248.

Conklin, J. R. & Battley, P.F. (2011). Impacts of wind on individual migration schedules of New Zealand bar-tailed godwits. *Behavioural Ecology*, 22: 854-861.

Conklin, J.R., Battley, P.F. & Potter, M.A. (2013). Absolute consistency: Individual versus population variation in annual-cycle schedules of a long-distance migrant bird. *PLoS ONE*, 8: e54535.

Cooper, N.W., Murphy, M.T. & Redmond, L.J. (2009). Age- and sex- dependent spring arrival dates of Eastern Kingbirds. *Journal of Field Ornithology*, 80: 35-41.

Delord, K., Barbraud, C., Pinaud, D., Ruault, S., Patrick, S.C. & Weimerskirch, H. (2019). Individual consistency in the non-breeding behaviour of a long-distance migrant seabird, the Grey petrel *Procellaria cinerea*. *Marine Ornithology*, 47: 93-103.

Fifield, D.A., Montevecchi, W.A., Garthe, S., Robertson, G.J., Kubetzki, U. & Rail, J.F. (2014). Migratory tactics and wintering areas of Northern gannets (*Morus bassanus*) breeding in North America. *Ornithological Monographs*, 79: 1-63.

Franklin, K.A., Norris, K., Gill, J.A., Ratcliffe, N., Bonnet-Lebrun, A.S., Butler, S.J., Cole, N.C., Jones, C.G., Lisovski, S., Ruhomaun, K., Tatayah, V. & Nicoll, M.A.C. (2022). Individual consistency in migration strategies of a tropical seabird, the Round Island petrel. *Movement Ecology,* 10: 13.

Forstmeier, W. (2002). Benefits of early arrival at breeding grounds vary between males. *Journal of Animal Ecology*, 71: 1-9.

Fraser, K.C., Shave, A., de Greef, E., Siegrist, J. & Garroway, C.J. (2019). Individual variability in migration timing can explain long-term, population-level advances in a songbird. *Frontiers in Ecology and Evolution*, 7: 324.

Gill, J.A., Alves, J.S., Sutherland, W.J., Appleton, G.F., Potts, P.M. & Gunnarsson, T.G. (2014). Why is timing of bird migration advancing when individuals are not*? Proceedings of the Royal Society B*, 281: 20132161.

Gunnarsson, T.G., Gill, J.A., Atkinson, P.W., Gélinaud, G., Potts, P.M., Croger, R.E., Gudmundsson, G.A., Appleton, G.F. & Sutherland, W.J. (2006). Population-scale drivers of individual arrival times in migratory birds. *Journal of Animal Ecology*, 75: 1119-1127.

Hasselquist, D., Montràs-Janer, T., Tarka, M. & Hansson, B. (2017). Individual consistency of long-distance migration in a songbird: significant repeatability of autumn route, stopovers and wintering sites but not timing of migration*. Journal of Avian Biology*, 48: 91-102.

Hopp, S.L., Kirby, A. & Boone, C.A. (1999). Banding returns, arrival pattern, and site-fidelity of white-eyed vireos. *The Wilson Bulletin*, 111: 46-55.

Hötker, H. (2001). Arrival of pied avocets *Recurvirostra avosetta* at the breeding site: effects of winter quarters and consequences for reproductive success. *Ardea*, 90: 379-387.

Kentie, R., Marquez-Ferrando, R., Figuerola, J., Gangoso, L., Hooijmeijer, J.C.E.W., Loonstra, A.H.J., Robin, F., Sarasa, M., Senner, N., Valkema, H, Verhoeve, M.A. & Piersma, T. (2017). Does wintering north or south of the Sahara correlated with timing and breeding performance in black-tailed godwits? *Ecology and Evolution*, 7: 2812-2820.

King, D.T., Wang, G., Yang, Z. & Fischer, J.W. (2017). Advances and environmental conditions of spring migration phenology of American white pelicans. *Scientific Reports*, 7: 1-8.

Krietsch, J., Hahn, S., Kopp, M., Phillips, R.A., Peter, H.A. & Lisovski, S. (2017). Consistent variation in individual migration strategies of brown skuas. *Marine Ecology Progress Series*, 578: 213-225.

Krist, M., Munclinger, P., Briedis, M. & Adamík, P. (2021). The genetic regulation of avian migration timing: combining candidate genes and quantitative genetic approaches in a long-distance migrant. *Oecologia*, 196: 373-387.

Lawn, M.R. (2016). Individual consistency in the arrival dates of territorial male Willow warblers *Phylloscopus trochilus. Ringing and Migration*, 31: 63-67.

Liu, D., Zhang, G., Jiang, H., Chen, L., Meng, D. & Lu, J. (2017). Seasonal dispersal and longitudinal migration in the Relict Gull *Larus relictus* across the Inner-Mongolian Plateau. *PeerJ*, 5: e3380.

Liu, D., Zhang, G., Jiang, H. & Lu, J. (2018). Detours in long-distance migration across the Qinghai-Tibetan Plateau: individual consistency and habitat associations. *PeerJ*, 6: e4304.

López-López, P., García-Ripollés, C. & Urios, V. (2014). Individual repeatability in timing and spatial flexibility of migration routes of trans-Saharan migratory raptors. *Current Zoology*, 60(5): 642-652.

Lourenço, P.M., Kentie, R., Schroeder, J., Groen, N.M., Hooijmeijer, J.C.E.W. & Piersma, T. (2011). Repeatable timing of northward migration departure, arrival and breeding in Black-tailed godwits *Limosa l. limosa*, but no domino effects*. Journal of Ornithology*, 152(4): 1023-1032.

McFarlane Tranquilla, L.A., Montevecchi, W.A., Fifield, D.A., Hedd, A., Gaston, A.J., Roberston, G.J. & Phillips, R.A. (2014). Individual winter movement strategies in two species of murre (*Uria* spp.) in the Northwest Atlantic. *PLoS ONE*, 9: e90583.

Metcalfe, N.B. & Furness, R.W. (1985). Survival, winter population stability and site fidelity in the Turnstone *Arenaria interpres. Bird Study*, 32: 207-214.

Møller, A.P. (2001). Heritability of arrival date in a migratory bird. *Proceedings of the Royal Society B: Biological Sciences*, 268: 203-206.

Müller, M.S., Massa, B., Phillips, R.A. & Dell'omo, G. (2014). Individual consistency and sex differences in migration strategies of Scopoli's shearwaters *Calonectris diomedea* despite year differences. *Current Zoology*, 60: 631-641.

Ninni, P., de Lope, F., Saino, N., Haussy, C. & Møller, A.P. (2004). Antioxidants and condition-dependence of arrival date in a migratory passerine. *Oikos*, 105: 55-64.

Pearse, A.T., Metzger, K.L., Brandt, D.A., Bidwell, M.T., Harner, M.J., Baasch, D.M. & Harrell, W. (2020). Heterogeneity in migration strategies of Whooping Cranes. *Ornithological Applications*, 122(1): 1-15.

Pedersen, L., Jackson, K., Thorup, K. & Tøttrup, A.P. (2018). Full-year tracking suggest endogenous control of migration timing in a long-distance migratory songbird. *Behavioural Ecology and Sociobiology*, 72(8): 139.

Petersen, M.R. (1992). Reproductive ecology of emperor geese: annual and individual variation in nesting. *The Condor*, 94(2): 383-397.

Phillips, R.A., Silk, J.R.D., Croxall, J.P., Afanasyev, V. & Bennett, V.J. (2005). Summer distribution and migration of nonbreeding albatrosses: individual consistencies and implications for conservation. *Ecology*, 86: 2386-2396.

Potti, J. (1998). Arrival time from spring migration in male Pied flycatchers: individual consistency and familial resemblance*.* *The Condor*, 100(4): 702-708.

Ramírez, I., Paiva, V.H., Fagundes, I., Menezes, D., Silva, I., Ceia, F.R., Phillips, R.A. & Garthe, S. (2016). Conservation implications of consistent foraging and trophic ecology in a rare petrel species. *Animal Conservation*, 19(2): 139-152.

Rees, E.C. (1989). Consistency in the timing of migration for individual Bewick's swans. *Animal Behaviour*, 38(3): 384-393.

Rotics, S., Kaatz, M., Turjeman, S., Zurell, D., Wikelski, M., Sapir, N., Egger, U., Fiedler, W., Jeltsch, F. & Nathan, R. (2018). Early arrival at breeding grounds: Causes, costs and a trade-off with overwintering latitude. *Journal of Animal Ecology*, 87: 1627-1638.

Ruthrauff, D.R., Tibbitts, T.L. & Gill, R.E. (2019). Flexible timing of annual movements across consistently used sites by Marbled godwits breeding in Alaska*.* *The Auk*, 136(1): 1-11.

Stanley, C.Q., MacPherson, M., Fraser, K.C., McKinnon, E.A. & Stutchbury, B.J.M. (2012). Repeat tracking of individual songbirds reveals consistent migration timing but flexibility in route. *PLoS ONE*, 7: e40688.

Studds, C.E. & Marra, P.P. (2011). Rainfall-induced changes in food availability modify the spring departure programme of a migratory bird. *Proceedings of the Royal Society B: Biological Sciences*, 278: 3437-3443.

Tedeschi, A., Sorrenti, M., Bottazzo, M., Spagnesi, M., Telletxea, I., Ibàñez, R., Tormen, N., De Pascalis, D., Guidolin, L. & Rubolini, D. (2019). Inter-individual variation and consistency of migratory behaviour in the Eurasian woodcock. *Current Zoology*, 66: 155-163.

van Wijk, R.E., Bauer, S. & Schaub, M. (2016). Repeatability of individual migration routes, wintering sites, and timing in a long-distance migrant bird. *Ecology and Evolution*, 6: 8679-8685.

Vardanis, Y., Nilsson, J.A., Klaassen, R.H.G., Strandberg, R. & Alerstam, T. (2016). Consistency in long-distance bird migration: contrasting patterns in time and space for two raptors. *Animal Behaviour*, 113: 117-187.

Verhoeven, M.A., Loonstra, A.J., Senner, N.R., McBride, A.D., Both, C. & Piersma, T. (2019). Variation from an unknown source: large inter-individual differences in migrating black-tailed godwits. *Frontiers in Ecology and Evolution*, 7: 1-9.

Watson, J.W. & Keren, I.N. (2019). Repeatability in migration of Ferruginous Hawks (*Buteo regalis*) and implications for nomadism. *The Wilson Journal of Ornithology*, 131(3): 561-570.

Wellbrock, A.H.J., Bauch, C., Rozman, J. & Witte, K. (2017). 'Same procedure as last year?' Repeatedly tracked swifts show individual consistency in migration pattern in successive years. *Journal of Avian Biology*, 48: 897-903.

Whelan, S., Hatch, S.A., Irons, D.B., McKnight, A. & Elliott, K.H. (2020). Increased summer food supply decreases non-breeding movement in black-legged kittiwakes. *Biology Letters*, 16: 20190725.

Yamamoto, T., Takahashi, A., Sato, K., Oka, N., Yamamoto, M. & Trathan, P.N. (2014). Individual consistency in migratory behaviour of a pelagic seabird. *Behaviour*, 151: 683-701.

Chapter 3

Individual consistency in migration strategies of a tropical seabird, the Round Island petrel

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Individual consistency in migration strategies of a tropical seabird, the Round Island petrel

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Abstract

Background: In migratory species, the extent of within- and between-individual variation in migratory strategies can influence potential rates and directions of responses to environmental changes. Quantifying this variation requires tracking of many individuals on repeated migratory journeys. At temperate and higher latitudes, low levels of within-individual variation in migratory behaviours are common and may reflect repeated use of predictable resources in these seasonally-structured environments. However, variation in migratory behaviours in the tropics, where seasonal predictability of food resources can be weaker, remains largely unknown.

Methods: Round Island petrels (*Pterodroma* sp.) are tropical, pelagic seabirds that breed all year round and perform long-distance migrations. Using multi-year geolocator tracking data from 62 individuals between 2009 and 2018, we quantify levels of within- and between-individual variation in non-breeding distributions and timings.

Results: We found striking levels of between-individual variation in at-sea movements and timings, with non-breeding migrations to different areas occurring across much of the Indian Ocean and throughout the whole year. Despite this, repeat-tracking of individual petrels revealed remarkably high levels of spatial and temporal consistency in within-individual migratory behaviour, particularly for petrels that departed at similar times in different years and for those departing in the austral summer. However, while the same areas were used by individuals in different years, they were not necessarily used at the same times during the non-breeding period.

Conclusions: Even in tropical systems with huge ranges of migratory routes and timings, our results suggest benefits of consistency in individual migratory behaviours. Identifying the factors that drive and maintain between-individual variation in migratory behaviour, and the consequences for breeding success and survival, will be key to understanding the consequences of environmental change across migratory ranges.

Keywords: annual cycle, geolocator, flexibility, individual variation, non-breeding period, *Pterodroma*, repeatability

Introduction

Rapid changes in environmental conditions are affecting ecosystems, communities and species worldwide (Walther et al., 2002). For migratory species that are dependent upon the availability of habitats, resources and conditions in multiple locations across migratory ranges, differing rates of change in these areas can greatly increase the potential for deleterious impacts at some point in the annual cycle (Robinson et al., 2009). Consequently, species lacking variability and flexibility in their migratory traits which might facilitate responses to changing environmental conditions could be at a disadvantage (Gilroy et al., 2016). For example, among European breeding birds, species which have shown little or no phenological change in recent decades tend to also be those that are currently in population decline (Møller et al., 2008). In order to identify potential constraints on migratory species' responses to environmental change, we therefore need to understand variability and flexibility in migratory behaviour.

Recent advances in remote tracking technology have facilitated numerous studies following the movements of birds across multiple annual cycles (López-López, 2016). These repeated measures of individuals allow investigation of spatiotemporal consistency (or, conversely, flexibility) in migration strategies within and among individuals (e.g., Brown et al., 2021; McFarlane Tranquilla et al., 2014). As a result, there are now many avian studies which have investigated individual consistency in migratory timings (reviewed in Chapter 2; Both et al., 2016), and non-breeding locations (Delord et al., 2019; Phillips et al., 2005) and, more recently, year-to-year fidelity in migratory routes (van Bemmelen et al., 2017) and stopovers (Brown et al., 2021; Hasselquist et al., 2017). Most studies have revealed high individual time- (Gill et al., 2014) and site-fidelity across years (Grist et al., 2014), with variation existing between individuals. However, some studies have also recorded individuals changing migratory behaviours between years (Dias et al., 2011; McFarlane Tranquilla et al., 2014). The occurrence and persistence of individual consistency in migratory behaviour may have emerged as a result of spatial and temporal predictability of resource availability (McNamara & Dall, 2010), with familiarity of conditions at known locations and times being more beneficial than trying to locate optimal conditions at any given time (Brown et al., 2021; Winger et al., 2018). Predictable resource distributions might therefore be expected to result in low within-individual variation in space and time across years, and resource landscapes that are heterogeneous and predictable might be expected to result in between-individual variation and within-individual consistency (Abrahms et al., 2019). By contrast, migratory species in environments in which resources are less predictable in space and time might be expected to show higher levels of within-individual flexibility. As most tracking studies have been conducted on species breeding at temperate and higher latitudes, levels of migratory consistency in less seasonal and unpredictable environments, such as tropical systems, remains unclear (Chapter 2; Ceia & Ramos, 2015).

Seabirds wintering in temperate and polar regions often associate with physical oceanographic features, such as oceanic fronts, shelf and ice edges or upwellings. These features, along with seasonal temperature and salinity gradients, tend to lead to temporally and spatially predictable prey aggregations (Wakefield et al., 2009). Individual birds in these systems tend to have predictable migrations to one or more of these high-productivity ocean areas and show high levels of migration fidelity between years (e.g., Phillips et al., 2005). By contrast, large areas of tropical oceans are often considered low in productivity and prey abundance, and have less marked seasonal variation in temperature, making prey aggregations unpredictable (Weimerskirch, 2007; but see Kumar et al., 2009). Seabirds foraging at lower latitudes also often rely on subsurface marine predators, such as dolphin and tuna, that drive prey to the surface (Au & Pitman, 1986; Jaquemet et al., 2004; Spear et al., 2001), and these events are likely to be less predictable than static oceanographic variables related to marine productivity. Non-breeding migrations of tropical species may therefore be less predictable both within- and between-individuals. However, only a very restricted number of studies have tracked individual tropical seabirds on multiple migrations (Jaeger et al., 2017; Pinet et al., 2011), and typically in such small sample sizes that quantifying within-individual variability has not yet been possible. So far for tropical seabirds, studies have mainly focused on variation in behaviours at breeding grounds, when individuals are constrained to a central location, and have revealed no consistent patterns in foraging site-fidelity (Cerveira et al., 2020; Oppel et al., 2017). Consequently, it remains unclear whether consistent individual migratory behaviours occur in less predictable, tropical environments.

We addressed these questions using a tropical, pelagic seabird, the Round Island petrel, as a model species. This population of gadfly petrels (genus *Pterodroma*) breeds all-year round on Round Island, Mauritius, in the western Indian Ocean, and has been the focus of a long-term geolocator tracking project (Nicoll et al., 2017). The mid-ocean location of Round Island means that petrel migrations could potentially occur in any compass direction and for a huge range of distances. Here we estimate how repeatable individual Round Island petrels are in their migratory timings (arrival to and departure from Round Island), and migration duration (time away from Round Island). We then use the earth mover's distance (EMD), an algorithm originally developed for image comparison (Rubner et al., 2000) and subsequently adapted to quantify similarity between spatial distributions (Kranstauber et al., 2017), to quantify a) spatial consistency of petrel migrations across the entire non-breeding distribution, and b) whether individuals consistently occur in the same locations at the same stages (~monthly) of their migration schedules.

Methods

Study site and species

This study was carried out at Round Island Nature Reserve (19.85° S, 57.78° E), a 219-ha island situated 22.5 km off the North coast of mainland Mauritius. The climate of Mauritius and the surrounding ocean is strongly seasonal and can be divided into two broad seasons: the austral winter (hereafter 'winter'), and the austral summer (hereafter 'summer'). The former typically runs from May to September and the latter from October to April, which reflects the influence of the monsoon circulation of the Indian Ocean (Schott & McCreary, 2001). Round Island is the only confirmed colony in the Indian Ocean of an unusual population of *Pterodroma* petrels, known as the Round Island petrel. Genetic evidence has shown this population to comprise at least three species of *Pterodroma* petrel (Trindade petrel, *P. arminjoniana*, Kermadec petrel*, P. neglecta* and Herald petrel, *P. heraldica*), which breed and extensively hybridise on the island (Booth Jones et al., 2017; Brown et al., 2010; Brown et al., 2011; Tatayah, 2007; Tatayah, 2010). Round Island petrels nest on the ground, typically under rock ledges or among piles of boulders. Eggs and chicks can be present in any month of the year, although there is a peak in egg-laying in August-October (Tatayah, 2010). As petrel breeding activity is typically lowest on the island in May each year, we selected 1 June as the start of the petrel breeding calendar and numbered days sequentially from this origin (Nicoll et al., 2017).

Geolocator deployment

Petrel surveys have been undertaken monthly since 2001, and involve regular visits to known nesting areas, ringing of adults and chicks (with South African Bird Ringing Unit numbered rings), and their subsequent recapture. Between 2009 and 2016, 421 light-level geolocators (GLS) were deployed on adult petrels. GLS were attached to the tarsus via a 1 or 0.75 mm thick Salbex (an industrial grade PVC; Sallu Plastics, Redditch, UK) colour-ring. Between 2009 and 2012, MK15 British Antarctic Survey geolocators (Cambridge, UK) were deployed, and during 2014 and 2016, Intigeo C250 and Intigeo C330 (Migrate Technology, Cambridge, UK) were deployed. The total device weight (including plastic ring) across all three tag types amounted to 3.6 - 3.9 g, which represents approximately 1.0% of the mean body mass of adult petrels (374 g). For the first three deployment periods, the tagged petrels were caught during targeted searches, whereas later GLS deployments occurred during the standard monthly petrel breeding surveys; these birds were predominantly resting on the island and not directly observed in a breeding attempt. Loggers were opportunistically recovered a minimum of one year later, during breeding surveys or during occasional specific searches. All loggers underwent a 3- to 5-day calibration period at a known location (Round Island, or mainland Mauritius (20.25° S, 57.44° E)) pre- and post- deployment. Details of the numbers of tags deployed and recovered until the end of December 2019 are provided in Table S3.1.

Geolocation data processing

At-sea locations for each individual were estimated from raw light-level data using the threshold method of estimating positions based on twilight events (i.e., sunrise and sunset transitions; Lisovski et al., 2012). Twilight events were defined using the preprocessLight function in the R package TwGeos (Lisovski et al., 2016) using a light intensity threshold of 4 and 1, for MK15 and Intigeo tags, respectively. The corresponding zenith angle was defined separately for each tag from the sunrise and sunset times recorded during the pre-deployment calibration period (range of 94.0° to 96.9° for MK15 tags and 96.8° to 99.0° for Intigeo tags). A Bayesian framework was used to refine the initial positions estimated from the threshold method and to derive uncertainty estimates. The R package SGAT (Wotherspoon et al., 2013) uses Markov Chain Monte Carlo (MCMC) simulations allowing the incorporation of: 1) a spatial probability mask, 2) sea-surface temperatures (SST) recorded by the tag in relation to global remote sensed SST maps, 3) prior definition of the error distribution of twilight events (twilight model) and 4) a flight speed distribution (behavioural model), to refine location estimates. The twilight model should reflect the expected error in detecting the real time of sunrise and sunset. Since the petrels spend a substantial amount of time sitting when at the breeding site (obscuring the light sensor) and can travel many hundreds of kilometres when still associated with the island, we could not use twilight times from a known location (i.e., Round Island) to parameterise the twilight model. We therefore used a rather conservative prior (log-normal distribution: meanlog = 2.2, sdlog = 1.0) describing a large variation in the discrepancy between the real and recorded twilight events. The spatial probability mask was constructed on the premise that birds only use marine environments when away from the colony (probability of 0 for positions on land). The probability at sea was further refined for each individual using remotely sensed sea-surface temperatures (weekly means on a 1.0° × 1.0° resolution downloaded from NOAA's Optimum Interpolation Sea Surface Temperature V2 dataset: https://www.esrl.noaa.gov/psd/data/gridded/data.noaa.oisst.v2.html) and the SST values recorded by the loggers. The potential flight speeds were modelled following a gamma distribution (shape = 2.0, rate = 0.1). For each individual, we used these parameters and started by drawing an initial 2000 samples for burn-in and tuning of the proposal distribution using a modified model with relaxed assumptions. Then a further 300 samples were drawn three times to evaluate chain convergence before drawing another 3,000 samples to describe the posterior distribution. Tracks were summarised to produce median tracks and 95% credible intervals.

Migratory timings

To identify the start and end dates of migration from GLS data, each day of GLS tracking was classified as one of two behavioural states (ashore on Round Island or at-sea) using a hidden Markov model (HMM). HMMs are a type of state-space model, which decompose observed time-series data into an observed sequence of discrete behavioural states. Behaviours were classified as either ashore or at-sea from the proportion of light interference during core daylight hours, the sum of daily wet records, and the distance from Round Island, using the R package depmixS4 (Visser & Speekenbrink, 2010). These variables were chosen as when petrels are frequenting the colony, we expect; 1) a high degree of shading of the tag as individuals are sitting, 2) longer periods without immersion, and 3) petrels to remain close to the colony. Distance from colony (km) was derived from the SGAT processed median location estimates and calculated using the distGeo function in the R package geosphere (Hijmans, 2019), whereas light and immersion data were from the respective raw GLS files. All GLS models sampled light every minute and logged the maximum light recorded at 10-minute intervals. To calculate light interference, we used the twilight times defined from the preprocessLight function to select out light recordings during daylight hours only. In contrast to the MK15 GLS, which record only low light levels, Intigeo GLS record the entire light range. Therefore, light samples with values of less than 64 or less than 100 were classed as interference for MK15 and Intigeo, respectively. Due to the different number of light samples that fall within each daylight period, this variable was calculated as the proportion of light samples with interference for each calendar day. GLS tested for saltwater immersion every 3 or every 30 seconds and stored the sum of positive tests at 10-minute intervals, resulting in values between 0 (entirely dry), and 200 or 20 (entirely wet), for the MK15 and Intigeo GLS, respectively. The sum of these 144 values (number of 10-minute periods in 24-hours) were calculated for each calendar day. A Gaussian distribution was used to describe both distance from Round Island and immersion data, and a binomial distribution to describe light interference. Migration periods were defined as a sequence of consecutive days that were assigned to the same behaviour (at-sea) by the HMM for a period of at least three months, before switching to the other behavioural state (ashore). The duration of the migratory period was calculated using these dates.

Spatial consistency

To investigate consistency in migratory locations within- and between-individuals, we used the median locations identified as the migration period from the HMM in combination with the earth mover's distance (EMD; Kranstauber et al., 2017) to create a matrix of space-use similarity estimates. In contrast to spatial overlap indices (where distributions with no spatial overlap have the same similarity value irrespective of their distance from one another), the EMD integrates a measure of spatial proximity in the similarity between different space-use distributions, by calculating the effort it takes to transform, for example, one migration track into another. EMD 'effort' values are therefore on a continuous scale, starting at zero for two identical migrations and increase with increasing dissimilarity. EMD was calculated for all petrel and year combinations, using Haversine distance with the 'emd' function in the R package move (Kranstauber et al., 2020), using geographical coordinates directly as inputs.

In order to show how EMD relates to a widely used method for quantifying home range overlap, we also calculated relative overlap of petrel migrations using Bhattacharyya's affinity (BA; Fieberg & Kochanny, 2005). BA estimates range between 0 (no overlap) to 1 (identical distributions) and therefore do not quantify how dissimilar migratory distributions are if they do not overlap. For each individual and year, migratory locations were used to generate kernel utilisation distributions (UDs) using the R package adehabitatHR (Calenge, 2006). A fixed smoothing parameter (*h*) of 200 km was used to account for precision error around location estimates (Phillips et al., 2004). BA was calculated between all possible paired combinations of petrel UDs using the 'kerneloverlap' function the R package adehabitatHR. This analysis was carried out in a Lambert azimuthal equal-area projection centred on the centroid of all positions. By comparing with BA, we were also able to investigate the impact of any scale-dependence on our analyses of EMD. As EMD is an absolute metric, individuals covering large migratory distances have greater capacity to differ and are thus more likely to generate large EMD values.

To investigate the spatiotemporal similarity of the same individual's migrations in different years, two different approaches were used to define time: each petrel's migrations was split into (1) 30-day periods irrespective of the migration start date (Fig. S3.1a), meaning that a short period of time may be excluded for within-individual migrations of different durations; and into (2) six stages of equal duration (average of 29.4 days ± 4.7 SD; Fig. S3.1b), meaning that the corresponding within-individual stage between migrations may be of a different length but in total spans the whole migratory period. EMD values were calculated for within-individual migrations for the same 30-day period/stage only (i.e., comparing the first 30-day period/stage of the first migration to the first 30-day period/stage of the second migration etc.), using the same method as described above.

Statistical analysis

Repeatability (R) of (a) arrival to, (b) departure from Round Island and (c) migration duration were each estimated in a mixed-effects model framework, using 1,000 bootstrap iterations to estimate confidence intervals (CIs), with the R package rptR (Stoffel et al., 2017). Arrival and departure dates were recorded as days from 1 June; individuals with consecutive migrations spanning 1 June, (e.g., arriving on 30 May (day 364) in year one, and 2 June (day 2) in year two, had the first date converted to a negative day value to overcome the circular nature of this variable (the inclusion or exclusion of negative values had no significant impact on the estimated repeatability values)). All three models were fitted with a Gaussian error family and included ‘individual identity’ as a random effect.

To investigate whether petrels arriving/departing in the different seasons differ in their levels of variability in migratory timings, the number of days between the earliest and latest date for each individual (i.e., within-individual variation) was calculated separately for arrival and departure dates, for petrels which consistently arrived or departed in either the summer or winter only. These values were included as the response variable in generalised linear models (GLMs) with gamma error family and log link function for arrival and departure dates separately, with season as a fixed effect.

To quantify spatial repeatability in individual petrel migrations and whether this varied with differences in departure timing, the EMD values comparing whole petrel migrations were included as the response variable in a GLM with the binary factor ‘same individual’ (0 as ‘no’ and 1 as ‘yes’), and the difference in days between the compared individuals’ departure dates from Round Island as fixed factors. An interaction between ‘same individual’ and difference in departure dates was also included. A significantly negative coefficient for the ‘same individual’ classification would indicate higher overlap (i.e., greater spatial similarity) within-individuals than between-individuals. The EMD values were continuous, non-negative and right-skewed; therefore, a gamma error family and identity link function were used. To examine if scale-dependence in EMD influenced these findings, we ran a second GLM with binomial error family and log link function with the same fixed factors, but this time with the BA values as the response variable.

To investigate within-individual consistency in distribution at different stages during the migration period, GLMs with gamma error family and identity link function were run with EMD values for each (a) stage or (b) period as the response variable, and difference in days between departure dates, and stage/period of migration (categorical variable including a level for whole migration) as fixed factors. An interaction between the two fixed factors was also included, to explore whether similar departure timing between years results in more consistent use of the same locations at the same time in each year. For all models, non-significant ($p < 0.05$) terms were sequentially removed using backwards stepwise deletion and significance of terms was determined using ANOVA. Pairwise comparisons among levels were calculated based on estimated marginal means and adjusted using post-hoc Tukey correction using the R package emmeans (Lenth, 2021). All analyses were conducted using R version 3.6.2 (R Core Team, 2019).

Results

A total of 337 retrieved GLS loggers provided data on 267 complete migration tracks of 198 Round Island petrel individuals between 2009 and 2019 (Table S3.1). This includes repeated tracking of the same individuals providing complete migration tracks during two (n = 57), three (n = 3) or four (n = 2) migratory periods. The five individuals with three or four migratory periods were a result of two separate non-consecutive GLS deployments, rather than birds evading capture for multiple years following deployment. These tracks provided arrival dates over a period of 2 to 4 years, and migration durations for up to 4 years, for 62 petrels. Due to logger failure during deployment, partial data recovery was possible for a number of GLS devices, providing a total of 76 petrels with between 2 and 5 departure dates from Round Island (Table 3.1).

Timing of migration

GLS tracking of sampled individuals covered departure and arrival dates of petrel migrations spanning all months. Repeated tracking of individual petrels indicated a much higher degree of consistency within- than between-individuals in all three migratory timings (arrival to, and departure from Round Island, and migration duration), with individual arrival dates to Round Island being the most repeatable (Fig. 3.1; Table 3.1). This repeatability was consistent across all years of the study period (Fig. 3.1). Although significantly repeatable, there is some variation within-individuals (median difference between latest and earliest departure date for each individual = 56 days (range 1-240 days) and for arrival = 47 days (range 2–220 days)), and individuals with a larger departure date range were also more likely to have a larger arrival date range (Pearson's correlation: $r = 0.64$, $t = 6.38$, $df = 60$, $p < 0.0001$). This within-individual repeatability in arrival and departure also differed between the two seasons which petrels arrived and departed, with the 17 birds departing in the winter (i.e. off-peak breeding period) having significantly higher within-individual variation than the 39 departing in the summer (i.e. peak breeding period, GLM: adjusted $R^2 = 0.25$, $\beta = 0.79$, $SE = 0.23$, $t = 6.55$, $p < 0.001$), and the 10 birds arriving in the summer, having significantly higher within-individual variation than the 37 arriving in the winter (GLM: adjusted $R^2 = 0.48$, $\beta = 56.21$, $SE = 8.58$, $t = 6.55$, $p < 0.0001$).

Migration durations of the 131 tracks (from the 62 repeatedly tracked petrels) lasted on average 175 days ± 28 SE (range: 104-256 days). Despite a lower repeatability value for migration duration (Table 3.1), individuals showed relatively small mean individual ranges (difference between the largest and smallest record for each individual, in days; 22.8 ± 19.6 SD), highlighting that this low *R* value may reflect relatively low variance in migration duration among individuals. The variance components for each of the repeatability estimates can be found in Table S3.8.

Table 3.1. Repeatability estimates (*R*) from adult Round Island petrels with repeated tracks (2-5 years) for departure date from the breeding colony, arrival at the colony and duration of the migratory period. Given are the number of individuals (N_{ind}), number of migratory tracks (N_{rep}), lower and upper 95% CIs, and p-values. Significant effects ($p < 0.05$) are highlighted in bold.

	N_{ind}/N_{rep}	*R*	Lower CI	Upper CI	P value
Departure date	76/169	0.7872	0.696	0.852	**< 0.001**
Arrival date	62/131	0.813	0.715	0.883	**< 0.001**
Duration	62/131	0.465	0.251	0.630	**< 0.001**

Spatial consistency in migratory journeys

Round Island petrels showed striking levels of between-individual variation in migratory journeys, with individuals undertaking non-breeding migrations to different areas across much of the Indian Ocean north of ~35°S (Fig. 3.2, Fig. S3.2). Most birds migrated north to the Somali Basin and further into the Arabian Sea, or east across the central Indian Ocean between 10 and 20°S. Comparatively few travelled into the Bay of Bengal or Western Australian Basin, but all petrels largely avoided nearshore/shelf waters (Fig. 3.2, Fig. S3.2). Despite this large between-individual spatial variation, repeated tracking of individual petrels for up to 4 years indicates remarkably high levels of spatial consistency (Figs. 3.2, 3.3), with within-individual petrel migrations being significantly more similar than between-individual migrations (Figs. 3.3, 3.4a; Table 3.2, Table S3.2). EMD values for within-individual petrel migration comparisons ranged from 156.0 – 1618.7 compared to a range of 226.4 – 5419.0 for between-individual migrations (Figs. 3.3, 3.4a). The highest EMD value of 5419.0 indicates, in this case, the difference between individuals travelling north to the Arabian Sea versus east to the Western Australian Basin (Fig. 3.3f). The relative overlap of this pair of migrations when calculated using BA revealed a very low overlap of 0.06 (Fig. S3.3a). However, as BA does not take into account the spatial distance between migrations, the same BA value can be observed across a range of EMD values, which represent paired migrations that are relatively close together in space (EMD = 2090.8; Fig. S3.3c) or far apart (EMD = 5419.0; Fig. S3.3a).

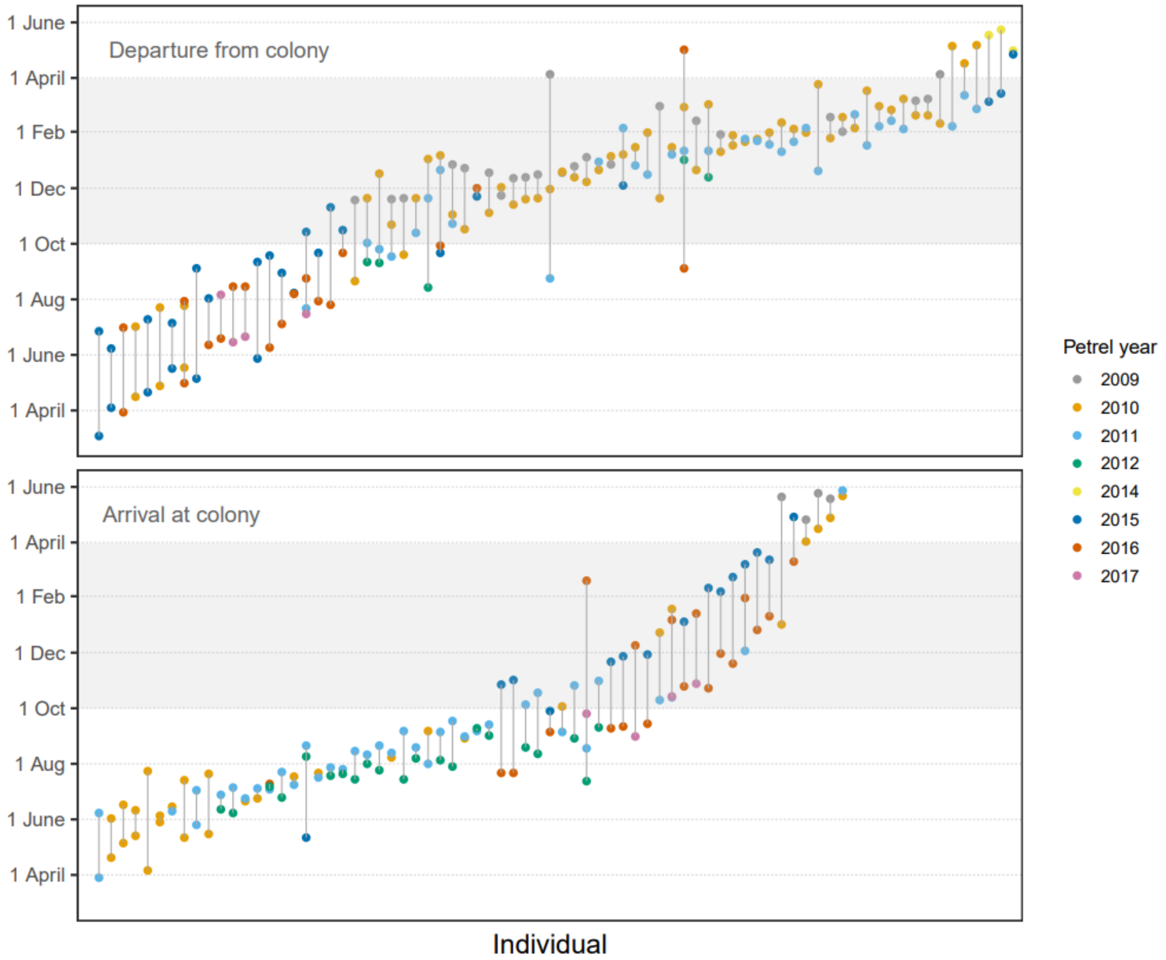

Figure 3.1. Dates of migration departure and arrival to/from the breeding colony (Round Island) of adult Round Island petrels tracked for more than one migration. Dates of the same individual are connected by vertical lines, and individuals are ordered from left to right by increasing mean date for departure and arrival, separately (therefore, individual one for departure is not the same as individual one for arrival). Filled circles are coloured by the petrel year (i.e., 2009 = 2009/2010) in which the departure or arrival took place. Grey shaded areas represent the austral summer.

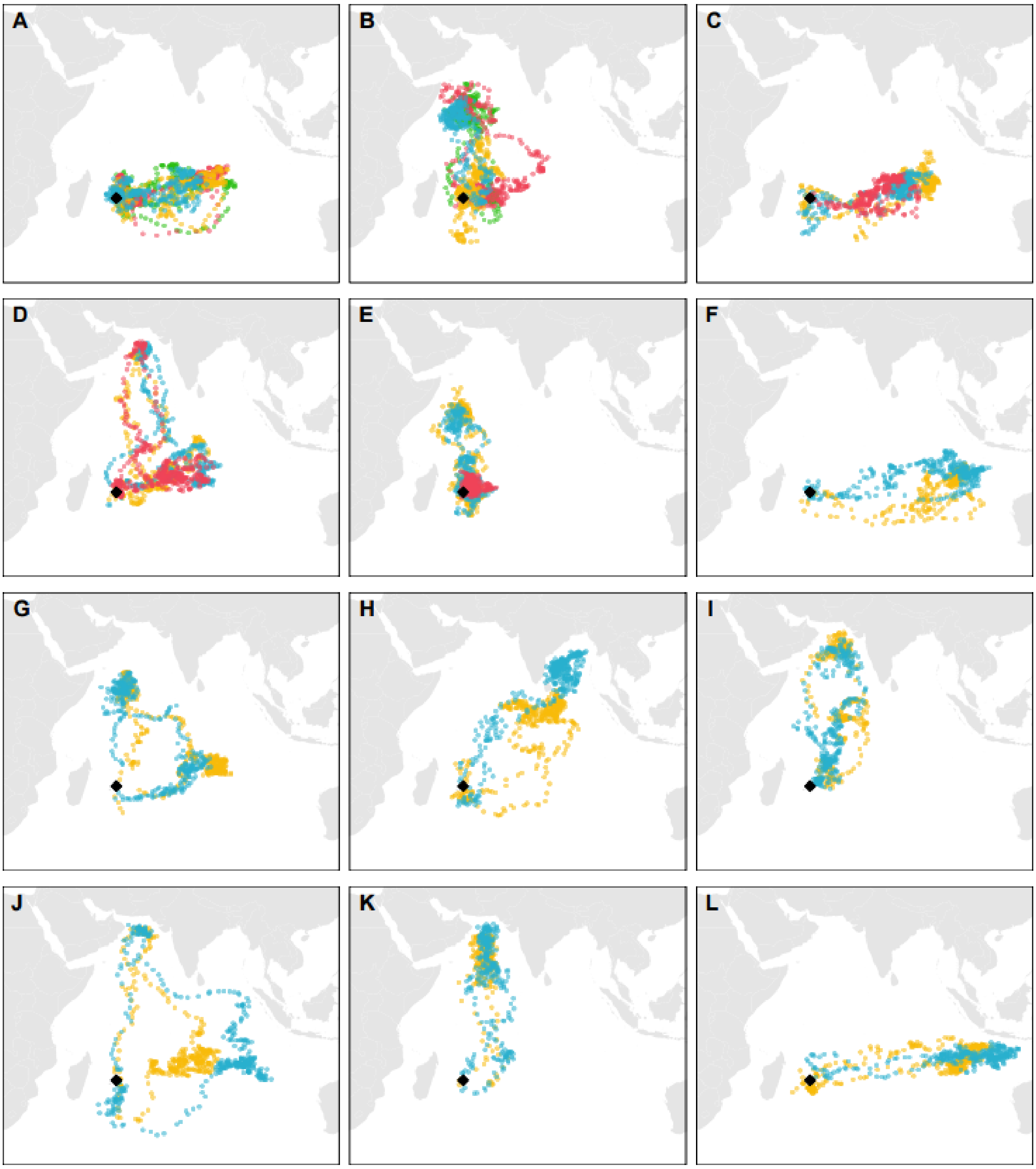

Figure 3.2. Example tracks of 12 individual Round Island petrels that have been tracked with geolocators over four (A, B), three (C-E), or two (F-L) migrations. Positions denote twice-daily median locations with different years illustrated in different colours. Black diamond indicates the location of Round Island, Mauritius. The tracking year that each set of colours represents can be found in Table S3.7. Note that positions often overlap between years and hence might be partly obscured.

Within-individual spatial consistency was also significantly higher for individuals that departed Round Island at more similar times in each year (Fig.

3.4b; Table 3.2, Table S3.2). However, this effect is very small in comparison to the large amount of variation in EMD values across the range of differences in departure timing (R2 = 0.020; Fig. 3.4). There was no significant interaction between ‘same individual’ and difference in departure dates meaning that the greater similarity of migratory ranges for birds departing at similar times applies both within- and between- individuals (Table S3.2). Overall, comparison with the BA analysis showed both methods yielded broadly consistent results suggesting any scale-dependence in EMD values does not vary systematically in relation to difference in departure date, and thus does not affect our conclusions (Tables S3.2, S3.3).

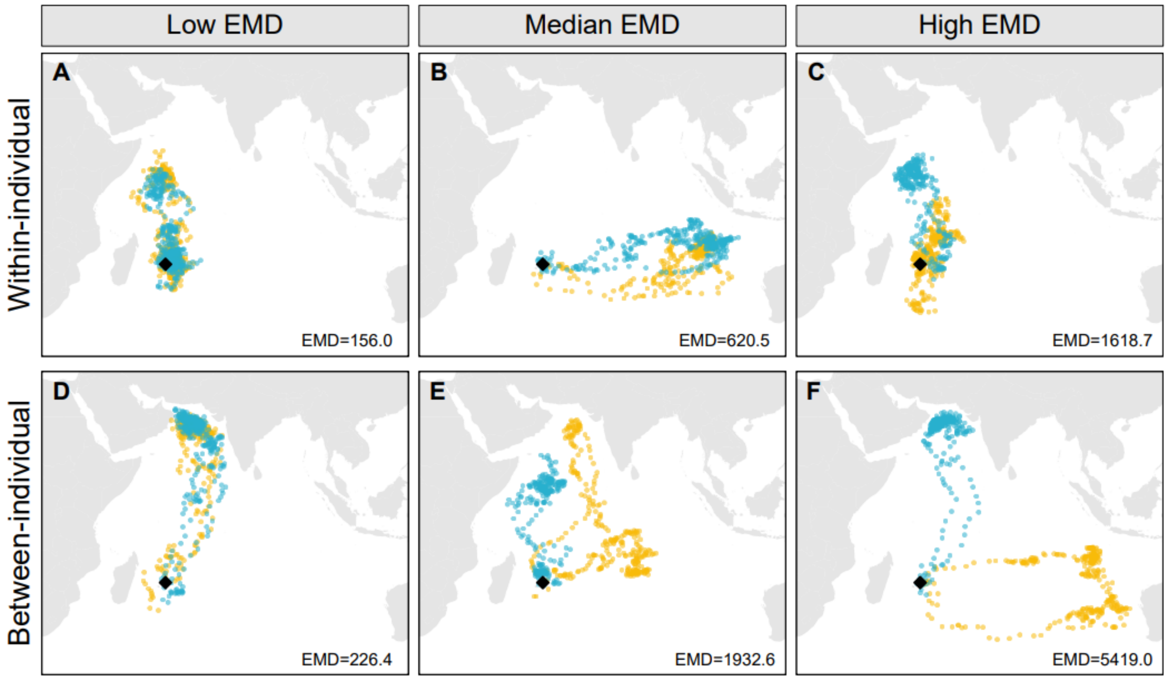

Figure 3.3. Example tracks of Round Island petrels with low (A, D), moderate (B, E), and high (C, F) within-individual (A-C) and between-individual (D-F) earth mover’s distance (EMD) migration comparisons. Moderate EMD values are based on the median values for within- and between-individual migration comparisons separately. Positions denote twice-daily median locations with the two different years illustrated in different colours. Black diamond indicates the location of Round Island, Mauritius. The tracking year that each set of colours represents can be found in Table S3.7.

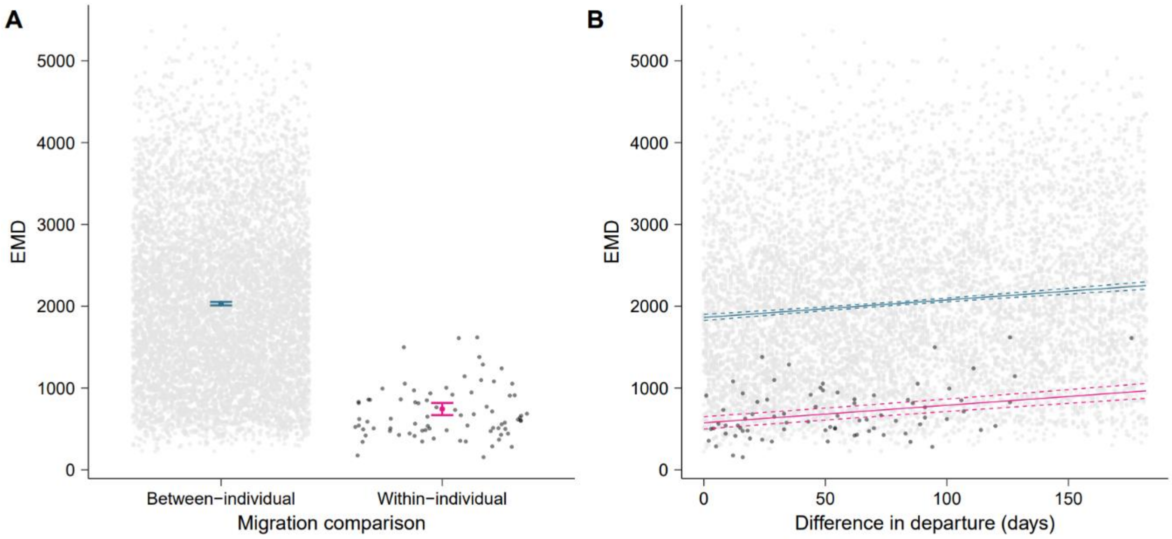

Figure 3.4. Predicted earth mover's distance (EMD) values (lower values indicate more similar migrations) from a generalised linear model (GLM) of A) between- and within-individual migration comparisons (error bars ± 95% confidence intervals), and B) the difference in departure timing (fitted lines ± 95% confidence intervals). Pink (within-individual) and blue (between-individual) estimates are from GLM and raw data (filled circles) are shown for within- (black) and between-individual (grey) EMD values, separately. Model predictions for A) are based on the median value for difference in departure of 79 days.

Despite high within-individual consistency in entire migratory journeys, individual Round Island petrels do not always use the same at-sea locations at the same stage or period within their migratory journeys. EMD values calculated for each stage/period of each petrel's migrations were slightly, but significantly, higher than the EMD values for the whole migration (Fig. 3.5; Table 3.2, S3.2, S3.4-3.6). These differences in the EMD values across stages/periods are not a result of individuals departing later or earlier in one migration compared to the other, as there was no significant interaction between stage/period and the difference in departure dates between years. Nonetheless, the overall pattern of petrels that departed Round Island at more similar times of year having more similar migrations still exists (Table 3.2).

Table 3.2. Results of generalised linear models to investigate a) the similarity of petrel whole migrations within- and between-individuals and b) the spatiotemporal similarity of within-individual petrel migrations when split into six equal stages, using earth mover's distance (EMD) 'effort' values. Minimum adequate models are shown and categorical variables are being compared to reference levels; for the 'same individual' binary variable, this is 0 (different individuals), and for 'stage', this is the whole migration. Significant effects ($p < 0.05$) are highlighted in bold.

Variable	**Estimate ± SE**	***t* value**	**P value**
a. Whole migration EMD comparisons ($R^2 = 0.020$)			
(Intercept)	1862.17 ± 19.17	97.14	< 0.001
1 (Same individual)	-1287.08 ± 39.38	-32.69	< 0.001
Difference in departure	2.15 ± 0.20	10.60	< 0.001
b. Six stage EMD comparisons* ($R^2 = 0.061$)			
(Intercept)	500.51 ± 62.80	8.0	< 0.001
Stage (1)	234.33 ± 90.04	2.6	0.01
Stage (2)	359.11 ± 98.47	3.6	< 0.001
Stage (3)	398.67 ± 101.20	3.9	< 0.001
Stage (4)	355.13 ± 98.20	3.6	< 0.001
Stage (5)	448.60 ± 104.67	4.3	< 0.001
Stage (6)	543.29 ± 111.35	4.9	< 0.001
Difference in departure	3.94 ± 0.84	4.7	< 0.001

* The full pairwise comparisons for the categorical variable 'stage' can be found in Table S4.

Discussion

Tropical, migratory Round Island petrels have striking levels of between-individual variation in at-sea movement patterns, with individuals undertaking migrations across much of the Indian Ocean and throughout the whole year. However, repeat tracking of individuals across the non-breeding period revealed very little within-individual variation, with migratory journeys being remarkably consistent in both space and time.

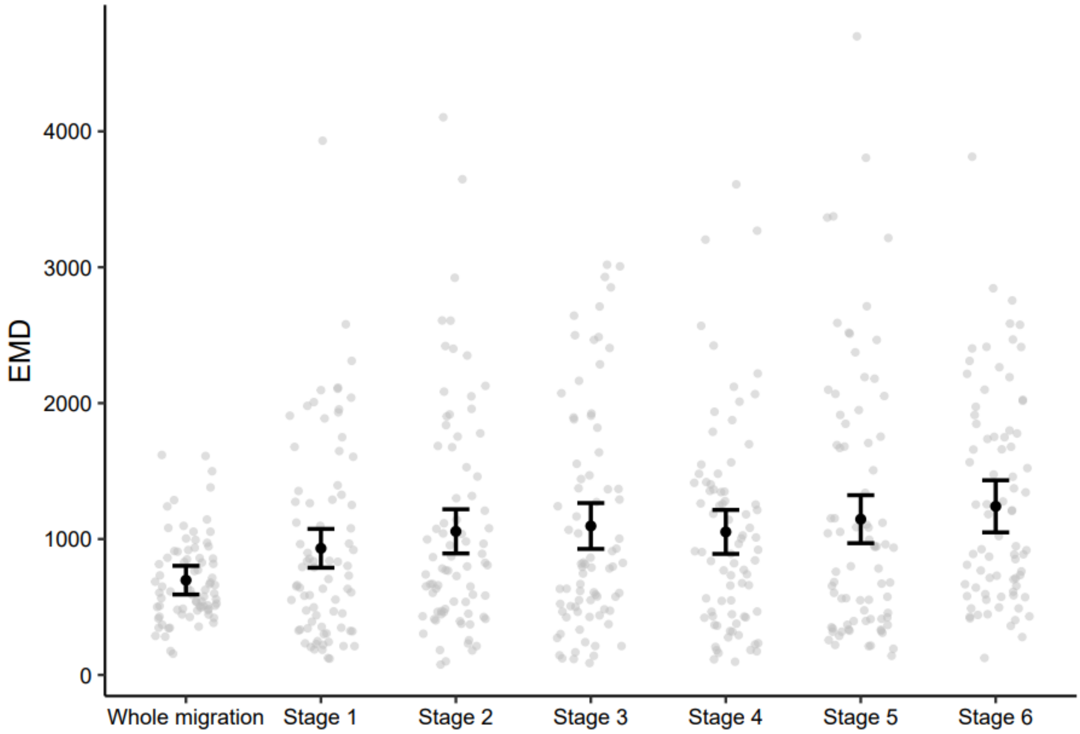

Figure 3.5. Predicted earth mover's distance (EMD) values from generalised linear model (error bars ± 95% confidence intervals) and raw data (grey circles) of within-individual migration comparisons, for whole migration comparisons, and migrations when divided into six stages of equal size. Model predictions are based on the median value (50 days) for difference in departure.

The areas frequented by Round Island petrels during migration cover much of the Indian Ocean north of ~35°S. Compared with most other studies tracking seabirds breeding in the western Indian Ocean, albeit in smaller numbers, the range of areas used by Round Island petrels during the non-breeding period is particularly large (Le Corre et al., 2012; Pinet et al., 2011). GLS tracking of sooty terns *Onychoprion fuscatus* from Bird Island, Seychelles, also revealed use of a range of different non-breeding areas, three of which (the Bay of Bengal, northeast to an area straddling the Chagos-Laccadive plateau, southeast to an area on each side of the 90 East Ridge; Jaeger et al., 2017) are also used by Round Island petrels. However, the majority of Indian Ocean seabirds for which migratory journeys have been tracked, including the closely related Barau's petrel *Pterodroma baraui*, which nests on nearby Réunion Island, tend to show consistent eastward migrations to specific areas of the central and eastern

Indian Ocean (Pinet et al., 2011). Systems with large non-breeding distributions, as seen in the Round Island petrel system, therefore provide ideal opportunities to explore the degree of within- and between-individual variation in migratory behaviour.

Although migration strategies were highly variable across the population, individuals used distinct areas within the overall range in a consistent manner across years. Individual consistency in space use has been shown for many migratory bird species, from great reed warblers *Acrocephalus arundinaceus* to Atlantic puffins *Fratercula arctica* (Guilford et al., 2011; Hasselquist et al., 2017); however, this topic has received very little attention for migratory birds breeding in the tropics (e.g., Jaeger et al., 2017). Our results suggest that familiarity with locations may be more beneficial than tracking current environmental conditions even when resources may be patchy and unpredictable, such as those in tropical systems (Ashmole, 1971; Weimerskirch, 2007). Further, the fact that individuals which depart closer together in time are likely to have more similar non-breeding distributions may suggest that the meteorological or oceanographic conditions at departure can influence individual non-breeding distributions (but see Dell'Ariccia et al., 2018). However, we also observed temporal variation in space use, with EMD values being higher (i.e., migrations were less similar) when split into stages/periods, compared to the migration as a whole. This suggests a degree of temporal flexibility, such that individuals use the same areas in different years, but not necessarily at the same time during the non-breeding period, which has also been shown for other seabirds (Merkel et al., 2020; van Bemmelen et al., 2017). This temporal flexibility therefore seems to only occur within the range of known areas for a particular individual, suggesting that relying on familiar areas is more beneficial than switching to a new location (McNamara & Dall, 2010), and implies that temporal variation in resource availability may not be very large at these scales. Additionally, gadfly petrel flying behaviour is strongly affected by wind conditions (Spear & Ainley, 1997; Ventura et al., 2020) and thus how fast petrels move through their environment may vary with the environmental conditions that they experience in each year. The EMD metric provided an effective method for measuring spatial dissimilarity in non-overlapping distributions. This is particularly valuable for systems with large, non-overlapping variation in the possible range of individual migratory distributions, such as Round Island petrels. This framework could easily be applied to other species to compare space-use patterns within and across taxa (although effects of scale-dependence may need to be considered).

Repeated tracking of individual petrels also indicated a high degree of consistency in migratory timings. This has been reported for many other species (mean ICC = 0.414 (95% confidence interval: 0.3–0.5; reviewed in Chapter 2) suggesting consistent individual differences in migration phenology to be a common feature of migratory systems. Recently, Trindade petrels breeding on Trindade Island in the South Atlantic Ocean have also shown to maintain their breeding schedules year-to-year (Leal et al., 2021). For tropical seabirds, breeding phenology can range from seasonal and synchronised breeders (e.g., Barau’s petrel; Pinet et al., 2009), to aseasonal breeders, albeit in varying numbers across the year (e.g., Round Island petrels; Tatayah, 2010). Consequently, it is important to note that repeatability of individual phenologies may be naturally inflated when a large number of viable phenologies exist in a population. Despite this, Round Island petrels were still remarkably repeatable in their migratory timings with much lower within- than between-individual variation. While the exact breeding status and/or outcome of individual petrels on Round Island is rarely known, other studies on seabirds have shown that failed breeders and non-breeders may depart earlier from their colony in comparison to successful breeders (Phillips et al., 2005; Yamamoto et al., 2014). Regardless of this, we still found high repeatability in migratory departure (although not as high as arrival) without accounting for breeding outcome (i.e., success, failure, or if breeding was attempted). Calculating repeatability in migratory timings requires consistent methods of classifying phenological events. In our study, we used HMMs in order to assign dates of arrival and departure from Round Island in an objective and reproducible manner, which was particularly important given that the low spatial resolution available from GLS tracks can make identification of departure times from location data alone problematic.

While most individuals seem to follow a consistent migratory schedule, the differing levels of within-individual variation between the seasons suggests an influence of prevailing environmental conditions on timings of departure and arrival. Petrels arriving at Round Island in the winter (which show more consistent timings of arrival) are likely to breed during the peak breeding period, and could thus experience greater competition for resources, including nest sites, than birds arriving during the summer period (which are less consistent in arrival times). Arriving at a consistent time each year may facilitate synchronous mate arrival (Gunnarsson et al., 2004), which may be particularly important if pairs are to compete for nest sites. Although the petrels nest in a range of conditions across the island, most nests occur within a relatively small number of colonies. Nesting sites within these colonies are likely to be in high demand, particularly during the peak breeding period, when broken eggs with peck marks and young chicks with head wounds are often observed (Tatayah, 2010). Observations from camera traps have also shown intra- and inter-specific fights at petrel nest sites (Franklin, pers. obs.). As the Round Island petrel is a hybrid species complex (Booth Jones et al., 2017; Brown et al., 2010; Brown et al., 2011), it means that the population comprises individuals with a great deal of genetic variation dictated by evolutionary histories. This, together with the fact that petrels have an asynchronous breeding period, means that interactions with different environmental conditions (such as the semi-annual wind reversals as a result of the two monsoon periods in the Indian Ocean; Schott & McCreary, 2001), may have given rise to the diverse range of migration patterns. However, it is not yet clear whether there is any temporal structuring in the genotypes of petrels on Round Island (i.e., are certain petrel hybrids on the island at certain times of year), or if different genotypes have different migratory distributions, which may contribute to individual phenological and spatial variation.

Conclusions

The small amount of within-individual variation suggests that consistency in migratory behaviours is favoured even in comparatively patchy and unpredictable tropical systems (Weimerskirch, 2007). This consistency, together with the fact that birds can be found breeding on Round Island all year round, means that different individuals are potentially exposed to different environmental conditions and human-associated impacts, with potentially important consequences for breeding success (e.g., Fayet et al., 2016), survival and, ultimately, the status of this population. The Round Island petrel population appears to have arisen relatively recently in time through range expansions of different *Pterodroma* taxa (Booth Jones et al., 2016; Brown et al., 2010; Brown et al., 2011). The high level of individual migratory consistency means that future changes in non-breeding distributions and timings will most likely reflect changes in the numbers of individuals undertaking different journeys. Determining what is driving the large levels of between-individual variation in this system will be key in revealing the implications of individual consistency for population demography, and the potential consequences of future environmental changes across the migratory range.

Acknowledgements

This work would not have been possible without the many staff and volunteers from the Mauritian Wildlife Foundation (MWF) and National Parks and Conservation Service (NPCS) who have helped with the Round Island petrel research programme. In particular, we would like to thank Vimul Nundlaul, Richard Baxter, Pat Banville, Katherine Booth Jones, Lucy Rouse, Helen Gath, Luke A’Bear and Johannes Chambon in facilitating the deployment and recovery of GLS on the island. We would also like to thank Stephen Vickers and Martin Stoffel for statistical advice, and the associate editor, Matthieu Le Corre and an anonymous reviewer who provided valuable feedback that greatly improved the manuscript. The main EMD analysis was conducted on the High Performance

Computing Cluster supported by the Research and Specialist Computing Support service at the University of East Anglia. KAF was funded by a John and Pat Warham PhD studentship from the British Ornithologists' Union (BOU). The petrel tracking programme was supported by the Natural Environmental Research Council (NERC; UK) (Grant NE/H5081500) and Research England. JAG was also supported by NERC (Grant NE/M012549/1).

Data accessibility

Tracking data are deposited on the Seabird Tracking database (www.seabirdtracking.org) handled by BirdLife International (ID: 1810).

R scripts to reproduce analysis can be found on Github (https://github.com/kirstyfranklin/RIpetrel-consistency).

Supplementary materials to Chapter 3: Individual consistency in migratory strategies of a tropical seabird, the Round Island petrel

Table S3.1. Details of all geolocator deployments and recoveries on adult Round Island petrels from 2009-2019, and number of complete migrations which took place in each petrel year for the 62 petrels with repeat migrations.

Petrel year	**Number deployed**	**Number recovered***	**Petrel year which migration took place**						
			2009	**2010**	**2011**	**2014**	**2015**	**2016**	**2017**
2009	135	110	20	24					
2010	84	79		24	25				
2011	28	18							
2012	79	64							
2014	49	36				3	20	6	
2015	21	15					1	5	1
2016	25	15						2	
Total	**421**	**337**	**20**	**48**	**25**	**3**	**21**	**13**	**1**

* Geolocators recovered between October 2010 and December 2019.

Table S3.2. Results of ANOVA tests for generalised linear model selection for the similarity of petrel migrations within- and between- individuals, using a) the earth mover's distance (EMD) 'effort' values, and b) Bhattacharyya's affinity (BA), and the spatiotemporal similarity of within-individual petrel migrations when split into c) six equal size stages, and d) 30-day periods, both using EMD. Significant effects ($p < 0.05$) are highlighted in bold.

Model	df	Deviance	F value	P value
a. Whole migration EMD comparisons				
EMD ~ Same individual*Difference in departure EMD ~ Same individual + Difference in departure	1	0.096	0.409	0.522
EMD ~ Same individual EMD ~ Same individual + Difference in departure	1	26.728	113.11	**< 0.001**
EMD ~ Difference in departure EMD ~ Same individual + Difference in departure	1	62.679	265.24	**< 0.001**
b. BA comparisons				
BA ~ Same individual*Difference in departure BA ~ Same individual + Difference in departure	1	0.727	0.73	0.394
BA ~ Same individual BA ~ Same individual + Difference in departure	1	22.316	22.32	**< 0.001**
BA ~ Difference in departure BA ~ Same individual + Difference in departure	1	41.415	41.42	**< 0.001**
c. Six stage EMD comparisons				
EMD ~ Stage*Difference in departure EMD ~ Stage + Difference in departure	6	2.310	0.779	0.587
EMD ~ Stage EMD ~ Stage + Difference in departure	1	11.186	22.792	**< 0.001**
EMD ~ Difference in departure EMD ~ Stage + Difference in departure	6	15.975	5.425	**< 0.001**
d. 30-day period EMD comparisons				
EMD ~ Period*Difference in departure EMD ~ Period + Difference in departure	7	4.744	1.43	0.190
EMD ~ Period EMD ~ Period + Difference in departure	1	11.977	25.23	**< 0.001**
EMD ~ Difference in departure EMD ~ Period + Difference in departure	7	16.362	4.92	**< 0.001**

Table S3.3. Results of generalised linear model to investigate the similarity of petrel whole migrations within- and between-individuals, using Bhattacharyya's affinity (BA) values. Minimum adequate model is shown. Note, the binary categorical variable ‘same individual’ is being compared to the reference level of that variable, which is 0 (different individuals). Significant effects ($p < 0.05$) are highlighted in bold. $R^2 = 0.007$.

Variable	**Estimate ± SE**	**z value**	**P value**
Whole migration BA comparisons			
(Intercept)	-0.829 ± 0.024	-34.355	< 0.001
1 (Same Individual)	0.634 ± 0.063	10.110	< 0.001
Difference in departure	-0.001 ± 0.000	-4.787	< 0.001

Table S3.4. Pairwise comparisons between each level of the categorical variable ‘stage’ from the generalised linear model examining the spatiotemporal similarity of petrel migrations when split into six equal size stages, using earth mover’s distance (EMD) ‘effort’ values. Significant effects ($p < 0.05$) are highlighted in bold.

Contrast	**Estimate ± SE**	**P value**
Whole migration – Stage 1	-243.3 ± 90.0	0.1251
Whole migration – Stage 2	-359.1 ± 98.5	**0.0049**
Whole migration – Stage 3	-398.7 ± 101.2	**0.0016**
Whole migration – Stage 4	-355.1 ± 98.2	**0.0055**
Whole migration – Stage 5	-448.6 ± 104.7	**0.0004**
Whole migration – Stage 6	-543.3 ± 111.4	**< 0.0001**
Stage 1 – Stage 2	-124.8 ± 110.1	0.9180
Stage 1 – Stage 3	-164.3 ± 112.5	0.7685
Stage 1 – Stage 4	-120.8 ± 109.9	0.9285
Stage 1 – Stage 5	-214.3 ± 115.7	0.5123
Stage 1 – Stage 6	-309.0 ± 121.7	0.1458
Stage 2 – Stage 3	-39.6 ± 119.4	0.9999
Stage 2 – Stage 4	4.0 ± 116.8	1.0000
Stage 2 – Stage 5	-89.5 ± 122.3	0.9907
Stage 2 – Stage 6	-184.2 ± 128.1	0.7810
Stage 3 – Stage 4	43.5 ± 119.1	0.9998
Stage 3 – Stage 5	-49.9 ± 124.5	0.9997
Stage 3 – Stage 6	-144.6 ± 130.2	0.9250
Stage 4 – Stage 5	-93.5 ± 122.1	0.9881
Stage 4 – Stage 6	-188.2 ± 127.8	0.7618
Stage 5 – Stage 6	-94.7 ± 132.9	0.9919

Table S3.5. Results of generalised linear model to investigate the spatiotemporal similarity of within-individual petrel migrations when split into 30-day periods, using earth mover's distance (EMD) 'effort' values. Minimum adequate model is shown and categorical variable 'period' is being compared to reference level of whole migration. Significant effects ($p < 0.05$) are highlighted in bold. $R^2 = 0.067$.

Variable	**Estimate ± SE**	**t value**	**P value**
(Intercept)	490.85 ± 61.98	7.9	**< 0.001**
30-day period*			
First period	226.15 ± 88.06	2.6	**0.01**
Second period	391.87 ± 99.15	4.0	**< 0.001**
Third period	440.96 ± 102.52	4.3	**< 0.001**
Fourth period	319.85 ± 94.27	3.4	**< 0.001**
Fifth period	493.25 ± 106.90	4.6	**< 0.001**
Sixth period	476.44 ± 123.96	3.8	**< 0.001**
Seventh period	546.10 ± 212.03	2.6	**0.01**
Difference in departure	4.21 ± 0.85	5.0	**< 0.001**

Table S3.6. Pairwise comparisons between levels of the categorical variable '30-day period' from the generalised linear model examining the spatiotemporal similarity of petrel migrations when split into 30-day periods, using earth mover's distance (EMD) 'effort' values. Significant effects ($p < 0.05$) are highlighted in bold.

Contrast	**Estimate ± SE**	**P value**
Whole migration – first 30-day period	-226.2 ± 88.1	0.1676
Whole migration – second 30-day period	-391.9 ± 99.1	**0.0020**
Whole migration – third 30-day period	-441.0 ± 102.5	**0.0005**
Whole migration – fourth 30-day period	-319.9 ± 94.3	**0.0159**
Whole migration – fifth 30-day period	-493.2 ± 106.9	**0.0001**
Whole migration – sixth 30-day period	-476.4 ± 124.0	**0.0031**
Whole migration – seventh 30-day period	-546.1 ± 212.0	0.1648
First 30-day period – second 30-day period	-165.7 ± 110.0	0.8040
First 30-day period – third 30-day period	-214.8 ± 113.0	0.5502
First 30-day period – fourth 30-day period	-93.7 ± 105.6	0.9873
First 30-day period – fifth 30-day period	-267.1 ± 117.0	0.3030
First 30-day period – sixth 30-day period	-250.3 ± 132.9	0.5625
First 30-day period – seventh 30-day period	-320.0 ± 217.5	0.8230
Second 30-day period – third 30-day period	-49.1 ± 121.8	0.9999
Second 30-day period – fourth 30-day period	72.0 ± 115.0	0.9985
Second 30-day period – fifth 30-day period	-101.4 ± 125.5	0.9928
Second 30-day period – sixth 30-day period	-84.6 ± 140.5	0.9989
Second 30-day period – seventh 30-day period	-154.2 ± 222.3	0.9972
Third 30-day period – fourth 30-day period	121.1 ± 117.9	0.9704
Third 30-day period – fifth 30-day period	-52.3 ± 128.2	0.9999
Third 30-day period – sixth 30-day period	-35.5 ± 142.9	1.0000
Third 30-day period – seventh 30-day period	-105.1 ± 223.8	0.9998
Fourth 30-day period – fifth 30-day period	-173.4 ± 121.7	0.8461
Fourth 30-day period – sixth 30-day period	-156.6 ± 137.1	0.9475
Fourth 30-day period – seventh 30-day period	-226.3 ± 220.1	0.9703
Fifth 30-day period – sixth 30-day period	16.8 ± 146.1	1.0000
Fifth 30-day period – seventh 30-day period	-52.9 ± 225.8	1.0000
Sixth 30-day period – seventh 30-day period	-69.7 ± 234.1	1.0000

Table S3.7. Colour of geographic coordinates in figures (main text and Supplementary material) and the corresponding year/s of each migration.

Figure	**Colour of geographic coordinates**			
	Orange	**Blue**	**Red**	**Green**
3.2a	2016/17	2017	2011	2010/11
3.2b	2016/17	2017	2012	2011
3.2c	2015/16	2016/17	2011	-
3.2d	2011	2012	2015/16	-
3.2e	2011	2011/12	2015/16	-
3.2f	2015/16	2016	-	-
3.2g	2010	2011	-	-
3.2h	2011	2012	-	-
3.2i	2011	2011/12	-	-
3.2j	2009/10	2010/11	-	-
3.2k	2015	2016	-	-
3.2l	2015/16	2016	-	-
3.3a	2011	2011/12	-	-
3.3b	2015/16	2016	-	-
3.3c	2016/17	2017	-	-
3.3d	2012	2011	-	-
3.3e	2012	2016	-	-
3.3f	2009/10	2009/10	-	-
S3.3a	2009/10	2009/10	-	-
S3.3b	2017	2010	-	-
S3.3c	2015/16	2016/17	-	-

Table S3.8. The variance components and repeatability estimates (*R*) from adult Round Island petrels with repeated tracks (2-5 years) for departure date from the breeding colony, arrival at the colony and duration of the migratory period.

	Between-individual variance	**Within-individual variance**	***R***
Departure date	8148.0	2203.2	0.787
Arrival date	8669.5	1998.7	0.813
Duration	369.76	425.62	0.465

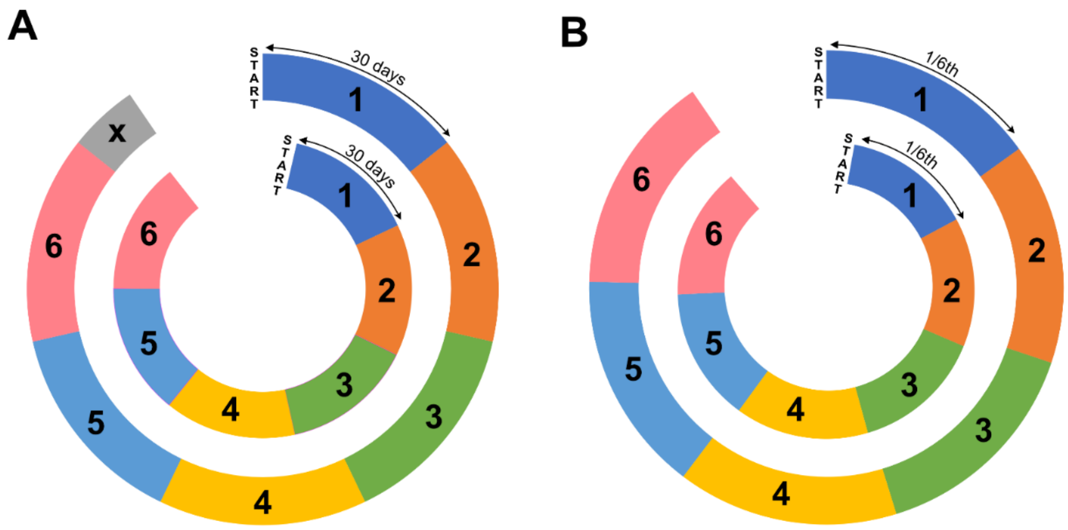

Figure S3.1. Earth mover's distance (EMD) values are calculated for both A) consecutive 30-day periods, irrespective of start date, and B) by splitting the migration into six equal stages. For A), this typically means that a short period of longer within-individual migrations is not included, however, there was evidence of individual consistency in migration duration and so this often only comprises a small proportion of the whole migration. Whereas for B), if one migration is longer than the other then each stage will comprise of more days than the other corresponding stage.

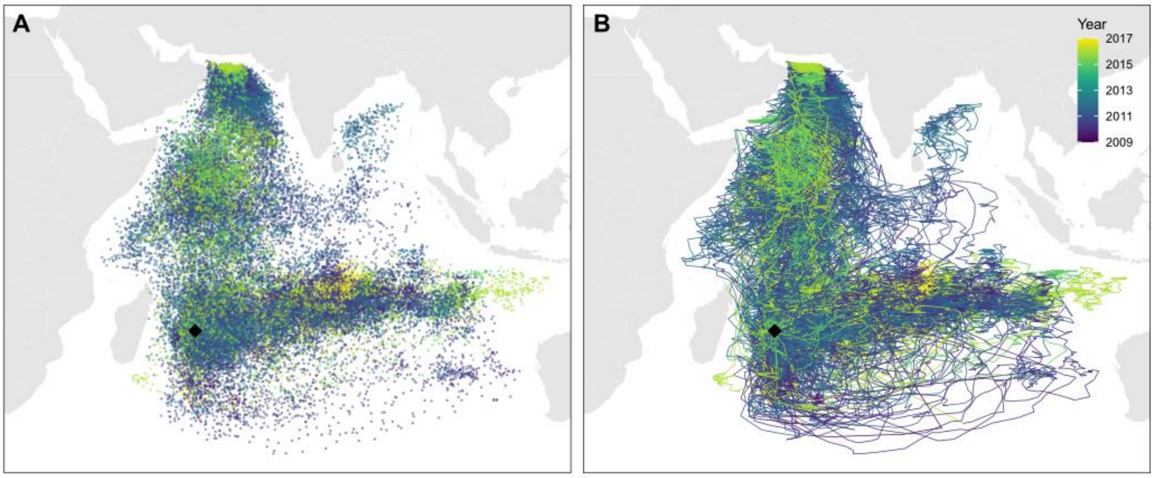

Figure S3.2. Geographic coordinates (a) and tracks (b) from 62 adult Round Island petrels that have been tracked over multiple complete migrations (n=131) with geolocators. Colours of lines and points represent the year of tracking (2009-17). Black diamond indicates the location of Round Island, Mauritius.

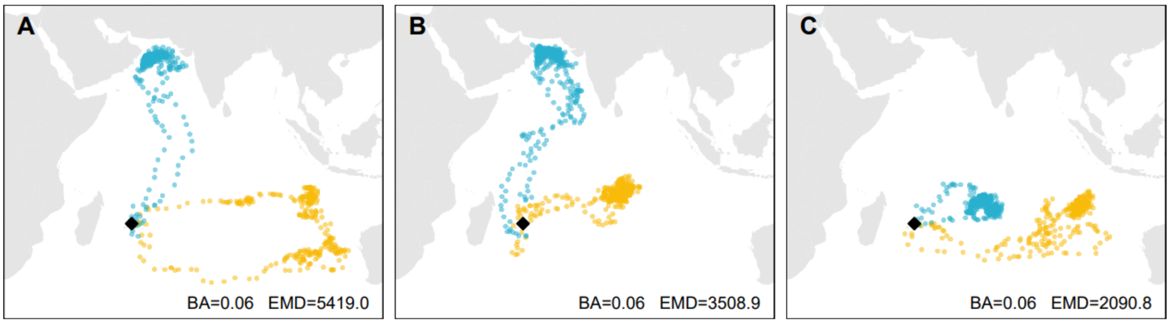

Figure S3.3. Example tracks of between-individual Round Island petrel migration comparisons with the same relative overlap value (Bhattacharyya's affinity (BA) = 0.06), but with comparatively high (A), moderate (B), and low (C) earth mover's distance 'effort' values. Positions denote twice-daily median locations with the two different years illustrated in different colours. Black diamond indicates the location of Round Island, Mauritius. The tracking year that each set of colours represents can be found in Table S3.7.

Chapter 4

Drivers of ocean movement patterns in Round Island petrels

Photo: Sam Napaul

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Drivers of ocean movement patterns in Round Island petrels

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Abstract

Migratory strategies can vary within and between populations of many taxa, with potentially important consequences for individual fitness, population dynamics, and conservation. However, the mechanisms influencing which strategies are used by which individuals are often poorly understood. For example, individual migratory journeys could be influenced by conditions (environmental and/or social) that are encountered at departure or *en route*, which in turn may vary with individual timing of migration. In tropical systems, species often have extended breeding seasons, and thus a broad range of individual migration timings, making them good systems in which to explore potential causes of individual migration strategies. On Round Island, Mauritius, in the tropical western Indian Ocean, a population of *Pterodroma* petrels breed all-year round, and thus migrates year round, in a strongly seasonal environment. This, together with the fact that the population is made up of a hybrid complex of at least three species of *Pterodroma* petrel, provides a unique opportunity to explore potential causes of individual migration strategies. Here we combine a long-term geolocator tracking dataset, a novel Bayesian Mixtures Analysis, and microsatellite genotyping analysis, finding large levels of between-individual variation in migratory strategies, with petrels migrating to different areas across much of the Indian Ocean. We identified nine different migratory strategies but, despite the diverse phenological and genotypic variation within the petrel population, we found limited evidence that individuals with similar genetic composition or timing of migration have similar strategies. The disproportionate use of each of the nine strategies across the tracked population, together with the fact that individuals are highly repeatable in their migratory journeys, suggests that conditions experienced early in life may be important in shaping migratory journeys. Understanding at-sea behaviour and the individual fitness costs of migrating to different areas within the non-breeding range, and tracking across life stages, will be key in understanding the subsequent consequences for population dynamics and how between-individual variation emerges and persists.

Introduction

Animal migration is a widespread phenomenon found across all major taxonomic groups and at all latitudes, although it increases in frequency with distance from the equator (Newton & Dale, 1996). Within and across species, remarkable diversity in migratory strategies has been documented (Newton, 2010; Schofield et al., 2010), both in terms of when and where individuals go, and the routes they take to get there. This means individuals of the same species and/or population may experience very different environmental conditions, with potentially important consequences for individual fitness and population dynamics (Alves et al., 2013). Understanding the processes that influence individual migratory journeys is integral to predicting how animals might encounter and respond to environmental change. For many migratory species, this is often quite difficult, owing to the wide range of temporally and spatially distributed habitats and resources that they depend on across the annual cycle (Robinson et al., 2009).

Birds are some of the world's greatest travellers and are renowned for the huge distances they can cover across the globe. Remote tracking technology has revolutionised our understanding of these long-distance migrations, with the best-known examples including the Arctic tern *Sterna paradisaea* which undertakes huge pole-to-pole migrations every year (Egevang et al., 2010), and the Bar-tailed godwit *Limosa lapponica baueri* for the longest non-stop flight (Gill et al., 2009). Like many other migratory taxa, birds show a diverse range of non-breeding strategies within- and between- species (e.g., Brown et al., 2021; Kopp et al., 2011). A range of factors influence individual migratory journeys, such as conditions experienced at departure and/or *en route*. For example, the environmental conditions, particularly wind strength and direction, may be important in shaping migratory journeys of soaring and gliding birds (Mellone et al., 2011; Vansteelant et al., 2017). Conditions experienced at departure or on migratory journeys may also be socially influenced, especially for species that travel in groups (Oestreich et al., 2022; Teitelbaum et al., 2016).

At the individual-level, migratory journeys are often highly repeatable, with individuals arriving at and departing from the breeding grounds at a similar time (reviewed in Chapter 2) and migrating to the same non-breeding areas (Chapter 3; Kürten et al., 2022), year after year (but see Dias et al., 2011; McFarlane Tranquilla et al., 2014). If between-individual variation in migratory distributions is high and within-individual variation low, this may mean that individuals of the same species will experience very different environmental conditions and anthropogenic pressures depending on the migratory strategy they undertake. Therefore, if individuals repeatedly follow the same migratory strategy from an early age, it may be likely that the conditions experienced early in life are important in determining individual migration strategies and the subsequent survival of those individuals undertaking specific strategies (Gill et al., 2019).

High levels of diversity in migratory strategies are common in seabird populations (e.g., Dell'Ariccia et al., 2018; Jaeger et al., 2017; Weimerskirch et al., 2017). Some species are resident year-round (Schacter & Jones, 2018), some disperse widely during the non-breeding period (Fayet et al., 2017), others engage in basin-scale or pole-to-pole migrations (Egevang et al., 2010). The migratory strategies undertaken by individuals are also often highly repeatable, in space and time (Chapter 2; Chapter 3; Kürten et al., 2022). The availability of food resources, itself influenced by large-scale environmental conditions, is suggested to be an important driver of seabird at-sea distributions (but see Lambert & Fort, 2022). This may be particularly evident in temperate and polar regions where environmental conditions undergo strong seasonal changes making availability of prey resources more predictable (Weimerskirch, 2007). In contrast, tropical environments are typically more oligotrophic, making marine productivity both less seasonal and less predictable (Weimerskirch, 2007; but see Kumar et al., 2009). Tropical seabirds, therefore, often have extended and/or asynchronous breeding seasons in response to their less predictable environments and are commonly described to be more wide-ranging (Soanes et al., 2021). Tropical species therefore often display a broad range of individual migratory timings and distributions, meaning the range of conditions which migrating individuals can experience might very greatly, making them ideal systems in which to explore potential causes of individual migration strategies.

The Round Island petrel (*Pterodroma* sp.) is a tropical, pelagic seabird which breeds all-year round in Mauritius, in a strongly seasonal environment in the western Indian Ocean. The population is particularly interesting as it consists of at least three species of *Pterodroma* petrel, with one species (Trindade petrel, *P. arminjoniana*) originating from the Atlantic, and two species (Kermadec petrel, *P. neglecta* and Herald petrel, *P. heraldica*) from the Pacific, and contains two- and three-way hybrids of these species (Booth Jones et al., 2017; Brown et al., 2010; Brown et al., 2011). Previous research has shown large levels of between-individual variation in Round Island petrel migrations, with petrels undertaking long-distance migrations to different areas across much of the Indian Ocean (Chapter 3). However, repeat tracking of individuals across the non-breeding period has revealed individual migratory journeys to be remarkably consistent in both space and time (Chapter 3). Yet, the factors driving the large levels of between-individual variation are yet to be explored. The migratory journeys of Round Island petrels might be influenced by the evolutionary history of their ancestral species (Trindade, Kermadec and/or Herald petrel) and by the conditions that individuals experience during the non-breeding season, which can span any months of the year. Consequently, this is an ideal system in which to explore individual variation in migratory distributions.

Using a long-term geolocator tracking dataset and microsatellite genotyping analysis from Round Island petrels, we quantify 1) the range of migratory strategies that adult Round Island petrels undertake, 2) whether petrels with differing genotypes depart Round Island at differing times of year (and may thus experience differing conditions during migration), and 3) whether migratory strategies differ among individuals with differing genotypes and timings of departure.

Methods

Study site and species

Fieldwork was carried out at Round Island Nature Reserve (19.85° S, 57.78° E), Mauritius, in the western Indian Ocean. The climate of Mauritius and the surrounding ocean is strongly seasonal and can be divided into two broad seasons: a cool and dry austral winter (1st May – 30th Sep), and a warm and humid austral summer (1st Oct – 30th April; Senapathi et al., 2009). These periods reflect the influence of the monsoon circulation of the Indian Ocean, with the south-western monsoon dominating during the winter and the north-eastern monsoon in the summer. These atmospheric dynamics in the Indian Ocean are characterised by biannually reversing monsoon winds in the northern Indian Ocean (Schott & McCreary, 2001). The months of May and October are commonly known as the transition months, reflecting the inter-annual variation in the timing of the wind reversal (Mauritius Meteorological Services).

Round Island is the only location in the Indian Ocean where a hybrid complex of at least three *Pterodroma* species breeds. They are long-lived, medium-sized gadfly petrels which nest on the ground, typically under rock ledges or herbaceous vegetation (Nicoll et al., 2017). Petrels can be found breeding all-year round, although in varying numbers across the year. We therefore define a petrel year as starting in June and ending in May (when the number of petrels on the island is at its lowest), and thus spans two calendar years i.e., 2009 = 2009/2010 (Nicoll et al., 2017).

Data collection and processing

Between 2009 and 2016, 421 geolocation-immersion loggers (hereafter 'geolocators') were deployed on adult Round Island petrels (Table S4.1). Two brands of geolocator were used: British Antarctic Survey model MK15 were deployed between 2009 and 2012 and Migrate Technology Intigeo models C250 and C330 during 2014 and 2016. Geolocators were recovered at least a year after deployment (note, tags deployed in 2012 and subsequently recovered did not yield any useable data, likely due to tag age; Figure 4.1) and were mounted on different coloured 1 or 0.75 mm thick Salbex (an industrial grade PVC; Sallu Plastics, Redditch, UK) colour-rings and attached to the tarsus, with colours representing different deployment years to avoid early recapture of recently-deployed tags. The total mass of the attachments ranged from 3.6 - 3.9 g, representing approximately 1.0 % of the mean body mass of adult petrels (374 g). Previous analyses found no evidence of geolocators affecting the short- or long-term survival of adult petrels (Nicoll et al., 2022).

Petrels were caught by hand, predominately while resting on the island away from nest sites. For the first three deployments, the tagged petrels were caught during targeted searches, whereas later geolocator deployments occurred during regular petrel breeding surveys. Petrel breeding surveys have been undertaken every month or two since 2001, and involve regular visits to known nesting areas, with petrels found during these visits either fitted with rings (South African Bird Ringing Unit numbered rings) or recorded as recaptures, and their breeding status recorded. All individuals which were ringed (and had a geolocator attached) also had blood samples taken (see Booth Jones et al., 2017 for details). Geolocators were opportunistically recovered a minimum of one year later, during breeding surveys or during occasional specific searches. All geolocators underwent a 3- to 5-day calibration period at a known location (Round Island, or mainland Mauritius (20.25° S, 57.44° E)) pre- and post-deployment. Details of the numbers of geolocators deployed and recovered until the end of December 2019 are provided in Table S4.1.

Twice-daily at-sea locations for each individual were estimated using the R package SGAT (Wotherspoon et al., 2013). Detailed procedures related to geolocator processing can be found in Chapter 3. In short, the applied Bayesian method makes use of Markov Chain Monte Carlo (MCMC) simulations and allows incorporation of a twilight model (prior definition of the error distribution of twilight events), a movement model, and a spatial mask to improve location estimates and estimate uncertainty (Lisovski et al., 2020).

The arrival and departure dates of migration were identified using a two-state hidden Markov model (HMM) using the R package depmixS4 (Visser & Speekenbrink, 2010). This HMM uses the proportion of light interference during core daylight hours, the sum of daily wet/dry records, and the distance from Round Island to classify each calendar day for each petrel as ashore or at-sea. Migration periods were defined as a sequence of consecutive days that were assigned to the same behaviour (at-sea) by the HMM for a period of at least three months, before switching to the other behavioural state (ashore; for more details see Chapter 3).

Genetic background

Blood samples taken during ringing and/or geolocator deployment were genotyped by KABJ using a suite of 12 microsatellite markers. These samples were analysed using STRUCTURE v.2.3.4 (Falush et al., 2003; Pritchard et al., 2000) along with genotyped individuals from potential source populations, including Trindade petrels from Trindade Island, and a range of Pacific islands representing the distributions of Kermadec, Herald, Phoenix (*P. alba*), and Murphy's (*P. ultima*) petrels. Results from this analysis suggested a total of four genetic clusters and provided estimated membership (Q) values for each individual to each cluster. The four clusters are as follows: Trindade-type petrels, Kermadec-type petrels, Herald- or Phoenix-type petrels, and Murphy's-type petrels. As Trindade-type petrels are the most dominant genotype on Round Island, the Q value of each individual to the Trindade-type cluster (probability of 0-1, with 1 being pure Trindade-type) was used as a measure of genetic background. For full details of microsatellite genotyping and genetic analysis methods see Booth Jones et al. (2017).

Identifying migratory strategies

We used a Bayesian Mixtures Analysis (BMA) to group petrels into spatially similar migratory distributions (Holloway et al., in review). We only used the first complete migration for each individual in this analysis (n = 198; rather than including repeat tracks), as petrels have previously been shown to be remarkably consistent in their migratory timings and distributions (see Chapter 3). First, the BMA requires the overall distribution space of all tracked individuals to be divided. We used a 40x40 grid over the tracking area (Fig. S4.1), with each grid square approximately 200x200 km in order to account for the spatial inaccuracies of geolocator location estimates (Halpin et al., 2021; Phillips et al., 2004). The number of location estimates which fall within each grid square for each individual are then compared between individuals, and individuals are grouped based on similarities and differences in the whole track distribution with others in the BMA. For each cluster, we then generated the kernel utilisation distribution (UD) of individuals undertaking that strategy using the whole migratory track. To do so, we used the kernelUD function in the adehabitatHR R package (Calenge, 2006), using a fixed smoothing parameter of 200 km to account for precision error around location estimates. Distributions (delineated by 50, 75 and 95% density contours) were then extracted using the getverticeshr function.

Statistical analysis

To investigate whether there is any seasonal structuring in the presence of differing genotypes of petrels on Round Island, a beta regression model with probit link function was fitted, with petrel genetic background (Trindade-type Q values) as the response variable, and season (summer or winter) as an explanatory variable using the betareg R package (Cribari-Neto & Zeileis, 2010). To take into account the inter-annual variation in when the trade-winds shift (and thus the monsoon season changes), we also fitted the same model as above, but with season as either a three-level categorical variable, combining the two monsoon transition periods into one level, or as a four-level categorical variable with the May and October transition periods accounted for separately.

Next, using the six most common petrel migratory strategies as identified from the BMA, we used a binomial generalised linear model (GLM) with probit link function to investigate the relationship between season of departure and migratory strategy. The two-level variable of season (summer or winter) was included as the response variable, and migratory strategy as the fixed effect. For this analysis, we used all individuals incorporated in the BMA (n = 198) regardless of availability of genotype information. As a complete separation would have occurred in binomial regression with one strategy containing individuals of only one season of departure, a bias reduction method was implemented using ‘brglmFit’ as the fitting method for GLMs within the brglm2 R package (Kosmidis, 2021; Kosmidis & Firth, 2021).

To investigate the influence of petrel genetic background and season of departure (and thus the environmental conditions experienced) on petrel migratory distributions, we fitted another GLM with a cauchit link function using only the two common petrel migratory strategies as identified from the BMA. The other migratory strategies, particularly when using only the subset of individuals for which genotyping data were available, had insufficient sample sizes for analysis but are described in the results. Petrel genetic background and season (summer or winter) were fitted as fixed effects, as well as their interaction. We also fitted the same model, but with the different ways of categorising season (three- or four-level categorical variable), as above. For all models, non-significant ($p < 0.05$) terms were sequentially removed using backwards stepwise deletion and significance of terms was determined using ANOVA. Pairwise comparisons among levels were calculated based on estimated marginal means and adjusted using post-hoc Tukey correction using the R package emmeans (Lenth, 2021). All analyses were conducted using R version 3.6.2 (R Core Team, 2019).

Results

In total, 421 geolocators were deployed on adult Round Island petrels across the study period. Deployments spanned all months, however, the majority of geolocators (~68%) were deployed between November and April of each petrel year (Fig. 4.1), when numbers of petrels at the colony are highest. Of the 421 deployed, 337 geolocators were retrieved, resulting in an overall retrieval rate of 80% (see Table S4.1 for timings and numbers). This provided 267 complete migration tracks from 198 individuals and, due to logger failure during deployment, an additional 46 incomplete migration tracks (which include a departure date from Round Island but insufficient information to identify migratory strategy) for 46 petrels.

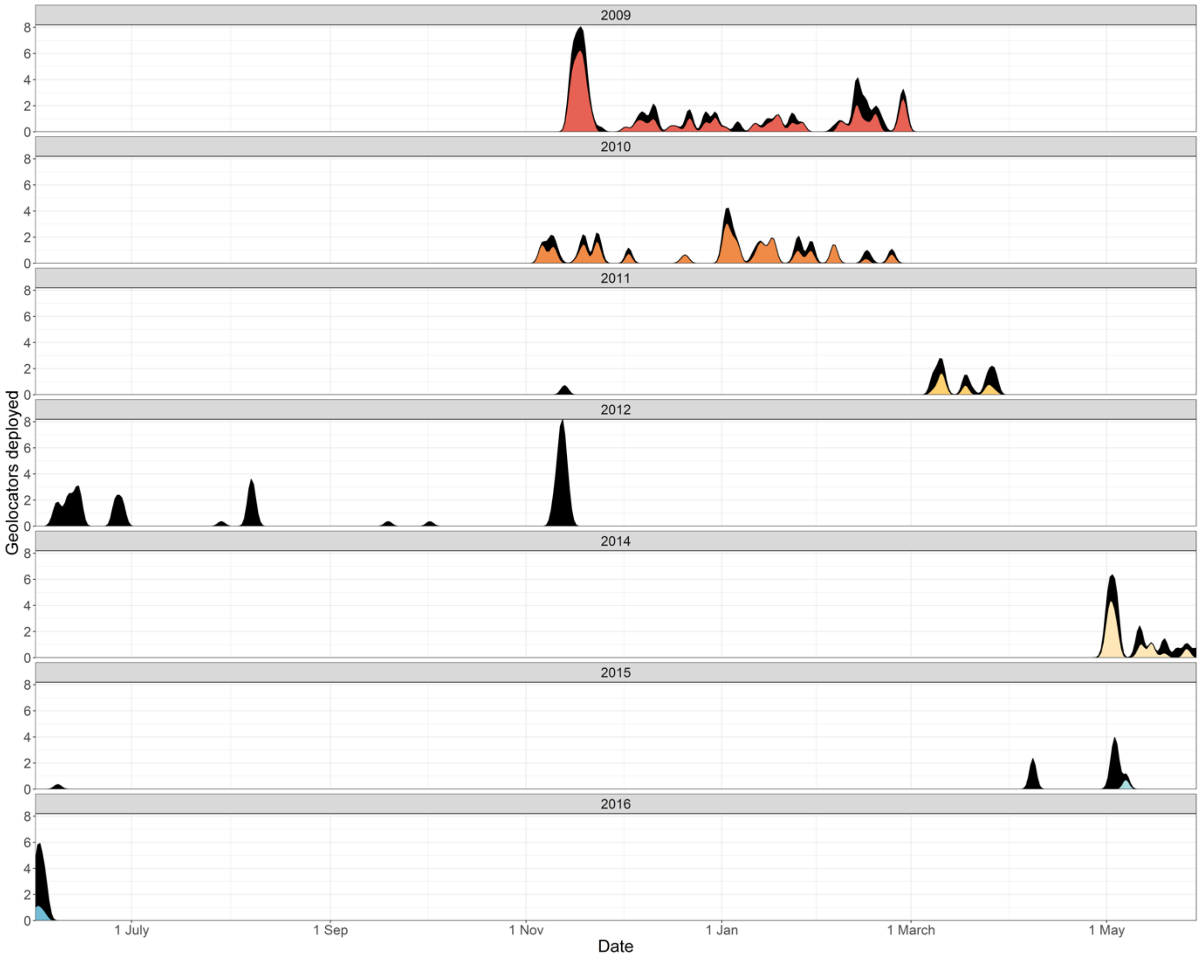

Figure 4.1. Temporal distribution of geolocator deployments (black) and the number of those geolocators which provided a sufficiently complete migration track to identify the migratory strategy (n = 198; coloured) on adult Round Island petrels across deployment years. Note that the petrel year starts in June and ends in May, thus a deployment year spans two calendar years (i.e., 2009 = 2009/2010).

Migration timing of petrel genotypes

Of the 244 Round Island petrels with either complete (n = 198) or incomplete migrations (n = 46; but including a departure date from Round Island), 181 had a blood sample taken and were successfully genotyped, providing each individual with an estimated membership (Q) value to the Trindade-type cluster. Of these, 124 individuals (68.5%) had a Q value of > 0.5. Tagged petrels departed Round Island in all months and petrels with differing genotypes did not vary significantly in the season (austral winter or austral summer) in which they departed Round Island (Fig. 4.2; Table S4.3), regardless of whether season included or excluded the inter-monsoon transition periods (Table S4.3).

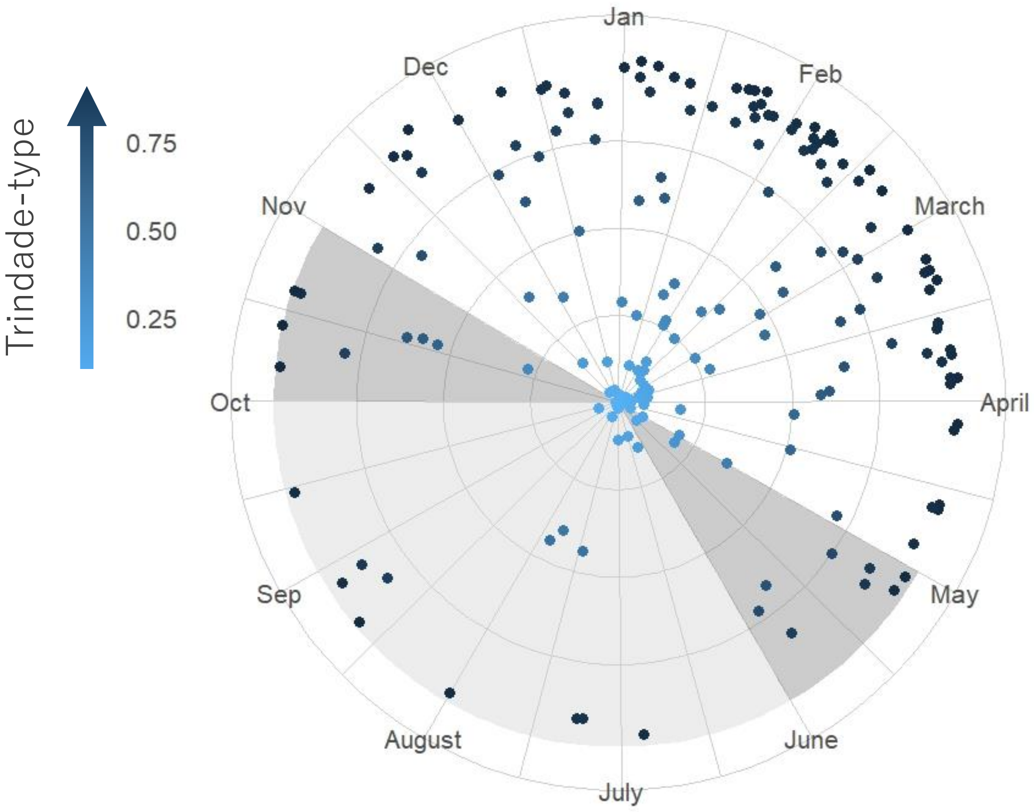

Figure 4.2. Distribution of migration departure dates for 181 adult Round Island petrels tracked with geolocators, with individual genetic background represented by point colour and location (with points closer to the centre and lighter in colour having a lower estimated membership to the Trindade-type cluster). Grey shaded areas represent the austral winter (May-Sep, inclusive), and the monsoon transition periods (dark grey) at the start of the austral winter and austral summer.

Petrel migratory strategies

Migrations of tracked Round Island petrels covered much of the Indian Ocean (Fig. S4.1), with individuals migrating in all directions from Round Island. The BMA of areas used by individual petrels during their non-breeding period identified nine distinct clusters of petrel migratory strategies (Fig. 4.3). Each cluster included between one and 88 individual petrels and, for those with multiple individuals, petrel migrations spanned all tracking years (Table S4.2). The most common strategies involved petrels migrating eastwards and then north to the Somali Basin (strategy two; 44% of tracked petrels) or directly north into the Arabian Sea (strategy four; 38%), while comparatively few individuals migrated east towards the central Indian Ocean or Ninety East Ridge (strategies one and six; 8%), northeast to an area straddling the Chagos-Laccadive plateau (strategy five; 5%), to the Bay of Bengal (strategy three; 3%), or an alternative strategy (strategies seven, eight or nine; 2%; Fig. 4.3).

Does petrel migratory strategy differ with genotype and phenology?

Of the six migratory strategies with more than two individual petrels, all exhibited large variation in dates of departure and petrel genetic background (Fig. 4.4). The inclusion of migratory strategy against departure season significantly improved the fit of the model over the null (GLM: χ^2 (5) = 14.822, p = 0.012), suggesting that individuals undertaking certain strategies were more likely to depart during certain seasons. However, pairwise comparisons (adjusted for multiple p-values) showed no significant differences in season of departure between strategies (Table S4.4), suggesting no strong patterns of variation in departure timing across strategies.

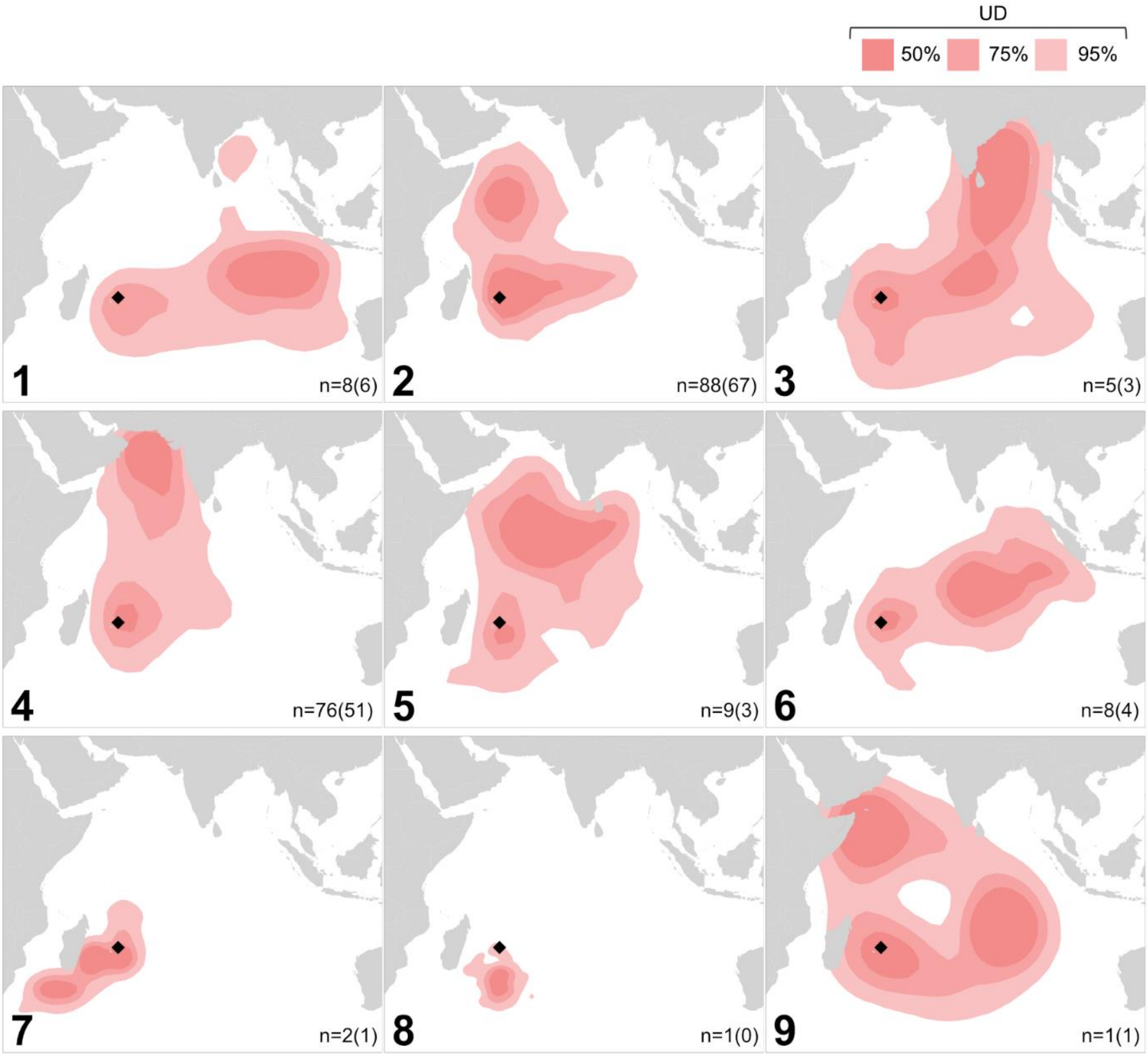

Figure 4.3. Distributions of the nine Round Island petrel migratory strategies covering much of the Indian Ocean identified by the Bayesian Mixtures Analysis. The number of individuals (n; with (and without) genotype information) which make up each distribution is noted for each strategy. Black diamond indicates the location of Round Island, Mauritius.

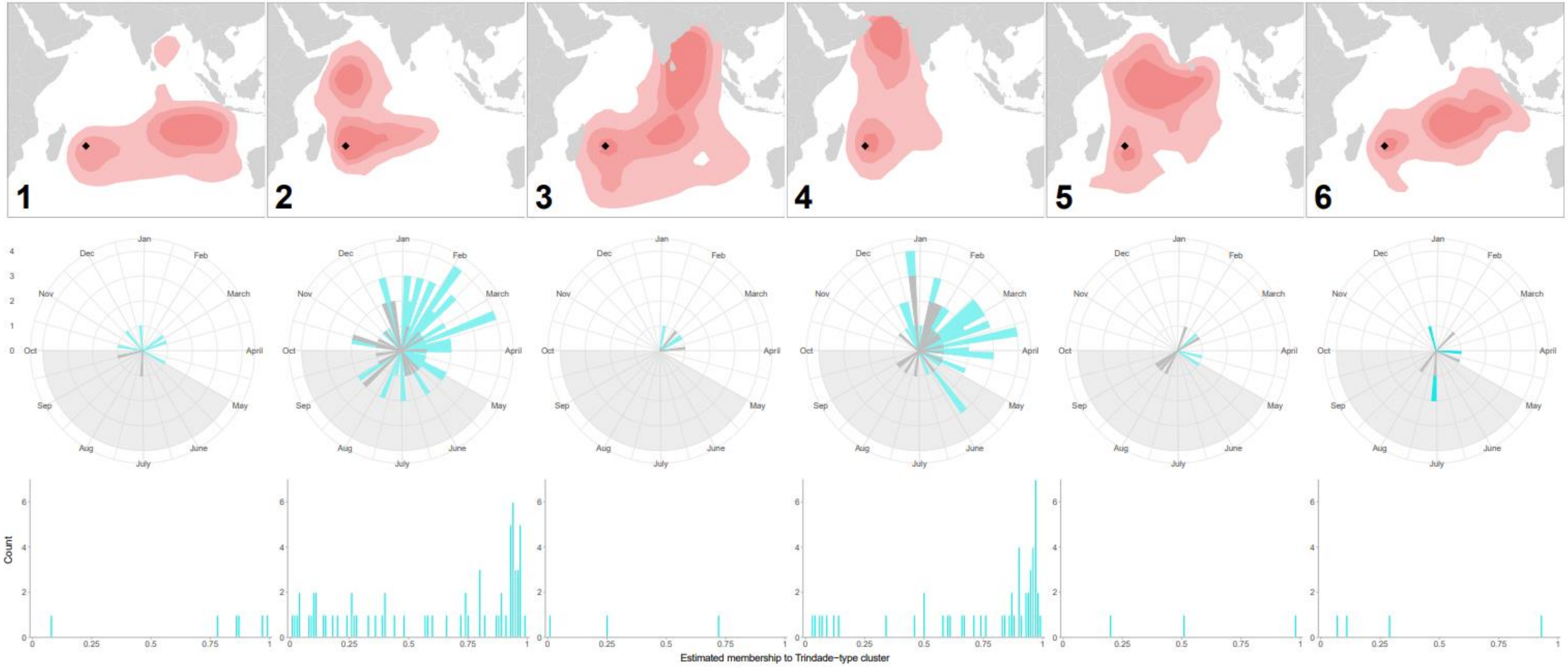

Figure 4.4. Distributions of Round Island petrels in each of the six most common migratory strategy clusters as identified by the Bayesian Mixtures Analysis (top panels), with differing times of departure from Round Island (middle panels) and with differing genotypes (bottom panels). Colour of lines in middle and bottom panels represent individuals with (blue) and without (grey) genotype data. Black diamond indicates the location of Round Island, Mauritius. Dates of departure in polar plots are binned into periods of 5 days for clarity, with length of bars representing the number of individuals (centre = 0, edge = 4) departing in that period, and grey shaded areas represent the austral winter (May-Sep).

Of the strategies with sufficient sample sizes to investigate the effect of petrel genotype and season of departure (to the Somali Basin (strategy two) or Arabian Sea (strategy four)), petrels departed in both seasons (and across all months), and there was no significant interaction between petrel genetic background and season of departure on the probability of using strategy two or four (Tables 4.1 & 4.2). Petrels following the two strategies did not differ significantly in genetic background or timing of departure although models containing only genetic background or departure timing suggested that petrels with more Trindade-like genotypes and petrels departing in the austral summer were slightly more likely to migrate to the Arabian Sea (Tables 4.1 & 4.2). For example, of those going to the Arabian Sea, a higher percentage of individuals (92.2% and 88.2% when including all individuals or only using those which have genotype data, respectively) departed during the austral summer (Fig. 4.5).

Table 4.1. Results of generalised linear model to investigate the influence of genetic background and season of departure (austral summer or austral winter) on migratory strategy for the petrels which have genotype information (n=164). Maximum model is shown. Nagelkerke pseudo $R^2 = 0.086$.

Variable	**Estimate ± SE**	**Z value**	**P value**
(Intercept)	0.768 ± 0.453	1.696	0.090
Trind	-0.968 ± 0.571	-1.696	0.090
Season (Winter)	1.198 ± 2.120	0.565	0.572
Trind*Season	-0.265 ± 2.658	-0.100	0.921

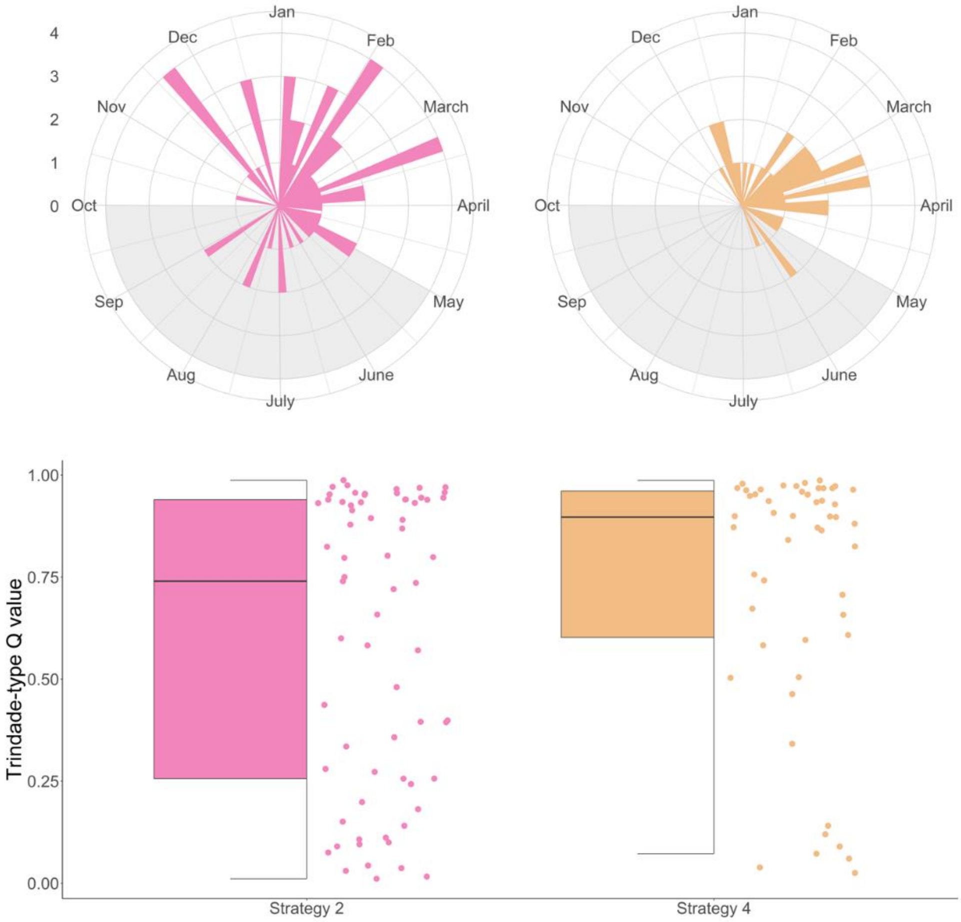

Figure 4.5. Individual petrel departure dates (top) and estimated membership (Q) values to the Trindade-type cluster (bottom) for petrels migrating to the Somali Basin (strategy two; pink) and the Arabian Sea (strategy four; orange), for petrels with genotype information only (n = 67 and 51, for strategy two and four, respectively). Dates of departure in polar plots are binned into periods of 5 days for clarity, with length of bars representing the number of individuals (centre = 0, edge = 4) departing in that period, and grey shaded areas represent the austral winter (May-Sep).

Table 4.2. Results of ANOVA tests for generalised linear model selection for the effect of petrel genetic background and season of departure (austral summer or austral winter) on migratory strategy for the petrels which have genotype information (n=164). Significant effects ($p < 0.05$) are highlighted in bold.

Model	df	Deviance	P value
a. Two-level categorical variable of season			
Strategy ~ Trind*Season	1	0.012	0.915
Strategy ~ Trind + Season			
Strategy ~ Trind + Season	1	3.214	0.073
Strategy ~ Trind			
Strategy ~ Trind + Season	1	3.780	0.052
Strategy ~ Season			
Strategy ~ Trind	1	4.634	**0.031**
Strategy ~ null			
Strategy ~ Season	1	4.068	**0.044**
Strategy ~ null			

Discussion

Migratory populations often show a diverse range of non-breeding strategies of movement and distribution, yet the factors influencing where individuals go is often poorly understood. Using an unusual hybrid population of tropical *Pterodroma* petrels from Round Island, we find large levels of between-individual variation in non-breeding distributions with petrels migrating to different areas across much of the Indian Ocean. We identified nine distinct migratory strategies and found a disproportionate use of each of the strategies across our tracked population, with only two strategies including more than 10 individuals. Petrels following these two strategies did not clearly differ in genetic background or timing of migration, although Trindade-type petrels and those migrating in the austral summer may be slightly more likely to go to the Arabian Sea.

Tracked Round Island petrels migrated widely over the Indian Ocean and employed nine different migratory strategies. Similarly large variations in migratory ranges have been documented in seabirds across the oceans (Dias et al., 2013; Shaffer et al., 2006), including in the tropical Indian Ocean (Jaeger et al., 2017), yet this pattern does not seem to be widespread across all species (Catry et al., 2009; Le Corre et al., 2012; Pinet et al., 2011). For example, sooty terns *Onychoprion fuscatus* from Bird Island in the Seychelles follow a similar dispersive pattern of movements to those of Round Island petrels, visiting a similar range of non-breeding areas in different distances and directions (Jaeger et al., 2017). By contrast, tracking studies on other Procellariforms, including the closely related Barau's petrel *Pterodroma baraui* which nests on nearby Réunion Island, and wedge-tailed shearwaters *Puffinus pacificus* from the Seychelles, both of which are synchronous breeders, have shown all individuals to perform very directed and consistent eastward migrations to the central Indian Ocean (Catry et al., 2009; Pinet et al., 2011). To the best of our knowledge, this is the only species of petrel in the Indian Ocean (tracked from a single colony) with such a large non-breeding distribution; however, the historical neglect of tracking studies on tropical seabirds (Bernard et al., 2021) means data for other species is limited.

The two most common Round Island petrel strategies (82% of tracked petrels) involved birds migrating to the more productive areas of the Indian Ocean, the Arabian Gulf and upwelling of Somalia (Catry et al., 2009; Dalpadado et al., 2021; Lévy et al., 2007). The high percentage of birds migrating to the Arabian Sea during the summer coincides with peak productivity in that area (Lévy et al., 2007), suggesting that Round Island petrels aggregate in these more productive areas. This contrasts with other tracking studies on Procellariforms in the western Indian Ocean (Catry et al., 2009; Pinet et al., 2011), where birds travelled to the low-productivity and low-variability areas in the Indian Ocean (Dalpadado et al., 2021). However, small numbers of Round Island petrels do migrate to these less productive areas, such as the central Indian Ocean, and Bay of Bengal.

Variation in environmental conditions could contribute to the unequal number of individuals using each of the migratory strategies. For example, the variation in conditions and resource availability across the non-breeding range may make particular strategies more energetically costly than others (Alves et al., 2013; Fayet et al., 2017). Individuals migrating to more advantageous locations may therefore be more likely to survive and return to the breeding grounds which, together with the fact that geolocators are archival loggers and must be recovered for data to be obtained, may bias observed non-breeding distributions. However, geolocator retrieval rates in our study were particularly high (~ 80%), and annual adult apparent survival probability of Round Island petrels is estimated to be > 0.9 (Nicoll et al., 2022). In addition, other species predominately migrate to these less productive areas (Catry et al., 2009; Pinet et al., 2011) which are less commonly used by Round Island petrels, again suggesting that high mortality of Round Island petrels in these areas is unlikely to be the case.

The unequal distribution of tracked petrels across migratory strategies could also be influenced by our sampling of breeding adult petrels only. For example, selective pressure against birds that choose uneconomical migration paths may result in favourable paths being more highly represented amongst those surviving to adulthood (Rotics et al., 2016; Sergio et al., 2014). The distribution of geolocator deployments is also not spread equally across or between tracking years (Fig. 4.1), with the majority having been deployed in the first few years of the tracking study and in the months when petrel attendance at Round Island is at its highest (Nicoll et al., 2017; Tatayah, 2010). Although tagged birds in this study departed Round Island in all months of the year, more targeted tracking of birds breeding at times of year when numbers are generally lower may be helpful. However, it would seem unlikely to greatly alter the patterns of at-sea distribution, given the scale of the disparity in numbers using each strategy.

Despite the large variation in petrel non-breeding distribution, we found no strong signal for genotype or environmental conditions influencing where petrels go during the non-breeding season. The Round Island petrel population appears to have arisen relatively recently in time through range expansions of different *Pterodroma* taxa from outside of the Indian Ocean (from Atlantic and Pacific Oceans; Booth Jones et al., 2017; Brown et al., 2010; Brown et al., 2011), originating from very different ocean regimes. Birds from different origins could, therefore, differ in individual migration phenotypes and may show adaptations to the local conditions in which they evolved (Friesen, 2015). Among birds, migratory trajectory is often thought to be underpinned by (epi)genetically inherited information (Helbig, 1991; Merlin & Liedvogel, 2019), typically thought to comprise ‘clock and compass’ navigation (Mouritsen & Larsen, 1998; Yoda et al., 2017) or an inherited ‘map-location’ (Thorup et al., 2020), and hybrids may inherit parental or intermediate migratory behaviours (Austin et al., 2019; Delmore & Irwin, 2014; Väli et al., 2018; Veen et al., 2014). However, tagged petrels varied greatly in genetic background and petrels of all genotypes migrated at all times of year and in all directions, suggesting either little ancestral influence on migration behaviour, or that ancestral types have similarly variable migration behaviours. Non-breeding tracking data from the parental species, and of *Pterodroma* petrels more generally (< 50% of species accounted for on the Seabird Tracking Database; BirdLife International, 2022) is limited. However, published data from Trindade petrels breeding on Trindade Island in the South Atlantic Ocean revealed two different migratory patterns: migrating directly north to the main non-breeding area at the centre of the North Atlantic Ocean or moving eastwards before finally moving north to the main non-breeding area (Fig. S4.2; Krüger et al., 2016; Leal & Bugoni, 2021). The main northwards movement is similar to that of Round Island petrels migrating to the Arabian Sea; the strategy in which individuals had a higher estimated membership to the Trindade-type cluster (although this was only apparent in the univariate model). In addition, the majority of tracked petrels with genotype information (68.5%) had a Q value to the Trindade-type cluster of > 0.5, which could explain why a northwards (Trindade-like) migration was the most common. In contrast to the Atlantic Ocean, these northerly migrations are constrained partly by the Eurasian landmass acting as physical barriers for tropical Indian Ocean seabirds. A larger sample of individuals with genetic data, both within and across more tracking years (as our subset of data is limited to early years of tracking which is focused on the peak breeding period) may help.

Additionally, a better understanding of the non-breeding distributions of the parental species across their full breeding range may aid interpretation.

Migratory behaviour could vary with genotype for non-genetic reasons. For example, if individuals with more similar genotypes vary in their timing of occurrence on Round Island, they may be more likely to experience similar environmental and/or social conditions that may influence the direction and duration of subsequent migratory journeys. However, we found no temporal segregation of the petrel species on Round Island, with petrels with a high estimated membership value to the Trindade-type cluster present all year round. This may not be surprising, as both Trindade and Kermadec petrels are recorded to breed year-round (albeit with peaks in breeding at certain times of year) in their natal range (Luigi et al., 2009; Veitch, 1997).

It is perhaps surprising that environmental conditions at migratory departure, as characterised by the two main seasons of the tropical western Indian Ocean, did not have a strong influence on petrel migratory distribution. Gadfly petrel, and Procellariforms in general, flying behaviour is strongly affected by wind conditions (Spear & Ainley, 1997; Ventura et al., 2019), and petrels have been shown to take advantage of wind on foraging routes rather than flying directly to highly productive waters (Ventura et al., 2019). Elsewhere in the Indian Ocean, Barau's petrels have been shown to take advantage of strong winds and seasonal phytoplankton blooms in their wintering migrations and Pinet et al. (2011) hypothesise that the unfavourable wind regime (direction and speed) north of 10°S (which Round Island petrels cross) would make these waters unsuitable for wintering Barau's petrels. However, oceanic wind patterns may not have been responsible for individual variability in migratory behaviour in other Procellariforms (Dell'Ariccia et al., 2018). The high repeatability in migratory routes of adults, a strong indication of learning, suggests the use of particular strategies is based on the familiarity of previously used locations. Another possibility is that timing of departure of recently fledged juveniles, and the consequent social and/or environmental conditions experienced, could influence individual migratory strategies, which are subsequently repeated throughout their lives (Gill et al., 2019). However, the timing of departure from Round Island of breeding adults may differ from their initial (post-fledging) timing of departure, for example because of the influence of timing of return as a recruiting adult, timing of mate formation and/or impacts of breeding success or failure in any given year on timing of departure. Consequently, timing of departure could be strongly associated with migratory strategy in early life but poorly associated in adulthood. Finally, if the use of certain strategies has not been inherited (epi)genetically or culturally, an alternative mechanism has been proposed, particularly for the development of migratory routes in long-lived species called 'exploration-refinement' (Campioni et al., 2020; Guilford et al., 2011). In the exploration–refinement hypothesis, young animals spend their first few years exploring potential non-breeding areas, and gradually refine their migration route as they age. Their migration would therefore not be under genetic or cultural control but rather rely on learning, experience, and memory (Fayet et al., 2020). Tracking of juveniles is therefore required but is difficult in long-lived species which spend years at sea before returning to breed. Initial tracking of Round Island petrel fledglings for the first year or two of migration (before geolocators fail), shows individuals to migrate northwards, primarily into the Arabian Sea and the Bay of Bengal (Nicoll et al., 2017), with less direct and more exploratory movements than those of adult petrels suggesting this to be a likely explanation. However, repeated tracking of the same individuals across life stages will be needed to investigate the detailed mechanisms by which exploration and refinement of migration routes are achieved.

In conclusion, despite the diverse phenological and genotypic variation within the Round Island petrel population, we found no strong evidence for petrel genetic background or timing of departure influencing the large variation in petrel migratory distributions. Thus, changes in at-sea conditions in any part of the non-breeding range would appear to be unlikely to disproportionately affect particular components of the petrel population. However, tracking of petrels more evenly across the phenological range, and structured sampling of the genotypic variation may be needed to quantify the real influence of these predictors. Ultimately, identifying how these strategies emerge will require studies which repeatedly follow individuals across life stages, from fledging through to breeding. Currently, this is quite difficult because survival rates in early life are typically low, and battery life of tags for deployment on long-lived species is limited, but technological advances will hopefully make this possible in the near future. Studies focusing on migratory behaviour and the fitness costs of different strategies will also be particularly valuable for understanding how migratory distributions and demographic rates are shaped (e.g., Alves et al., 2013). A better understanding of all these processes and how they influence between-individual variation in migratory strategies will be integral to predicting how populations might encounter and respond to environmental change.

Acknowledgments

This work would not have been possible without the many staff and volunteers from the Mauritian Wildlife Foundation (MWF) and National Parks and Conservation Service (NPCS) who have helped with the Round Island petrel research programme. In particular, we would like to thank Vimul Nundlaul, Richard Baxter, Pat Banville, Lucy Rouse, Helen Gath, Luke A'Bear and Johannes Chambon in facilitating the deployment and recovery of GLS on the island.

Data accessibility

Tracking data are deposited on the Seabird Tracking database (www.seabirdtracking.org) handled by BirdLife International (ID: 1810).

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Supplementary materials to Chapter 4: Drivers of ocean movement patterns in Round Island petrels

Table S4.1. Details of all geolocator deployments and recoveries on adult Round Island petrels from 2009-2019.

Petrel year	Number deployed	Number recovered* (%)
2009	135	110 (81.5)
2010	84	79 (94.0)
2011	28	18 (64.3)
2012	79	64 (81.0)
2014	49	36 (73.5)
2015	21	15 (71.4)
2016	25	15 (60.0)
Total	**421**	**337 (80.0)**

* Geolocators recovered between October 2010 and December 2019.

Table S4.2. Table showing which 'year' migrations are in each of the nine clusters. Brackets show the subset of those with genotype data. Note, for this table, a year starts in October and ends in September to cover the two monsoon periods and are based on petrel departure dates.

	Year which migration took place					
Cluster	**2009**	**2010**	**2011**	**2014**	**2015**	**Total**
1	3 (3)	2 (2)		2 (0)	1 (1)	8 (6)
2	37 (32)	29 (25)	6 (6)	7 (3)	9 (1)	88 (67)
3	2 (2)	3 (1)				5 (3)
4	43 (33)	24 (16)	3 (2)	4 (0)	2 (0)	76 (51)
5	2 (1)	2 (1)	1 (1)	3 (0)	1 (0)	9 (3)
6	5 (3)	1 (1)		1 (0)	1 (0)	8 (4)
7	1 (1)				1 (0)	2 (1)
8				1 (0)		1 (0)
9			1 (1)			1 (1)
Total	92 (74)	62 (47)	11 (10)	18 (3)	15 (2)	198 (136)

Table S4.3. Results of generalised linear models to investigate whether there is any temporal structuring in the genotypes of petrels on Round Island, using season as a) a two-level categorical variable of austral summer and austral winter, b) a three-level categorical variable which includes the transition months as one period, or c) as a four-level categorical variable with the transition periods included separately. In all models, the categorical variable of season is being compared to that of the reference level (summer).

Variable	Estimate ± SE	z value	P value
a. Two-level categorical variable of season			
(Intercept)	0.305 ± 0.063	4.843	< 0.001
Season			
Winter	-0.207 ± 0.150	-1.378	0.168
b. Three-level categorical variable of season			
(Intercept)	0.302 ± 0.065	4.652	< 0.001
Season			
Winter	-0.263 ± 0.186	-1.411	0.158
Transition 1	-0.043 ± 0.172	-0.248	0.804
c. Four-level categorical variable of season			
(Intercept)	0.302 ± 0.065	4.656	< 0.001
Season			
Winter	-0.263 ± 0.186	-1.412	0.158
Transition 1	-0.113 ± 0.227	-0.496	0.620
Transition 2	0.038 ± 0.243	0.157	0.875

Table S4.4. Pairwise comparisons between each level of the categorical variable 'strategy' from the generalised linear model examining differences in departure seasons between petrel migratory strategies. P-values are adjusted using post-hoc Tukey correction.

Contrast	**Estimate ± SE**	**P value**
Strategy 1 – Strategy 2	0.211 ± 0.471	0.998
Strategy 1 – Strategy 3	1.177 ± 0.957	0.823
Strategy 1 – Strategy 4	0.505 ± 0.478	0.899
Strategy 1 – Strategy 5	-0.683 ± 0.622	0.882
Strategy 1 – Strategy 6	-0.578 ± 0.636	0.944
Strategy 2 – Strategy 3	0.966 ± 0.857	0.870
Strategy 2 – Strategy 4	0.294 ± 0.214	0.741
Strategy 2 – Strategy 5	-0.894 ± 0.452	0.355
Strategy 2 – Strategy 6	-0.789 ± 0.471	0.548
Strategy 3 – Strategy 4	-0.672 ± 0.860	0.971
Strategy 3 – Strategy 5	-1.860 ± 0.948	0.364
Strategy 3 – Strategy 6	-1.755 ± 0.957	0.444
Strategy 4 – Strategy 5	-1.188 ± 0.459	0.100
Strategy 4 – Strategy 6	-1.083 ± 0.478	0.208
Strategy 5 – Strategy 6	0.105 ± 0.622	1.000

Table S4.5. Results of ANOVA tests for generalised linear model selection for the effect of petrel genetic background and season on petrel migratory strategies, with season included as a) a three-level categorical variable which includes the transition months as one period, or b) as a four-level categorical variable with the transition periods included separately.

Model	df	Deviance	P value
a. Three-level categorical variable of season			
Strategy ~ Trind*Season Strategy ~ Trind + Season	2	1.822	0.402
Strategy ~ Trind + Season Strategy ~ Trind	2	5.200	0.074
Strategy ~ Trind + Season Strategy ~ Season	1	3.911	**0.048**
Strategy ~ Trind Strategy ~ null	1	4.634	**0.031**
Strategy ~ Season Strategy ~ null	2	5.920	0.052
b. Four-level categorical variable of season			
Strategy ~ Trind*Season Strategy ~ Trind + Season	2	1.896	0.388
Strategy ~ Trind + Season Strategy ~ Trind	3	6.046	0.109
Strategy ~ Trind + Season Strategy ~ Season	1	4.000	**0.046**
Strategy ~ Trind Strategy ~ null	1	4.634	**0.031**
Strategy ~ Season Strategy ~ null	3	6.680	0.083

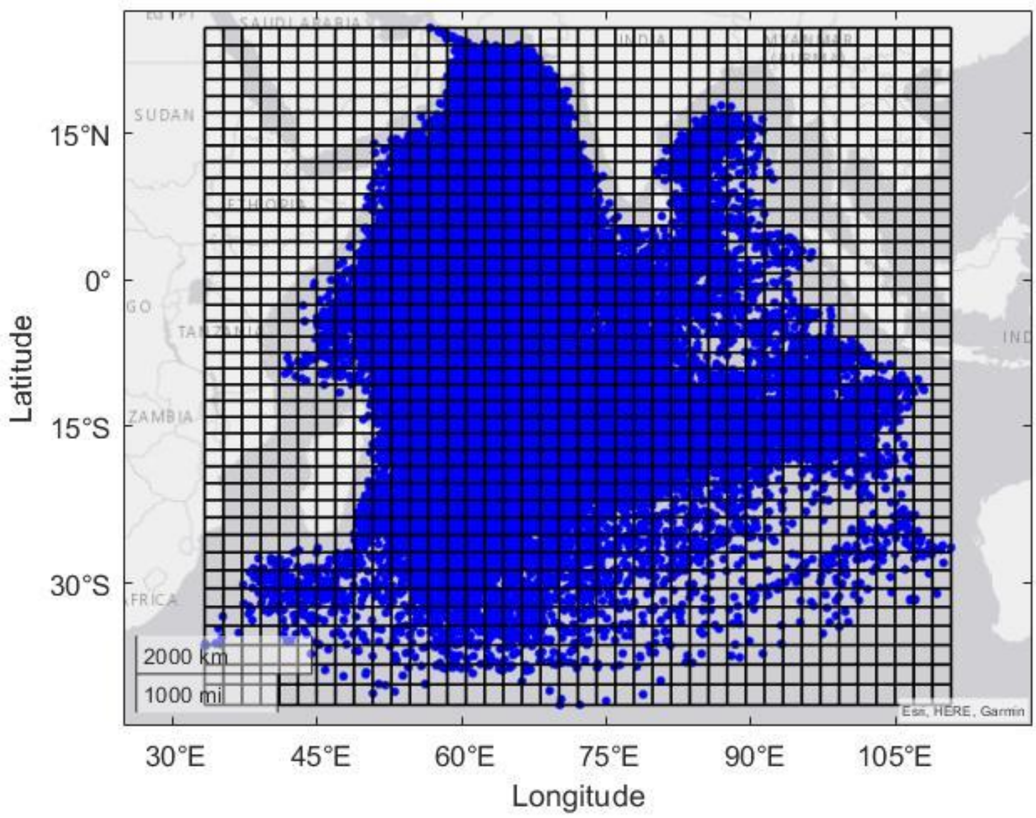

Figure S4.1. Non-breeding locations (blue points) from all Round Island petrels (n=198) tracked with geolocators. Overlaid is the 40x40 grid used for the Bayesian Mixtures Analysis. Figure kindly provided by Garth Holloway.

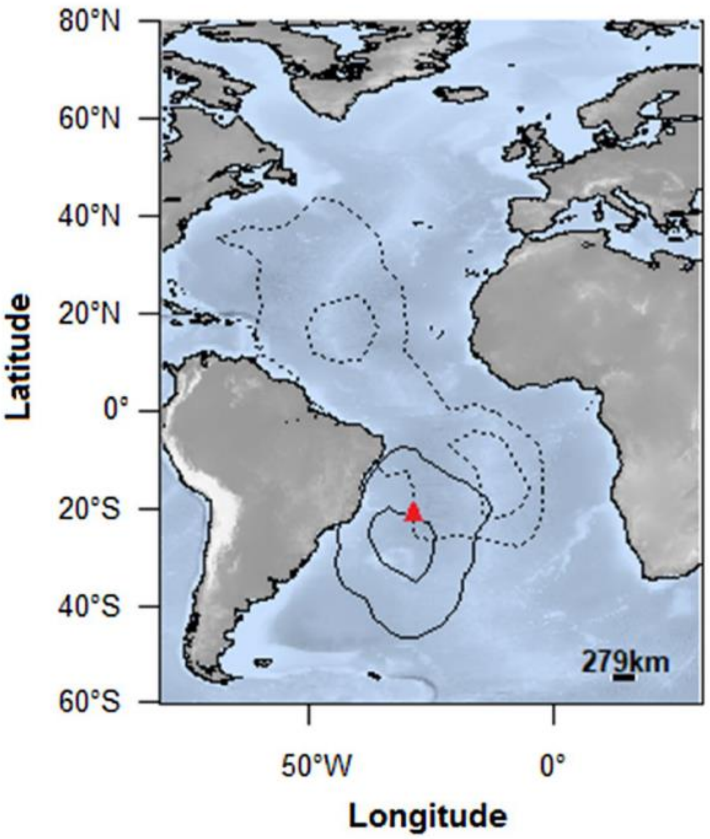

Figure S4.2. Utilisation distributions (50 and 95%) showing the two different migratory patterns of Trindade petrels tracked from Trindade Island (red circle) in the Atlantic Ocean: 1) migrating directly north to the main non-breeding area at the centre of the North Atlantic Ocean or 2) moving eastwards before finally moving north to the main non-breeding area. Solid line represents the breeding period, and dashed line the non-breeding period. Figure taken from Leal & Bugoni (2021).

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Chapter 5

Variation in night-time activity of tropical gadfly petrels with lunar cycles and at-sea locations

Photo: Sam Napaul

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Variation in night-time activity of tropical gadfly petrels with lunar cycles and at-sea locations

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Abstract

Within migratory populations, individuals can differ markedly in their migratory strategies of where they go and when they go there. Thus, substantial variation in conditions and resources across different migratory strategies has the potential to influence individual fitness and population dynamics. In marine environments, productivity and resource abundance can vary at differing spatial and temporal scales. For example, for seabirds, the availability of their marine prey can vary in abundance spatially in relation to oceanographic features, and temporally in relation to lunar and seasonal cycles. Here, using a long-term geolocator tracking dataset from nearly 200 individuals, we examined the night-time activity patterns of Round Island petrels (*Pterodroma* sp.) across their widely distributed non-breeding areas. Specifically, we ask how petrel night-time behaviour varies spatially across the tropical Indian Ocean and with the lunar cycle. We found petrel night-time at-sea activity to exhibit a clear cycle of $\sim$ 29 days, with time on the water being lowest during full moon periods and closely tracking the lunar cycle. Petrel migratory distributions cover much of the Indian Ocean, and activity patterns vary among migratory strategies, but track the lunar cycle in all cases. These results suggest that similar prey resources are likely being exploited by all petrels across the entire non-breeding range, despite the characteristically very different oceanographic conditions experienced. Variation in the numbers of tracked individuals using different migratory strategies is therefore unlikely to reflect substantial variation in prey resources and associated costs.

Introduction

Migratory species often range over large geographical areas as individuals move between geographically distinct breeding and non-breeding areas (Newton, 2010). Within populations, migratory behaviours of individuals can vary greatly, with journeys differing in route and timing, as well as distance and direction (Newton, 2010). These high levels of diversity in migratory strategies may therefore mean that individuals from the same population experience very different environmental conditions depending on when and where they go on migration (Alves et al., 2013). Substantial variation in conditions experienced during differing migratory strategies could influence the energetic costs of undertaking those journeys, with potential implications for survival rates and thus the numbers of individuals undertaking different strategies within a population (Acker et al., 2021). Understanding migratory behaviour and the fitness costs of different strategies will therefore be particularly valuable for understanding how migratory distributions are shaped (Alves et al., 2013; Payo-Payo et al., 2022).

Marine ecosystems are highly dynamic, resulting in environmental conditions and resource distributions which vary both spatially and temporally (Hunt et al., 1999; Weimerskirch et al., 2005). However, variation in resources can be more predictable, both in space and time, in some parts of the world. For example, temperate and polar systems are highly seasonally structured and this, in combination with oceanographic features (such as oceanic fronts, shelf and ice edges or upwellings), can lead to patchy but predictable resources (Weimerskirch, 2007). Studies have demonstrated that many marine predators aggregate at predictable times and places (Block et al., 2011; Davies et al., 2021b), often in association with these areas of abundant resources. By contrast, large areas of tropical oceans are often considered low in productivity and prey abundance, and have less marked seasonal variation in temperature, making prey aggregations unpredictable (Weimerskirch, 2007; but see Kumar et al., 2009). Only in very small areas of the tropics may periodic climatic phenomena (such as monsoons or seasonal upwellings) deliver relatively predictable patterns of prey availability and distribution (Wiggert et al., 2000). In systems in which resources vary in space and time, migratory strategies might be expected to vary widely (for example, because of individuals moving to locate resources), and the number of individuals undertaking different strategies might fluctuate, as the costs and benefits of different strategies might vary between years.

In addition to annual and seasonal variation in resource distributions, resource availability can also vary at much shorter time scales. For example, regular cycles in the marine environment, such as tidal and lunar cycles, can have important influences on ecosystem dynamics (Benoit-Bird et al., 2009; Embling et al., 2012). For seabirds that feed on prey that either follow or are influenced by these regular and predictable cycles, they can have significant effects on where, when, and how foraging animals can locate resources (Ramos et al., 2016; Trevail et al., 2018). Patterns in pelagic seabird behaviour have been commonly recorded to follow the lunar cycle (Pastor-Prieto et al., 2019; Ramos et al., 2016), which influences the diel vertical migration (DVM) of their prey base (such as zooplankton, squid, and fish; Benoit-Bird et al., 2009). For example, common guillemots *Uria aalge* dive deeper when nocturnal illumination is high to match the DVM patterns of their main prey (Regular et al., 2009), and many Procellariforms (such as albatrosses, petrels, and shearwaters) spend more time in flight during full moon conditions (Bonnet-Lebrun et al., 2021; Phalan et al., 2007). The availability of food resources for these predators can therefore be highly constrained by the diel cycles of their vertically migrating prey, which will vary spatially and temporally, thus having important consequences for individual behaviour and potentially also for fitness of the predators.

Technological advancements in recent decades have provided the opportunity to investigate the at-sea behaviour of seabirds when relieved from the spatial and temporal constraints of reproduction (e.g., Berg et al., 2019; Mackley et al., 2010). In particular, light-level geolocators with built-in saltwater immersion switches can be used to record individual activity throughout the non-breeding period. Ambient light levels recorded by these devices can be used to estimate geographical locations (with latitude estimated by daylength, and longitude estimated by the timing of local midday or midnight; Hill, 1994), and immersion data can be used to provide insights into the activity of the focal species, thus in combination they can provide information on the spatial distribution of patterns of activity (Dias et al., 2012b).

Here, using an extensive dataset with nearly 200 individual non-breeding migrations tracked using geolocation immersion loggers, we study the night-time at-sea behaviour of the Round Island petrel (*Pterodroma* sp.) in their widely distributed non-breeding areas. Breeding on Round Island, Mauritius, in the western Indian Ocean, these tropical gadfly petrels (*Pterodroma* sp.) have been shown to repeatedly undertake long-distance migrations to different parts of the Indian Ocean (Chapter 3), ranging from the Somali Basin and Arabian Sea to the north, to the Bay of Bengal, and elsewhere in the Indian Ocean (Chapter 4). Previous research has shown that tracked petrels vary in the frequency with which they migrate to these different areas (Chapter 4), yet whether this is related to the different costs and consequences of undertaking each strategy is unclear. The different areas used by the petrels differ markedly in their oceanographic conditions, including with respect to primary productivity. For example, despite both being in the tropical northern Indian Ocean, the Arabian Sea in the northwest is one of the most productive oceanic regions in the world, whereas the Bay of Bengal in the northeast Indian Ocean is traditionally considered to be a region of lower biological productivity (Dalabehara & Sarma, 2021; Prasanna Kumar et al., 2002; Zhou et al., 2022). Round Island petrels therefore provide an ideal system in which to investigate how individual activity patterns vary across large geographical and environmentally contrasting areas. We pay particular attention to night-time activity, as gadfly petrels feed mainly on mesopelagic fishes and squids (Cherel & Bocher, 2022), the activity patterns of which are in turn influenced by the lunar cycle (Benoit-Bird et al., 2009). Consequently, we ask, 1) does petrel activity vary in relation to the lunar cycle, 2) does petrel activity vary spatially across different areas of the Indian Ocean (using previously defined migratory strategies), and 3) does the link between activity and lunar cycle vary with migratory strategy?

Materials and methods

Geolocator deployment and processing

We collected data on the non-breeding migrations and at-sea activity of 198 Round Island petrels from Round Island, Mauritius (19.85° S, 57.78° E) tracked over 9 years (2009-2018) using tarsus-mounted geolocation immersion loggers (hereafter 'geolocators'). Two brands of geolocator were used: British Antarctic Survey model MK15 and Migrate Technology Intigeo models C250 and C330. All geolocators measured light levels, saltwater immersion, and sea surface temperature (SST). The devices were deployed on adult petrels between November 2009 and June 2016 (see Table S5.1 for details). Petrels were caught by hand, and geolocators were deployed and recovered primarily during routine breeding surveys and during specific 1-week expeditions in 2009-2012. For more details on geolocation tagging see Chapters 3 and 4.

We used the R packages TwGeos (Wotherspoon et al., 2016) and SGAT (Lisovski et al., 2020; Lisovski & Hahn, 2012; Sumner et al., 2009) to estimate Round Island petrel locations from the raw light, immersion, and SST data collected by geolocators; see Chapter 3 for details. Briefly, SGAT uses a Bayesian framework to combine tag data with prior information on i) the twilight error distribution, ii) the flight speed distribution, as well as iii) a land and SST mask based on satellite maps from NOAA to sample the most likely locations of each individual. To identify start and end dates of petrel migration, these location estimates were then used (to calculate the distance from Round Island) along with the raw light and activity geolocator files, in a two-state hidden Markov model (HMM) for each individual to classify each calendar day as ashore or at-sea. Migration periods were defined as a sequence of consecutive days that were assigned to the same behaviour (at-sea) by the HMM for a period of at least three months, before switching to the other behavioural state (ashore; for more details see Chapter 3).

Migratory strategies and durations

To identify the different migratory strategies undertaken by the petrel population, we used a Bayesian Mixtures Analysis (BMA; Holloway et al., in review). This method groups individual petrels based on similarities and differences in the whole-track distribution with others in the BMA. For full details see Chapter 4. This resulted in nine different migratory strategies, with petrels migrating to the Somali Basin (n = 88), Arabian Sea (n = 76), central Indian Ocean or Ninety East Ridge (n= 8 and 8), an area straddling the Chagos-Laccadive plateau (n = 9), the Bay of Bengal (n = 5), or an alternative strategy (n = 2, 1, and 1).

The duration of the migratory period for each individual was calculated as the interval between departure and colony return, using the dates identified from the HMM. As migratory durations vary among individuals (mean: 177.5 days ± 2.0 SE, range: 106-275 days), they are presented as proportions of the total migration period to facilitate comparisons across individuals.

At-sea activity analysis

Immersion in seawater was measured every 3 s or every 30 s, for MK15 and C250/C330 tags, respectively, and recorded as 0 or 1. These data were then stored as the sum of positive tests at 10-minute intervals, resulting in values from 0 (entirely dry for 10 minutes) to either 20 or 200 (entirely wet for 10 minutes). To make the outputs from different geolocators equivalent, all sampling points from the C250/C330 geolocators were scaled by a factor of 10 (thus also ranging from 0 to 200). For each saltwater immersion value, we linearly interpolated positions using the GLS locations (available twice-daily at solar noon and solar midnight) for each individual using the interpolateTime function (with great circle distance) in the move R package (Kranstauber et al., 2020). This resulted in one geographical location every 10 minutes for each individual, with a corresponding activity value. All sun and moon data were extracted using the suncalc R package (Thieurmel & Elmarhraoui, 2019), and when altitudinal data were returned as radians, these were converted to degrees using the REdaS R package (Hatzinger et al., 2014; Maier, 2022). Solar elevations were then obtained for each of these locations and used to separate activity into daylight (> -6°) and darkness (≤ −6°). We did not distinguish day and night from twilight as the duration of twilight periods in the tropics is relatively short (Mills, 2008). The illuminated fraction of the moon (0 (new moon) to 1 (full moon)) was also extracted, but only retained during the night and when the moon was above the horizon (> 0°); values were otherwise recorded as 0. Activity data were then summarised over continuous day-night periods, and the average moonlight illumination per night calculated.

Statistical analysis

To investigate the influence of the lunar cycle on petrel night-time activity, we used a binomial generalised additive mixed model (GAMM) with logit link function using the mgcv R package (Wood, 2011). Models were fitted using the 'bam' rather than the 'gam' function of mgcv owing to the large size of the dataset. The response variable was the proportion of the night spent dry, created using a two-column matrix containing the sum of dry sampling points (in our case, the successes) and the sum of wet sampling points (failures). The illuminated fraction of the moon (averaged across the night, as described above) was included as a fixed effect. To examine if petrel behaviour varied spatially, we also included migratory strategy as a fixed effect, as well as a two-way interaction between moonlight and strategy. We included petrel identity as a random term, and the proportion of migration duration as a smoothing term. Migration duration was included as a proportion (rather than as a continuous count of days) to investigate how patterns in activity vary over the course of the migratory period while accounting for the different durations of petrel migrations. It was also included to control for temporal autocorrelation in activity data (i.e., activity of an individual on a given day is likely to be similar to its activity on the previous day). Non-significant ($p < 0.05$) terms were sequentially removed using backwards stepwise deletion and significance of terms was determined using ANOVA. All analyses were conducted using R version 3.6.2 (R Core Team, 2019).

Results

Round Island petrel night-time activity showed clear cyclical patterns (cycle length: ~ 29 days) across the non-breeding period (Fig. 5.1). These cyclical patterns occurred in all individual tracks and were significantly linked to moonlight, with petrels spending more time on the water during new moon and less during full moon (Fig. 5.2; Table 5.1). Patterns of activity across the lunar cycle varied significantly among the migratory strategies (Table 5.1) but the differences were slight (Fig 5.2). For the two migratory strategies with large numbers of tracked individuals (strategy two to the Somali Basin, and strategy four to the Arabian Sea), the proportion of time spent dry during a new moon was 0.29 and 0.26, and for a full moon was 0.91 and 0.87, for strategy two and four, respectively. Across all strategies, the proportion of time spent dry during new moon periods ranged from 0.13 (strategy eight, southwards migration close to Round Island) to 0.36 (strategy nine, long looping migration to the central the Indian Ocean and then on to the Somali Basin), and for full moon, ranged from 0.77 (strategy eight) to 0.92 (strategy one and six (central Indian Ocean and Ninety East Ridge)). However, these extremes are based on migratory strategies with few (< 10) tracked individuals, and strategies with more individuals were more similar. Regardless, there is a clear lunar-structured pattern in activity across all migratory strategies.

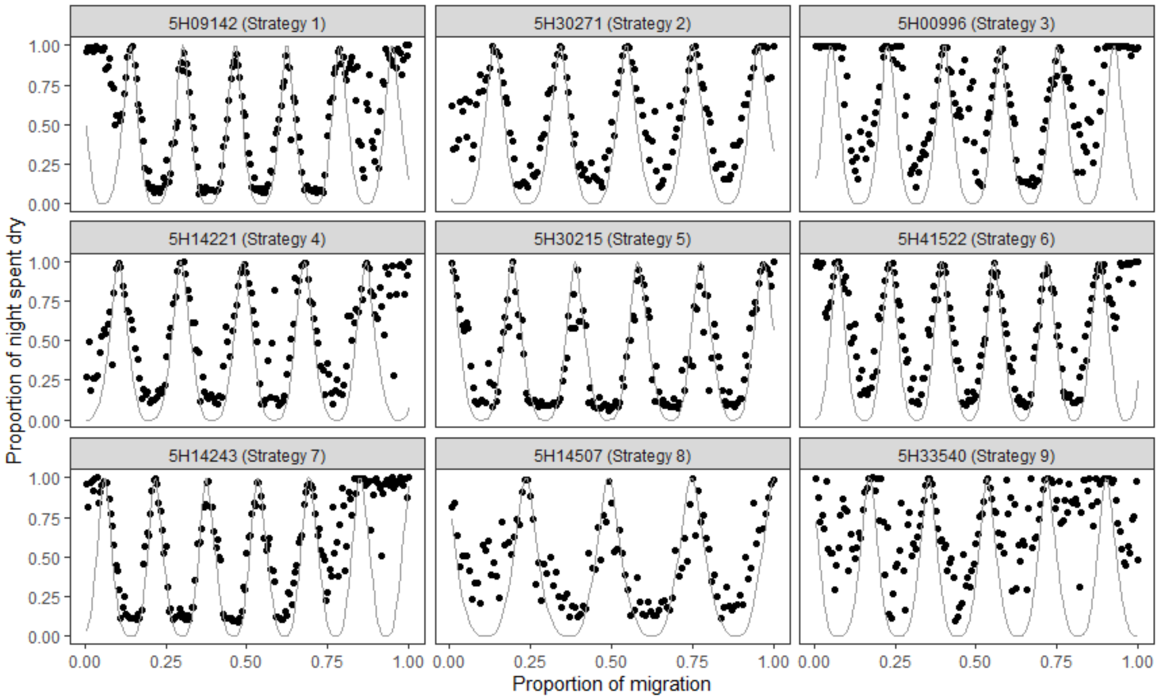

Figure 5.1. Proportion of night spent dry for nine randomly sampled Round Island petrels from each of the nine migratory strategies over the non-breeding period. Black points represent raw activity data from geolocator immersion loggers, and solid grey lines indicate lunar cycles. Note, individuals may be tracked in different years and migrations occur at different times.

Petrels also spent significantly less time on the water at the start and end of the migration period (Fig. 5.3; Table 5.1), likely representing more time spent flying during the in- and out-bound phases of individual migratory journeys. Daytime activity was not analysed in this study, but a similar pattern of less time in the water at the start and end of migration was also observed in the day (Fig. S5.2). However, these extended dry periods at the start and end of migration at night were not seen in all individuals, even when individuals were seemingly taking rapid directional movements to non-breeding areas, which might suggest that some individuals are spending more time on water (possibly foraging) during passage than others.

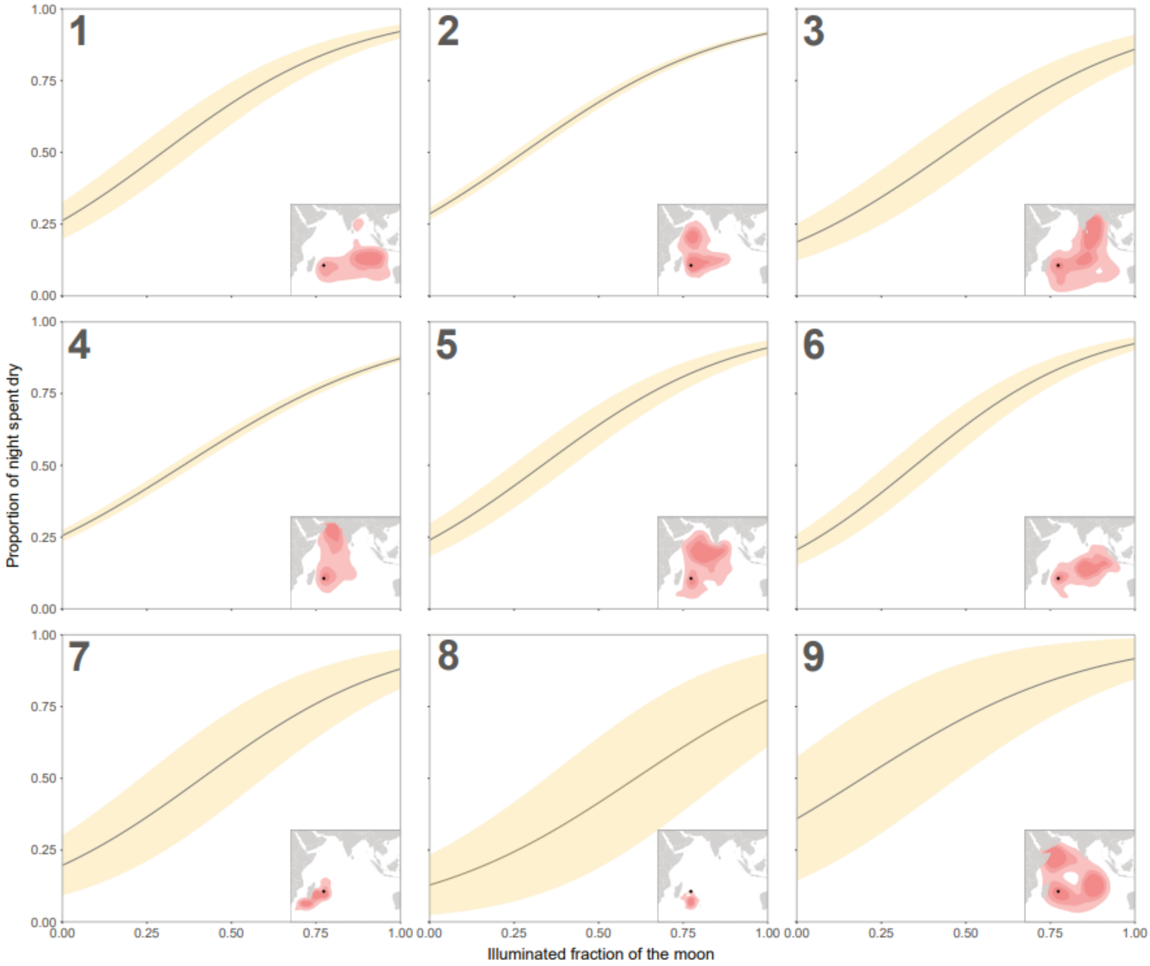

Figure 5.2. Predicted effect of moonlight on the nocturnal activity (proportion of time spent dry) of Round Island petrels during the non-breeding period from generalised additive mixed model (fitted lines ± 95% confidence intervals), split by migratory strategy (numbered). Map insets show the corresponding strategy, with the black diamond representing Round Island. Predictions use the population-level mean of the random effect of petrel ID, and are based on a migration proportion of 0.5. To see how lines for each strategy overlap (without CIs) see Figure S5.1. Sample sizes for migratory strategy 1-9 are: 8, 88, 5, 76, 9, 8, 2, 1 and 1.

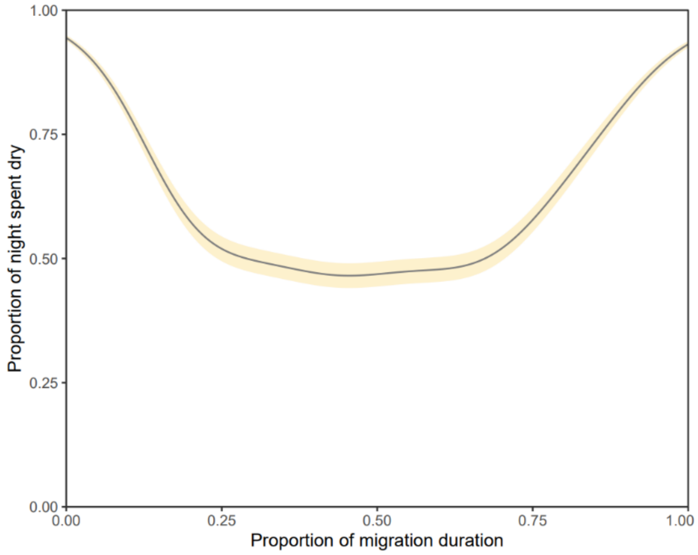

Figure 5.3. Predicted effect of the proportion of migration duration on the nocturnal activity (proportion of time spent dry) of Round Island petrels during the non-breeding period from generalised additive mixed model (fitted lines ± 95% confidence intervals). Predictions use the population-level mean of the random effect of petrel ID, and are based on the median moonlight intensity of 0.24, and the migratory strategy with the largest sample size (strategy 2).

Table 5.1. Results from generalised additive mixed model to investigate how petrel night-time activity varies spatially, across the lunar cycle, and across the migration period. The reference level for the categorical variable of migratory strategy is strategy 2 due to this level having the largest sample. Significant effects ($p < 0.05$) are highlighted in bold. Deviance explained = 64.7%.

Parametric coefficients	**Estimate**	**SE**	**Z value**	**P value**
(Intercept)	-0.180	0.051	-3.544	**< 0.001**
Moonlight	3.289	0.001	5238.438	**< 0.001**
Strategy 1	-0.119	0.176	-0.068	0.498
Strategy 3	-0.549	0.219	-2.505	**0.012**
Strategy 4	-0.156	0.075	-2.084	**0.037**
Strategy 5	-0.238	0.167	-1.424	0.154
Strategy 6	-0.433	0.176	-2.457	**0.014**
Strategy 7	-0.489	0.341	-1.434	0.151
Strategy 8	-0.999	0.480	-2.083	**0.037**
Strategy 9	0.337	0.480	0.703	0.482
Moonlight : Strategy 1	0.205	0.002	92.015	**< 0.001**
Moonlight : Strategy 3	-0.017	0.002	-6.788	**< 0.001**
Moonlight : Strategy 4	-0.294	0.001	-334.417	**< 0.001**
Moonlight : Strategy 5	0.172	0.002	85.220	**< 0.001**
Moonlight : Strategy 6	0.558	0.002	257.906	**< 0.001**
Moonlight : Strategy 7	0.121	0.004	32.257	**< 0.001**
Moonlight : Strategy 8	-0.145	0.006	-22.896	**< 0.001**
Moonlight : Strategy 9	-0.308	0.006	-49.041	**< 0.001**

Smoothed terms	**Effective degrees of freedom**	**Reference degrees of freedom**	**Chi squared**	**P value**
s(Proportion of migration)	9	9	37648182	**< 0.001**
s(Petrel ID)	189	189	15646498	**< 0.001**

Discussion

Night-time at-sea activity of tropical Round Island petrels followed repeated cycles (~ 29 days) which tracked lunar cycles, with petrels spending less time on the water during nights with higher moonlight intensity (around the full moon), and more on nights with little moonlight (around the new moon). This influence of the lunar cycle on night-time activity during the non-breeding period has been documented for many other seabirds, including other Procellariforms, such as albatrosses (Phalan et al., 2007), shearwaters (Yamamoto et al., 2008; Dias et al., 2012b), other gadfly petrels (Pastor-Prieto et al., 2019; Pinet et al., 2011; Ramírez et al., 2013; Ramos et al., 2016), as well as gulls (Cruz et al., 2013), but does not occur across all species (e.g., Bulwer's petrel *Bulweria bulwerii*; Dias et al., 2015; Dias et al., 2016). There are three non-mutually exclusive hypotheses as to why this might be the case. First, these patterns may reflect the diel vertical migrations of plankton and their predators which, following an endogenous lunar rhythym, come to the sub-surface layer where seabirds forage during lower moonlight intensities (Benoit-Bird et al., 2009). Although not much is known about the diet of Round Island petrels in the Indian Ocean, other gadfly petrels prey mainly upon mesopelagic fishes (chiefly myctophids) and squids, with their relative proportions depending on species and location (Cherel & Bocher, 2022). Round Island petrels may therefore be taking advantage of higher prey availabilty during periods with little moonlight (when prey come to the surface), thus spending more time sat on the water and feeding. Second, during a full moon, petrels appear to spend most of their time in flight, perhaps increasing their search effort for prey using the natural light source from the moon. For example, some species of seabird have been shown to increase flight and presumably foraging activity around twilight periods due to higher DVM prey availability at these times (Pajot et al., 2021; Ramos et al., 2016). Finally, less time spent on the water during the full moon may be a predator avoidance strategy, as predation risk by visual predators at sea may increase with light levels at night (Yamamoto et al., 2008). However, the large amount of time that Round Island petrels spend sitting on the water during the day makes the latter hypothesis less likely, unless predator activity levels are low during daylight hours.

Most studies of lunar effects on nocturnal, at-sea activity of seabirds, including this study, have been conducted using geolocation immersion loggers (e.g., Pinet et al., 2011; Ramírez et al., 2013; Ramos et al., 2016). However, these data only provide information on the time spent on water making it difficult to determine what that behaviour (e.g., foraging or loafing) actually represents. Studies using GPS loggers have been able to characterise finer-scale at-sea behaviours (as a result of higher resolution data; e.g., Pajot et al., 2021; Ravache et al., 2020). For example, GPS data from wedge-tailed shearwaters *Ardenna pacifica* in New Caledonia, albeit during the breeding season, revealed increases in nocturnal foraging activity during moonlit nights (Ravache et al., 2020). This, together with the fact that many species of petrel obtain the majority of their food at night (Imber, 1975), suggests that petrels vary in the amount of effort expended on foraging throughout the lunar cycle. Further investigation with the data from this study could explore variation in the frequency of landings on the sea across moonless and moonlit nights, with more frequent landings potentially suggesting greater foraging effort (Dias et al., 2012a).

Patterns of lunar-related activity varied statistically among the nine different petrel migratory strategies; however, the differences were quite small and there is a clear lunar-structured pattern in activity across all strategies. Even small differences in activity patterns could potentially reflect differences in prey type or abundance in different parts of the Indian Ocean, while more time spent in flight could mean that prey are more patchily distributed. However, further investigation will be needed to relate actual locations to environmental conditions that could influence petrel prey, such as sea surface temperatures and ocean bathymetry (e.g., Dias et al., 2012b). Further investigations could also include comparisons of diurnal and nocturnal petrel activity, to examine the influence of night-time activity on what individuals do during the day, which might reveal if there are costs carried over to subsequent days.

Round Island petrels spent significantly less time on the water at the start and end of the migration period. For some individuals, this was particularly evident as geolocator loggers were primarily dry for multiple conseqtutive nights, likely suggesting sustained periods of flight. However, some individuals did have periods of immersion during passage, which could suggest that foraging is either more possible or more of a necessity for some individuals travelling to their non-breeding grounds. This overall increase in flight time during passage, compared to residency at the non-breeding grounds, has been seen in many other seabird species (Bonnet-Lebrun et al. 2021; Dias et al., 2012a). As transit times were included within the analyses of spatial variation in activity, comparison of models that include and exclude passage periods could be a means of exploring their contribution to the spatial variation in activity. However, separating migratory journeys into transit and residency periods in this system, and likely some other tropical systems, may be difficult. For example, not all Round Island petrels show directed migrations and clear residency periods in non-breeding areas, like those of Barau's petrels *Pterodroma baraui* nesting on nearby Reunion Island (Pinet et al., 2011), and some exhibit a less direct 'looping' behaviour which is common of tropical seabird foraging behaviour (Soanes et al., 2021; Weimerskirch, 2007).

In conclusion, despite Round Island petrels migrating to characteristically very different parts of the Indian Ocean and at different times of year, all individuals show strongly lunar-structured night-time activity patterns with petrels spending less time on the water during nights with higher moonlight intensity. These results suggest that petrels feed on similar mesopelagic prey, which likely all display diel vertical migrations, across the entire non-breeding range. Variation in the numbers of tracked individuals using different migratory strategies is therefore unlikely to reflect substantial variation in prey resources and associated costs.

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Supplementary materials to Chapter 5: Variation in night-time activity of tropical gadfly petrels with lunar cycles and at-sea locations

Table S5.1. Details of all geolocator deployments and recoveries on adult Round Island petrels from 2009-2019.

Petrel year	Number deployed	Number recovered* (%)
2009	135	110 (81.5)
2010	84	79 (94.0)
2011	28	18 (64.3)
2012	79	64 (81.0)
2014	49	36 (73.5)
2015	21	15 (71.4)
2016	25	15 (60.0)
Total	**421**	**337 (80.0)**

* Geolocators recovered between October 2010 and December 2019.

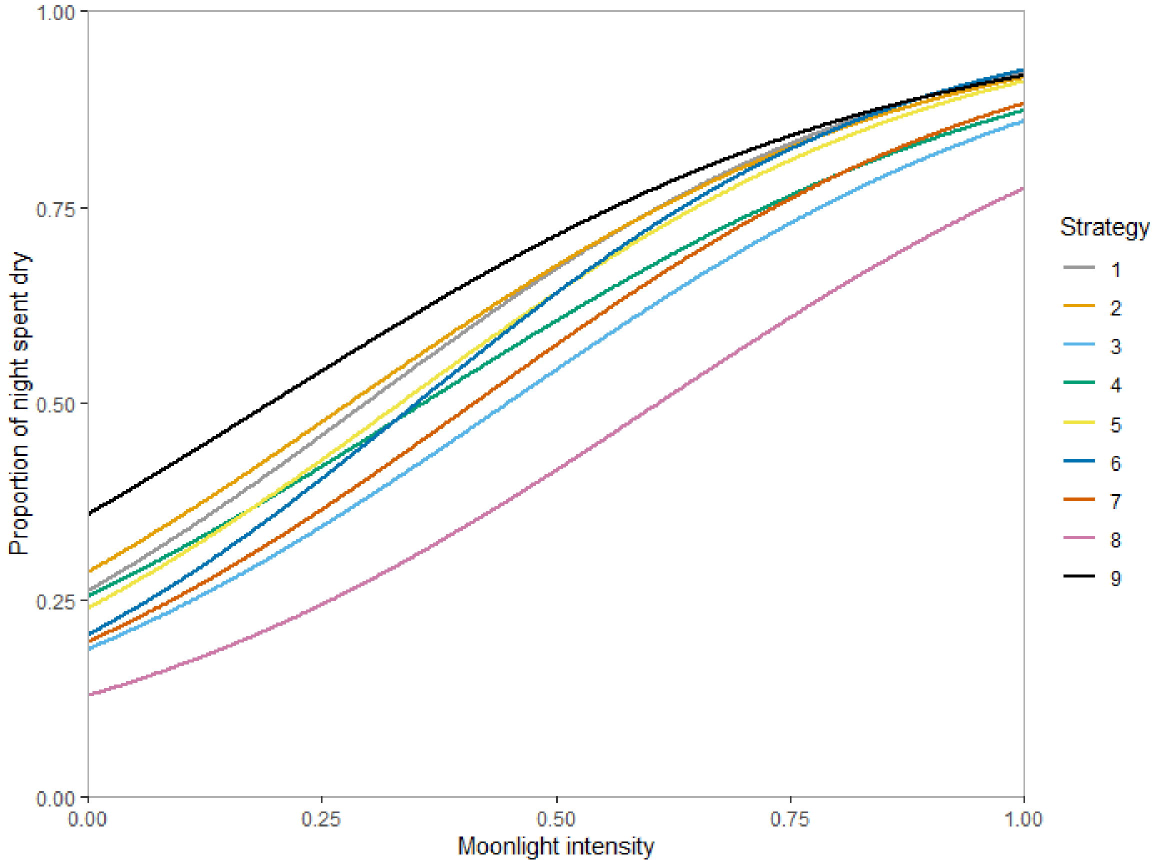

Figure S5.1. Predicted relationship between moonlight and night-time activity, coloured by strategy (confidence intervals not shown for clarity, but are shown in Figure 5.2).

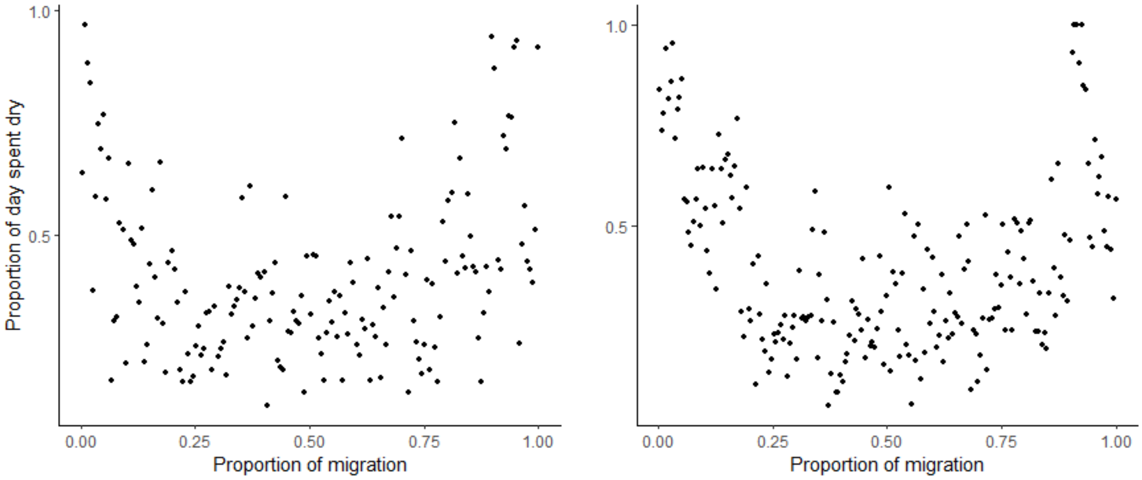

Figure S5.2. Proportion of day spent dry for two Round Island petrels over the non-breeding period. Black points represent raw activity data from geolocator immersion loggers and show the pattern of less time in the water at the start and end of migration.

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Chapter 6

Utility of automated time-lapse cameras to monitor breeding phenology and nest success of tropical ground-nesting seabirds

Photo: Sam Napaul

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Utility of automated time-lapse cameras to monitor breeding phenology and nest success of tropical ground-nesting seabirds

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Abstract

Variation in reproductive success is often a key contributor to population trends and can inform the design of conservation actions to address population declines. However, for many species these data are challenging to obtain. For example, many tropical seabirds breed year-round, often in difficult-to-access breeding colonies that can be easily disturbed by researcher presence. The use of time-lapse photography to capture breeding events for colonial seabirds is being increasingly used; however, it is not yet known how well this approach will work for tropical seabirds and in the challenging weather conditions of tropical systems. Here, we (a) test the utility of automated time-lapse photography as a tool for monitoring breeding phenology and nest success of tropical ground-nesting seabirds, using the Round Island petrel (*Pterodroma* sp.), found in the western Indian Ocean, as our study system and, by hosting our images on the Seabird Watch citizen science website, we (b) assess the consistency of image processing by researchers and citizen scientists. Ten time-lapse (one image per hour) cameras deployed at historically productive petrel sites successfully generated over 180,000 images over a two-year period, including periods with very high winds. Manual processing by researchers of a sample (26.2%) of images generated estimates of key breeding metrics consistent with previous field studies, and comparison of these images with a subsample (14.3%) annotated by citizen scientists revealed (i) that citizen scientists consistently underestimated the number of petrels in images in comparison to researchers, but typically only by missing one individual in an image, and (ii) that counts from cameras closer (< 3-4 m) to nest sites were more consistent among observers than those further away (> 7 m). Time-lapse cameras can thus be a viable tool for monitoring ground-nesting seabirds in tropical systems and, as this approach may be particularly valuable for species located in remote areas where year-round monitoring by fieldworkers is rarely possible, we provide recommendations for those interested in using this method.

Introduction

Understanding variation in reproductive success of populations is often important for identifying appropriate targets for management and conservation (Morrison et al., 2022). Long-term collection of information on breeding events provides opportunities to explore the effects of different direct and indirect threats on reproduction, and to understand causes of long-term population changes. However, collecting these data can be challenging for species that breed in remote locations, where time and resource constraints can limit opportunities for direct observations.

Seabird populations have declined faster than any other avian taxa in the last few decades (Croxall et al., 2012; Dias et al., 2019; Paleczny et al., 2015). The drivers of these declines can operate both on land at breeding sites, through threats such as the introduction of invasive alien species and habitat destruction, and at sea, through threats including fisheries bycatch, climate change, and various other anthropogenic pressures (Dias et al., 2019). Understanding where and why species are affected is therefore essential to help guide conservation actions to attempt to reverse these declines. Pelagic seabirds are most accessible to researchers when they attend their breeding colonies, making this stage of their annual cycle comparatively easier to monitor. However, many seabirds breed in remote locations, making collection of monitoring data expensive both in terms of time and money (Edney & Wood, 2021). Furthermore, direct observations of nests can sometimes introduce bias to breeding metrics, as nests may be more likely to fail from observer disturbance and nest abandonment (Carey, 2009).

Tropical seabirds can present unique challenges to monitoring work as they often breed on very remote, difficult to access, and uninhabited islands. This is reflected in the lack of studies on tropical seabirds in comparison to those that inhabit temperate and polar regions (Chapter 2). In addition, the often aseasonal and asynchronous nature of their breeding phenology (Carr et al., 2021; VanderWerf & Young, 2018) means that monitoring may have to span extended breeding seasons or capture irregular nesting in response to specific environmental conditions (e.g., Jaquemet et al., 2007). In practice, this can mean that multiple on-the-ground visits are required to adequately monitor breeding tropical seabirds.

A potential approach to overcome some of these challenges is the use of time-lapse photography (see Black, 2018; Edney & Wood, 2020). Recent advances in this technology, such as more affordable cameras, and improved storage capacity and battery life, have led to time-lapse cameras being increasingly used to research and monitor birds around the world (Black et al., 2017; De Pascalis et al., 2018; Otsubo & Higuchi, 2022). Time-lapse cameras are programmed to take images at predetermined time intervals (e.g., one image every hour or every day), and thus are suited to collecting long-term time series data. For example, time-lapse studies have proven successful in measuring breeding phenology and nest success (Hinke et al., 2018), patterns of nest occupancy and/or attendance (Bennett et al., 2022; Huffeldt et al., 2013), nest predation (Collins et al., 2014), and population counts (Kliska et al., 2022) in a range of seabirds. They are ideal for monitoring colonial species, such as surface- or cliff-breeding seabirds, in which a single vantage point can capture the activity of multiple individuals/nests. However, whilst autonomous time-lapse systems have the potential to greatly facilitate tropical seabird monitoring, their use has mainly been limited to temperate and polar species (Black et al., 2018a; Black et al., 2018b; De Pascalis et al., 2018), which have highly seasonal and synchronous annual cycles. So far, only a very restricted number of studies have used camera-traps to monitor tropical seabirds, and those have tended to focus on breeding and foraging behaviours (Hart et al., 2016; Le Corre et al., 2020; Mendez et al., 2017) or impacts of invasive species (Raine et al., 2019). Time-lapse camera systems have been used successfully to record year-round colony attendance patterns in penguins (Dodino et al., 2018) and so can potentially support the required fieldworker-hours as well as expanding the temporal and spatial coverage of tropical seabird monitoring, which is often year-round or for large parts of the year (Carr et al., 2021). For ground-nesting seabirds which nest in high densities, in-the-field monitoring can make it difficult to follow individual breeding attempts across time, whereas regular time-lapse images may make this easier. However, the utility of using time-lapse cameras to monitor individual tropical seabird breeding attempts has yet to be tested.

Time-lapse camera systems can potentially provide a solution to the impracticalities of year-round, large-scale monitoring by fieldworkers, but the wealth of photographic information produced can be challenging to process. One of the most common methods used is manual image processing (Edney & Wood, 2021). This requires researchers to examine images individually and record the appropriate information; however, this method can be very time-consuming, and the number of images can quickly exceed available researcher processing time. Instead, another method successfully proven to speed up image processing, particularly before automated machine-learning processes can be trained on a new species, is the engagement of citizen scientists (Green et al., 2022; Hsing et al., 2018; Jones et al., 2018). For example, one popular citizen science project focused on seabird monitoring is Penguin Watch. In this project, volunteers are asked to classify time-lapse camera images by tagging and counting juvenile and adult penguins (Jones et al., 2018). While this project has successfully validated the use of citizen science for annotating penguin images (Jones et al., 2018), it is important to note that data validation remains an important process and is required for citizen science-based projects on other species.

In this study, we test the utility of automated time-lapse cameras to monitor the breeding phenology and nest success of tropical ground-nesting seabirds. Our study is based on Round Island, Mauritius, in the western Indian Ocean, where a team of researchers are continuously based and carry out regular surveys of breeding seabirds, allowing us to establish cameras and assess the associated logistical requirements for deployment in remote areas. Specifically, we use the Round Island petrel (*Pterodroma* sp.) as a model system to assess, 1) the capacity of time-lapse cameras to capture consistent images over long time periods in tropical conditions and, 2) the frequency of daily time-lapse images required to capture key metrics of breeding phenology and success. By hosting our images on the Seabird Watch citizen science website (a sister project to Penguin Watch focused on black-legged kittiwakes *Rissa tridactyla*, guillemots *Uria* sp., and more recently Round Island petrels), we also assess 3) the consistency of image processing by researchers and citizen scientists in order to validate this processing approach. Finally, in light of our findings and experience we provide recommendations for those interested in using this method.

Methods

Study area and species

This study was conducted at Round Island Nature Reserve (19.85° S, 57.78° E), a 219-ha island situated 22.5 km off the north coast of Mauritius in the western Indian Ocean (Fig. 6.1). Five species of seabird breed on Round Island including an unusual population of *Pterodroma* petrels, known locally as the Round Island petrel. Recent genetic evidence has revealed this population to consist of a hybrid mix of at least three species of *Pterodroma* petrel: Trindade *P. arminjoniana*, Kermadec *P. neglecta*, and Herald *P. heraldica* (Booth Jones et al., 2017; Brown et al., 2010; Brown et al., 2011). Round Island petrels are medium-sized (300-500 g), surface nesters, breeding in a variety of habitats such as under rock ledges, in clusters of boulders, and in and under the native tussock grass (*Vetiveria arguta*) and Scaevola bushes. They breed all year round, with chicks and eggs found in any month of the year, although there is a peak in egg-laying in August-October (Nicoll et al., 2017; Tatayah, 2010). Since 2001, petrel surveys have been undertaken every month or two months and involve regular visits to known nesting areas to monitor breeding activity (including presence or absence of eggs and chicks), ringing of adults and chicks (with South African Bird Ringing Unit numbered rings), and their subsequent recapture.

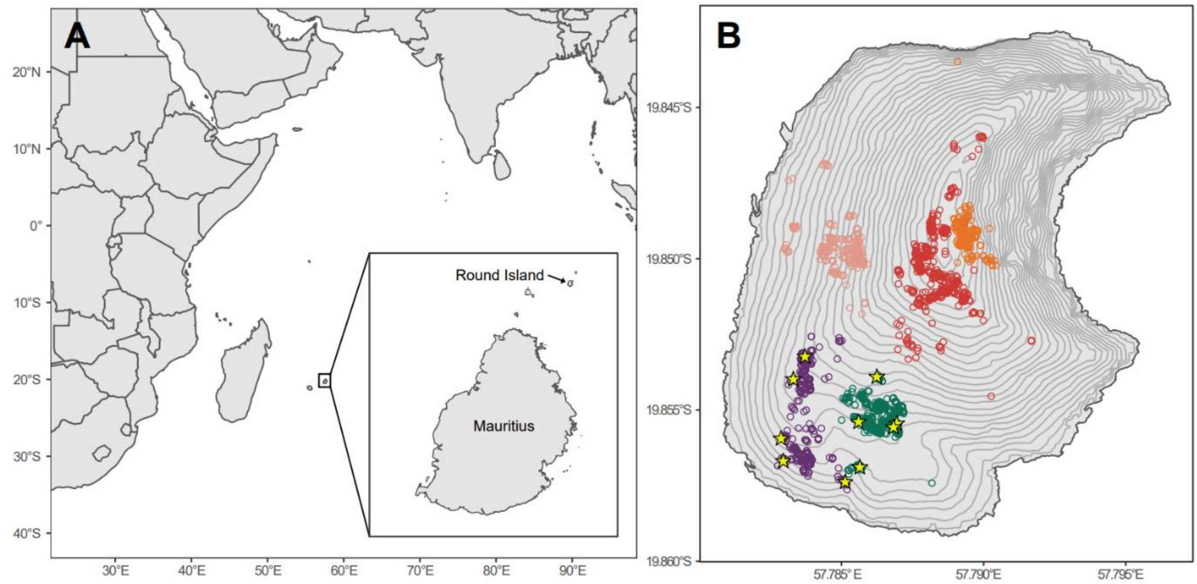

Figure 6.1. Locations of (A) Round Island in relation to Mauritius and the surrounding western Indian Ocean, and (B) Round Island petrel nest sites (open circles) and ten deployed time-lapse cameras (yellow stars). Petrel nest sites (as of 29th November 2019) are clustered into five main colonies: purple = 'south-west coast' (SWC), green = 'above camp' (ABC), pink = 'big slab' (BSL), red = 'summit' (SUM), and orange = 'crater' (CRA). Elevation contours are at 10 m intervals.

Camera deployment

We deployed 10 Reconyx camera traps (five each of Hyperfire HC600 and Hyperfire 2 HF2X, Reconyx, Holmen, USA) at sites at which productive breeding attempts had occurred within the last five years of petrel surveys (Fig. 6.1B). Each camera was attached to a vertical aluminium pole by a stainless-steel bracket (allowing the angle of the camera to be adjusted) and supported by four additional bars which were drilled into the rock (Fig. 6.2). The location of each camera was dictated by the number of marked nest sites that could be viewed without impairing the vision of nest contents (range of 2-10 m away), and by the angle of the sun. Camera sites were also determined opportunistically using locations with higher elevation for the central pole or elevated substrate for anchoring the camera system. The cameras were programmed in time-lapse mode to take photographs every hour across every 24-hour period between 04 December 2019 and 08 March 2022, and each camera captured contents of between two and five previously identified nest sites. Once installed, the cameras were maintained approximately every two months during routine petrel surveys in order to retrieve SD-cards, check operations, and change the (rechargeable Alkaline AA) batteries.

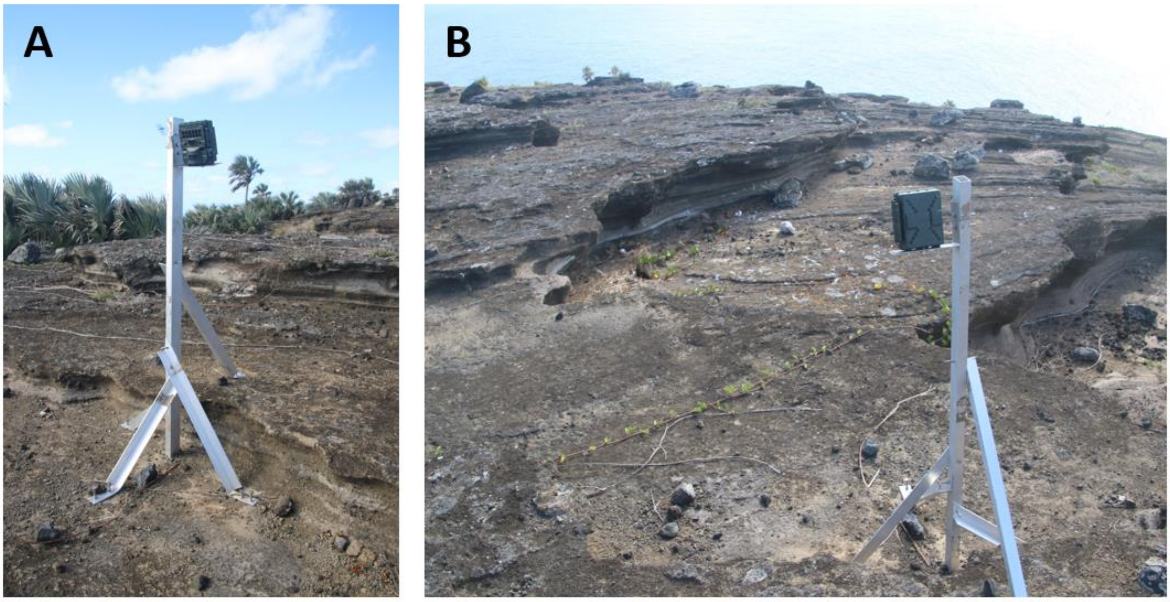

Figure 6.2. Front (A) and rear (B) view of one time-lapse camera trap and stand in situ on Round Island, Mauritius. Photo credit: Kirsty Franklin.

Photo classification

A subset of images (n = 47,570) from 04 December 2019 to 22 June 2020 were manually processed by two authors (KAF and MH). For each image, a range of image- and nest-level features of petrel breeding activity were recorded. Full descriptions and visual representations of each of these features can be found in Table 6.1 and the Supplementary material (Figures S6.1-S6.6). Key phenological dates were estimated using these nest-level features: the first date on which an egg or (apparently) incubating adult was identified at a nest site, and the first date on which a chick was observed, were estimated to be the dates of egg-laying and egg-hatching, respectively. The last date on which a large chick was observed at a nest site, or once it becomes undistinguishable from an adult, was estimated as the date of chick fledging.

Table 6.1. Image- and nest- level data on Round Island petrel breeding activity manually extracted from time-lapse camera images.

Variable recorded	Type	Description	Example image
Number of adult petrels	Continuous, whole number	The number of definite adult Round Island petrels in an image, including birds not attending nest sites but excluding flying birds	
Total number of adult birds	Continuous, whole number	Same as above, but includes unidentifiable adult birds difficult to distinguish from Round Island petrels (e.g., wedge-tailed shearwater)	
Breeding attempt	Continuous, whole number	Nest-level breeding attempt from start of monitoring, as multiple birds can breed in the same nest site	
Breeding activity	Categorical:	Nest-level description of breeding activity:	
	Apparently incubating	Adult petrel that appears to be incubating due to their posture and prolonged presence in a nest site	Figure S6.1
	Incubating	Incubating adult petrel confirmed only once an egg is observed	Figure S6.1
	Egg	A petrel egg visible in a nest site	Figure S6.2
	Chick	Petrel chick on own in nest site	Figure S6.2
	Adult and chick	Petrel chick accompanied by an adult	Figure S6.3
	Adult resting	Adult petrel resting in a nest site and not (apparently) incubating based on relaxed posture and frequent movement between images	Figure S6.1
	Empty	No petrel adults, chicks, eggs in the nest site	Figure S6.4
	Unclear	Nest contents unclear due to vegetation cover, poor visibility due to sunlight and/or heavy precipitation, or obstruction by other animals	Figure S6.5
Presence of other species	Binary (y/n)	Image-level presence or absence of any species which is not a Round Island petrel	
Name of other species	Categorical	Including species such as Telfair's skink (*Leiolopisma telfairii*), Aldabra giant tortoise (*Aldabrachelys gigantea*), ornate day gecko (*Phelsuma ornata*), night gecko (*Nactus coindemirensis*), zebra dove (*Geopelia striata*), Round Island boa (*Casarea dussumieri*), house sparrow (*Passer domesticus*), wedge-tailed shearwater (*Ardenna pacifica*), white-tailed tropicbird (*Phaethon lepturus*), crab (*Geograpsus* sp.), or unidentified.	Figure S6.6-8

To assess how estimates of key phenological dates varied with the temporal frequency (number of images per day) of time-lapse images, we randomly sampled our dataset using different frequencies (ranging from one to 23 images per day). Using these subsetted datasets, dates of egg-laying and -hatching were estimated as above. For each image frequency, this process was repeated 5000 times in order to randomly sample different hours across the 24-hour period. To standardise data, the difference in days between these dates and the ‘true’ phenological dates (estimated using all 24 images) was calculated, and the amount of error (in days) was calculated for each nesting attempt.

Citizen science processing

A total of 25,924 images taken at a set range of hours (11:00, 12:00, 13:00, 17:00, and 18:00) across the majority of the camera deployment period (December 2019 - May 2021) were selected for processing on the Seabird Watch citizen science project hosted on the Zooniverse web platform (https://www.zooniverse.org). The first set of images were uploaded and ready to be annotated on 10th December 2020, with additional images continuously uploaded once retrieved from cameras during routine maintenance. Prior to upload on the website, the raw image files were renamed and resized (Jones et al., 2018), with the ‘exiftoolr’ R package used to extract metadata from each image, including date, time, and temperature information (O’Brien, 2020).

On the Round Island petrel workflow on the Seabird Watch website, citizen scientists are shown a random image from any of the 10 cameras. If animals are present in the image, volunteers are asked to tag individuals by clicking on them, and classify them as ‘adult’, ‘chick’, ‘egg’, or ‘other’. For the Round Island petrel workflow, ‘other’ can be used to identify other species, such as the Telfair’s skink *Leiolopisma telfairii*, giant tortoises, or other seabirds. Each image is shown to eight different volunteers in order to increase data reliability. A clustering algorithm is then used to amalgamate the multiple volunteers clicks into a single ‘consensus click’ (see Fig. S6.9 for an example). We used the panotypes aggregation 3.6.0 software which is specifically designed for use by Zooniverse project researchers. First, raw clicks were formatted using the ‘point extractor by frame’ tool, which returns a list of x and y coordinates for every volunteer click on each image. Next, we clustered the coordinates using the DBSCAN (Density-Based Spatial Clustering of Applications with Noise) ‘point reducer’. With DBSCAN, a cluster is defined as a group of at least N_{min} samples that are all within a distance ε of each other. The parameter values we used were $N_{min} = 3$ (see Jones et al., 2018) and $ε = 20$.

To examine the agreement between citizen science (CS) consensus clicks and researcher (R) counts – and thus the reliability of Seabird Watch as a data processing tool – we ran a zero-inflated Poisson mixed model with the number of adults, chicks, or eggs counted in an image as the response variable. The stage (adults, chicks, or eggs), observer type (CS or R), and the camera from which images were taken (10-level categorical variable) were included as fixed effects, as well as a two-way interaction between camera and observer type, and observer type and stage. The image name was included as a random effect to account for multiple counts (of adults, chicks, and/or eggs per observer type) from a single image. Only CS images which were marked as complete (i.e., classified by eight different volunteers) by date of data extraction (17th November 2021) were included. We then ran the same model as above (zero-inflated Poisson mixed model) but replaced the fixed effect of camera site with the average distance of camera from nest sites, to explore whether closer cameras resulted in more consistent image classification. All models were run using the glmmTMB function in the R-package glmmTMB (Brooks et al., 2017). For all models, non-significant ($p < 0.05$) terms were sequentially removed using backwards stepwise deletion and significance of terms was determined using ANOVA. Pairwise comparisons among levels were calculated based on estimated marginal means and adjusted using post-hoc Tukey correction using the R package emmeans (Lenth, 2021). All analyses were conducted, and figures created, using R version 3.6.2 (R Core Team, 2019).

Results

A total of 181,635 images were taken between 04 December 2019 and 08 March 2022 across the 10 cameras deployed for this study. This resulted in a total of 7,669 camera trap days (sum of days each camera trap was operational; Table S6.1). Of the 10 cameras, eight continued functioning for the duration of the study, and only two failed; however, all cameras provided data for at least 15 months (Table S6.1). The two failures were due to casings of older cameras opening during deployment and thus moisture getting inside the camera. Three cameras required minor maintenance during deployment due to one camera not being closed properly after maintenance and two due to strong winds causing camera movement. This means there are short temporal gaps (accounting for only 2.9% of the total number of camera trap days) in the data set (see Table S6.1 for a summary of available data).

Of the 47,570 images that were manually processed, 58.56% of images were recorded to have an adult Round Island petrel, chick, and/or egg present (n = 27,857), 0.49% of these images also included a non-petrel species (n = 232), 0.55% contained a non-petrel species only (n = 260), and 40.95% of images were empty, and/or unclear due to heavy precipitation or vegetation (n = 19,481). Nine non-petrel species were identified (Table S6.2), with the most commonly recorded species being Telfair's skink (n = 182), wedge-tailed shearwater *Ardenna pacifica* (n = 172), and Aldabra giant tortoise *Aldabrachelys gigantea* (n = 37).

Nest phenology and breeding success

Across the ~ 6.5-month period which the manual image processing covered, a total of 23 breeding attempts were observed at 20 different nest sites from eight cameras. Of these, 18 were monitored to their final fate, and five were still in progress at the end of image processing. At the time of camera deployment, 13 of the breeding attempts were already in progress, either with incubating birds (n = 7) or chicks (n = 6) already present, whereas the remaining 10 were observed from egg-laying. Extracted lay dates for four of these breeding attempts spanned December till February (n = 4), and the remaining six were observed in May and June (Fig. 6.3). This provided observations of 17 breeding attempts from incubation, of which nine failed at the egg stage, three successfully hatched, and five which were still ongoing at the end of this subset of manually processed images, resulting in an observed hatching success of only

21.4%. Duration of incubation estimated from camera data (from the two breeding attempts with observed lay dates and successful hatching) lasted 52 and 53 days. During these two successful incubation periods, eggs were only observed and thus incubation confirmed in seven out of 1233 possible images (0.57%) and 34 out of 1242 possible images (2.74%). For unsuccessful breeding attempts observed from initiation but which failed at the egg stage, the shortest observed incubation period prior to an egg being lost was only 16 days (Fig. 6.3). The longest recorded incubation period (for an unsuccessful attempt) was much longer than the average duration for successful attempts (78 days), although eggs were observed on their own more often, and there were large gaps in incubation (Fig. 6.3).

Of the nine chicks observed in the camera images (six of which were present when the cameras were deployed), all nine were assumed to have successfully fledged (Fig. 6.3), having reached plumage indistinguishable from that of an adult (fledging success = 100%). Duration of the fledging period estimated from camera data (from the three breeding attempts with observed hatch dates) lasted, on average, 76 days ± 3.5 SE (range: 72-83 days).

Estimated lay dates varied very little when using a range of 1-24 images per day (Fig. 6.4A). Across all cameras, if only one photo was used per day, the dates estimated are likely to be on average 0.5 days later (range 0-2 days depending on the hours chosen) when compared to dates estimated using 24 daily images and are well estimated with > 6 photos per day (Fig 6.4A). For egg-hatching, the dates estimated are likely to be on average 3.3 days later (range 0-9 days) when only one image is used per day. The error in estimated egg-hatching dates decreases quite rapidly as the number of images used per day increases, but more images are required to get the same level of confidence as egg-laying (Fig. 6.4B).

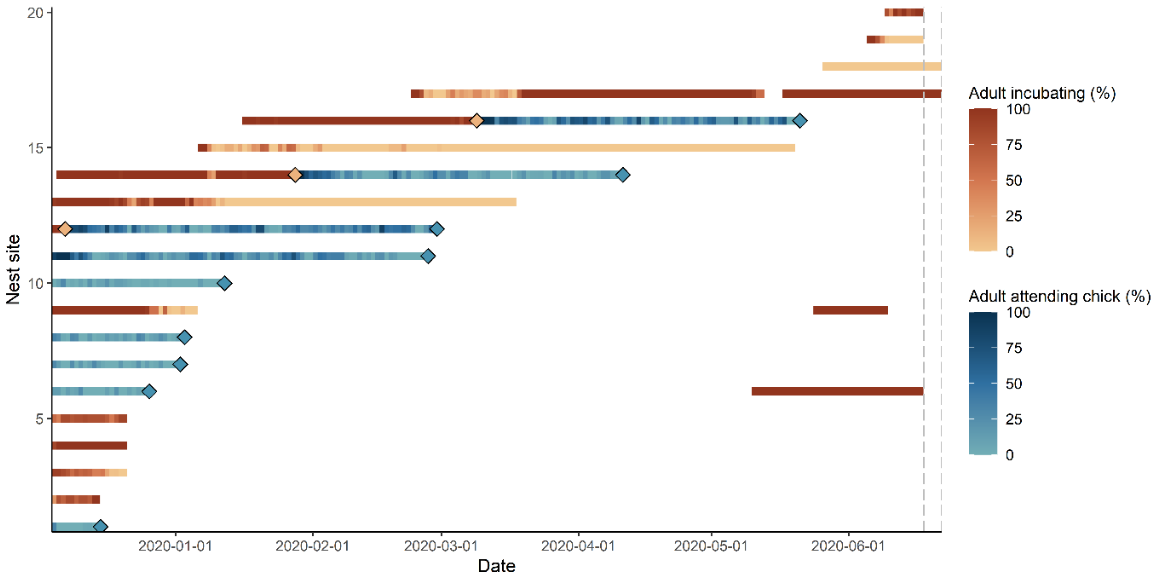

Figure 6.3. Chronology of 23 Round Island petrel breeding attempts (18 monitored to their final fate and five still in progress at the end of image processing) from 20 nests estimated from time-lapse camera images. Colours of lines represent the proportion of daily images containing eggs and/or chicks in which adults were present and either incubating an egg or attending a chick. Coloured diamonds represent dates of egg-hatching (orange) and chick fledging (blue). Small one-day gaps in data are a result of images being unclear for an entire day, whereas larger gaps (>6 days) represent consecutive breeding attempts in the same nest. Note, maintenance checks were conducted on two different dates, hence the last date of available images (grey dashed lines) are different for five of the cameras.

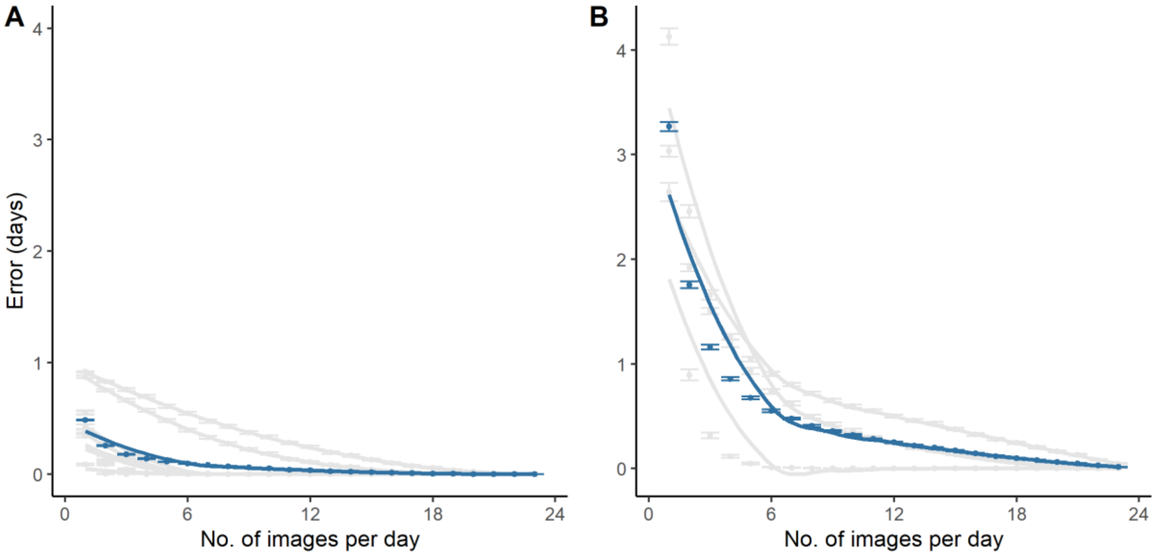

Figure 6.4. Amount of error (in days) in estimates of A) egg-laying, and B) egg-hatching with varying numbers of images classified (range 1-23) compared to the estimates when using all 24 daily images. Grey error bars (mean ± 95% confidence intervals)

represent data for each individual nesting attempt (n = 10 and n = 3 for egg-laying and egg-hatching, respectively), and blue represents error for all nests combined. Grey (individual nests) and blue (all nests) curves were fitted using a loess smoother to illustrate the non-linear change in error.

Comparison between researcher- and citizen science- derived data

By the date of data extraction from Zooniverse, full annotation by citizen scientists had been completed for 25,732 images of which 8,255 had also been classified by researchers. It took just over 11 months for these images to be annotated by citizen scientists. Of the 8,255 images, researchers recorded no animals to be present in 3019 images. Comparison with CS consensus clicks revealed a 98% agreement with researcher data (i.e., 2950 of 3019 were marked as containing no animals). When excluding the images which researchers and CS agreed to be empty (n = 2950) and only comparing images where the appropriate stage (adult, chick, and/or egg) were recorded as present according to researcher and/or CS data, volunteers consistently underestimated the number of adults, chicks and eggs in an image (Figs 6.5 & S6.10; Table S6.3). This underestimation was similar for eggs, chicks and adults (i.e., no statistically significant interaction between stage and observer type; Table S6.4; Fig. 6.5A) but was relatively small, with an average difference across all cameras and all stages combined (adults, chicks, and eggs) of only 0.61 ± 0.01 SE (ranging from an overestimation of four to an underestimation of seven). There was, however, significant variation in observer counts across camera sites, with model predictions of CS differing by only 0.3 petrels at camera site SWC5, and 1.06 at site ABC4 (Fig. S6.10; Tables S6.3 & S6.6). Some of this variation with camera site may be explained by distance of the camera from petrel nest sites, as the difference in counts between CS and researchers increased with increasing camera distance (Fig. 6.5B; Table S6.5).

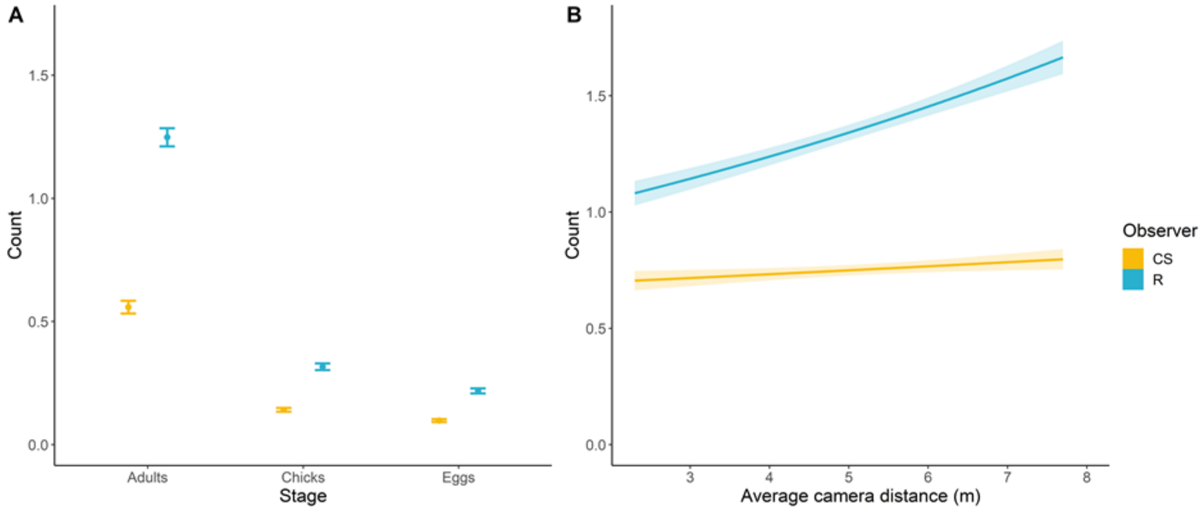

Figure 6.5. Predicted counts of the number of petrels in camera images from zero-inflated generalised linear mixed models of A) citizen science (CS; orange) and researcher (R; blue) stage (adult, chick, or egg) comparisons (error bars ± 95% confidence intervals), and B) the differences in counts between CS and R with average camera distance from nest sites (fitted lines ± 95% confidence intervals). For both models, predictions are averaged across all ten cameras and use the population-level mean of the random effect of image name. Whereas for B, model predictions are based on the adult stage only.

Discussion

Time-lapse photography is a powerful and flexible tool in seabird ecology. Our study demonstrates how automated time-lapse cameras can be successfully used year-round in remote areas to monitor tropical ground-nesting seabirds. In particular, we were able to individually follow 23 Round Island petrel breeding attempts, with researcher processing of images providing estimates of overall hatching and fledging success of 23.1% and 100%, respectively. The very small underestimation of petrel eggs, chicks and adults in images annotated by citizen scientists suggests that this type of processing would be an effective approach to capturing nesting phenology and success in these systems.

The majority of cameras deployed for this study successfully collected data for at least 15 months and were still functioning at the end of deployment. We lost two cameras due to equipment failure; however, these were older cameras which had been deployed elsewhere prior to being used in this study. We also have short temporal gaps in some of our data (accounting for < 3% of overall trap days) due to camera movement. Tropical cyclones occur regularly in this region (Nicoll et al., 2017) and did so during the 27 months in which cameras were deployed. Despite this, all cameras remained standing and active, thus performing exceptionally well even in these challenging conditions. The possibility of camera failure and/or movement is clearly important to consider when implementing time-lapse camera systems and avoiding any potential circumstances which could lead to time-lapse camera failure is crucial for these systems to work in remote places which researchers are unable to visit regularly. In this study, the presence of fieldworkers on the island allowed rechargeable batteries to be used, and these easily lasted the two to three months between changeovers (although battery efficiency did decrease across the deployment period, which is a known issue with rechargeable batteries in hot weather; Pebsworth & LaFleur, 2014). Alkaline and lithium batteries are recommended for longer time periods and are successfully used in time-lapse cameras that are only visited annually (e.g., Hinke et al., 2018) and solar-powered options are also becoming more affordable (Newbery & Southwell 2009). The latter option may be particularly suited to tropical systems.

Nearly 60% of all manually processed images were recorded to have a Round Island petrel (adult, chick and/or egg) present. The large number of empty and/or unclear photos in our dataset were due to factors including using photos from the end of the peak breeding season, when fewer petrels are on the island and when high levels of vegetation growth and sun glare (mainly around sunrise and sunset) often reduced visibility. Camera placement is therefore incredibly important and, where possible, placing cameras above nesting sites and facing downwards is likely to reduce issues of sun-glare and allow nest contents to be viewed more easily. Testing of camera systems and placement/orientation, such as across a full day and in different weather conditions, is therefore advised.

Time-lapse cameras were successfully used to estimate breeding phenology and nest success for Round Island petrels. The incubation period durations recorded for two successful nests (52 and 53 days) are similar to those estimated for other *Pterodroma* petrels. For example, the incubation period of Trindade petrels on Trindade Island is estimated to be 52-54 days (Luigi, 1995); for Kermadec petrels it was estimated to be 50-52 days (del Hoyo et al., 1992). Compared to in-the-field monitoring of Round Island petrels (56-57 days), our estimate is slightly lower, although this could reflect the less frequent checking of nest status that is typical of in the field research (approximately weekly for Round Island petrels; Tatayah, 2010). In comparison, for the fledging period, our average duration (76 days) was lower than that recorded from in the field monitoring of Round Island petrels (estimated between 92 and 99 days for a single nest; Tatayah, 2010), possibly because older Round Island petrel chicks often move around the nest site and out of view of the camera. For species with more defined nests (e.g., many cliff-nesting species), chicks moving out of view is likely to be less of a limitation. Round Island petrel fledglings also have a plumage similar to that of adults, making it sometimes difficult to distinguish between fully-grown fledglings and adults in camera images. The hatching and fledging success estimates (23% and 100%, respectively) reported here are raw estimates that do not account for nest failure prior to camera deployment, and may thus be overestimates (Mayfield, 1961; Mayfield, 1975). For example, several chicks which were recorded to successfully fledge were quite large at the start of monitoring, and larger chicks are more likely to survive than smaller ones. Further processing of images of more nests will allow more precise estimates to be modelled.

Regular monitoring of seabirds using camera traps can also allow researchers to observe important events which may be missed with conventional monitoring by nest visits. For example, the timings and causes of nest failure can often be missed (Collins et al., 2014), which can have important consequences for targeted management actions and conservation of seabirds. Time-lapse cameras also have the advantage that they are non-invasive, and disturbance is reduced by needing to visit nests less frequently (Carey, 2009; Tatayah, 2010).

Evaluation of daily image frequency revealed the number of daily images needed to estimate key breeding metrics. As little as one image per day could be used to estimate the start of incubation, but a higher frequency of images was required to confidently estimate egg-hatching, which is consistent with other studies. For example, after initial evaluation, Southwell and Emmerson (2015) re-programmed cameras to take 10 images each day, from an initial once-a-day, to confirm first egg lay of Adélie penguins *Pygoscelis adeliae*. Egg-hatching is inherently difficult to observe because adults typically continue brooding recently-hatched chicks, and so reliable detection requires more frequent observation. For this analysis, we randomly selected images across the 24-hour period, whereas in reality, timelapse settings of off-the-shelf cameras would not operate with this random structure and are programmed to take images at regular intervals (e.g., once an hour or once every two hours, possibly constrained within key periods of the day). However, the variation in error of estimates was small, suggesting that images captured at any time of day would be likely to effectively capture timing of egg-laying and -hatching (Fig. 6.4).

For studies using manual image processing, the trade-off between confidence in the metrics being extracted and the required image processing time is likely to be key, so identifying these required image frequencies will be particularly important. In our study, manual processing of nearly 50,000 images required ~ 50 hours in total. Alternatively, if image processing rather than storage capacity is the issue, the best approach may be to take regular photos but to only process one per day as the first pass. Once key events have been confirmed from those, the second pass could then be to work backwards from that date through more temporally refined images to improve precision. Additionally, it is important to note that this ~ 50 hours of manual image processing time provided us with relatively few nesting attempts, even though cameras were deployed in areas likely to capture several nests at once. This method may therefore be particularly suited to species which nest at high densities and in locations that are hard to access.

By hosting our images on the Seabird Watch website, members of the public annotated over 25,000 camera images over a period of 11 months. Comparison of images processed by researchers and citizen scientists revealed that citizen scientists slightly underestimated counts of petrels in images, and the difference in counts between researchers and citizen scientists was greater for cameras that were further from nest sites. Camera distance from the target sites should therefore be carefully considered, and minimised where possible, especially if citizen science approaches to image processing are to be used. For example, the team at Seabird Watch have recently deployed 11 long-range cameras to generate high quality images of cliff-nesting seabirds suitable for processing by citizen scientists. There is often a trade-off, however, between the distance of cameras from nest sites and the number of nests which are viewable.

There are several potential reasons why citizen scientists slightly undercounted petrels in camera images. First, Round Island petrels have a range of different colour morphs, but most common are the ‘dark morphs’ and all morphs have uniformly dark grey/brown upperparts (Tatayah, 2010). The dark plumage of the petrels, together with the shaded areas that they often nest in, can make it difficult to see petrels in some images. Species with contrasting plumage to that of the image background may be easier to identify. Second, sequential processing of images from the same camera, as is typical with manual image processing but not citizen science processing, can help to repeatedly identify individuals in the same or similar locations. However, as the underestimation with citizen science processing was very small (< 1 individual, on average), any impact on estimation of key breeding metrics is likely to be limited.

Although citizen scientists reduce image processing time for researchers, the amount of time it takes for all images to be analysed, particularly when multiple volunteers are required to look at one image, is often much longer. In this study, just over 25,000 images were annotated by citizen scientists in ~ 11 months. Another option for processing large numbers of images, which has been a recent focus of the camera trap literature, is the use of automated and semi-automated techniques (Edney & Wood, 2021). Machine learning algorithms can be trained to automatically and accurately identify and count species in camera trap images (Weinstein, 2017). These methods require a large set of pre-classified images for baseline training data, and images processed by citizen scientists can be the ideal platform for training these algorithms (Jones et al., 2020; Wright et al., 2017). For large projects, the development of such automated and semi-automated techniques will be key in making the use of camera traps for monitoring of breeding birds widespread for both conservation and management purposes. However, this will require more interdisciplinary collaborations between ecologists and computer scientists, and ultimately increased accessibility of techniques for non-computer scientists.

The use of autonomous time-lapse camera systems for monitoring seabird ecology is rapidly growing. In this study, we demonstrate the applicability of time-lapse cameras to monitor tropical seabirds and extract key breeding metrics, as well as the suitability for surviving challenging tropical conditions. While this method was developed and tested on surface-nesting *Pterodroma* petrels, it should apply generally to other medium- to large-sized tropical seabirds that are colonial breeders, and other similar systems. Depending on image processing methods used, this may be particularly useful for understudied tropical seabirds in very remote areas where year-round personnel and regular in the field monitoring is not possible. Camera traps could contribute to an improved understanding of a species' breeding ecology, that will be invaluable in prioritising conservation management decisions. Careful consideration must be given to selecting suitable camera locations and the processing methods to be used, but we hope the recommendations provided here will be useful for those interested in using this method.

Acknowledgements

This work would not have been possible without the many staff and volunteers from the Mauritian Wildlife Foundation (MWF) and National Parks and Conservation Service (NPCS) who have helped with the Round Island petrel camera trap project. In particular, we would like to thank Round Island wardens Ben Dymond, Bethan Govier, Jennifer Appoo, Pratiksha Bappoo and Pouvalen Seeneevassin for their assistance with camera maintenance and subsequent transfer of data. We would also like to thank Cliff Johnson for helping with data extraction and clustering of Zooniverse data.

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Supplementary materials to Chapter 6: Utility of automated time-lapse cameras to monitor breeding phenology and nest success of tropical ground-nesting seabirds

Table S6.1. Dates of operation and any missing periods for each of the 10 time-lapse cameras deployed on Round Island, Mauritius, and reasons for failure and/or missing data, if any.

Camera	Observation start date	Observation end date	Recording duration (days)	Missed periods	Missed periods (days)	Reasons
ABC1	04-12-2019	04-03-2022	822		0	
ABC2	04-12-2019	07-03-2022	825		0	
ABC3	04-12-2019	07-03-2022	825	16-09-2020 – 04-11-2020, 25-11-2020 –	67	Camera movement
ABC4	05-12-2019	19-03-2021	471	06-01-2021 – 20-01-2021	15	Camera failed early due to casing opening during deployment
ABC5	05-12-2019	07-03-2022	824		0	
SWC1	04-12-2019	08-03-2022	826		0	
SWC2	04-12-2019	08-03-2022	826	06-11-2021 – 13-01-2022	69	Data missing
SWC3	04-12-2019	01-02-2022	791	06-11-2021 – 13-01-2022	69	Data missing
SWC4	04-12-2019	27-08-2021	633	23-08-2021, 25-08-2021 – 27-08-2021	4	Camera movement, and failed early due to casing opening during deployment
SWC5	04-12-2019	08-03-2022	826		0	

Table S6.2. Number of images which a non-petrel species is observed in from manual image processing, from the 10 time-lapse cameras deployed on Round Island, Mauritius.

Species (common name)	Species (Latin name)	Number of images
Telfair's skink	*Leiolopisma telfairii*	182
Wedge-tailed shearwater	*Ardenna pacifica*	172
Aldabra giant tortoise	*Aldabrachelys gigantea*	37
Mauritius ornate day gecko or night gecko	*Phelsuma ornata* or *Nactus coindemirensis*	35
Zebra dove	*Geopelia striata*	30
Crab	*Geograpsus sp.*	15
Unidentified sp.	n/a	8
White-tailed tropicbird	*Phaethon lepturus*	8
Round Island boa	*Casarea dussumieri*	3
House sparrow	*Passer domesticus*	1

Table S6.3. Results for the effects of petrel stage (adult, chick, or egg), camera site, observer (citizen science or researcher), and the interaction between camera and observer on the number of petrels counted in images. Filename is included as a random term. Minimum adequate model is shown. Note, all variables are categorical and are being compared to the reference levels of adults, camera site ABC1, and citizen scientists. Significant effects ($p < 0.05$) are highlighted in bold. R^2m = 54.2% and R^2c = 59.8%.

Variable	**Estimate ± SE**	**z value**	**P value**
(Intercept)	-0.013 ± 0.029	-0.45	0.656
Stage (Chicks)	-0.404 ± 0.008	-53.16	**< 0.001**
Stage (Eggs)	-0.286 ± 0.009	-32.07	**< 0.001**
Camera (ABC2)	-0.211 ± 0.051	-4.16	**< 0.001**
Camera (ABC3)	-0.025 ± 0.039	-0.63	0.531
Camera (ABC4)	0.288 ± 0.054	5.30	**< 0.001**
Camera (ABC5)	0.385 ± 0.060	6.45	**< 0.001**
Camera (SWC1)	-0.140 ± 0.058	-2.42	**0.015**
Camera (SWC2)	-0.595 ± 0.039	-15.30	**< 0.001**
Camera (SWC3)	-0.149 ± 0.038	-3.93	**< 0.001**
Camera (SWC4)	0.224 ± 0.070	3.22	**0.001**
Camera (SWC5)	-0.206 ± 0.048	-4.30	**< 0.001**
Observer (Researchers)	-0.099 ± 0.017	-5.77	**< 0.001**
ABC2:Researchers	1.089 ± 0.029	37.08	**< 0.001**
ABC3:Researchers	0.816 ± 0.023	35.21	**< 0.001**
ABC4:Researchers	0.823 ± 0.036	22.78	**< 0.001**
ABC5:Researchers	0.728 ± 0.034	21.67	**< 0.001**
SWC1:Researchers	1.049 ± 0.034	30.91	**< 0.001**
SWC2:Researchers	1.504 ± 0.022	67.11	**< 0.001**
SWC3:Researchers	1.117 ± 0.022	50.28	**< 0.001**
SWC4:Researchers	0.844 ± 0.043	19.44	**< 0.001**
SWC5:Researchers	0.969 ± 0.028	35.10	**< 0.001**

Table S6.4. Results of ANOVA tests for zero-inflated generalised linear mixed model selection for the number of petrels counted in camera traps images using a) the camera as a 10-level categorical variable, and b) camera distance. Significant effects ($p < 0.05$) are highlighted in bold.

Model	**df**	**Deviance**	**Chi sq**	**P value**
a. Camera				
Count ~ stage*observer + camera*observer + (1|image ID)	26	52521	5.4998	0.064
Count ~ stage+ camera*observer + (1|image ID)				
Count ~ stage+ camera + observer + (1|image ID)	24	52575	548.07	**< 0.001**
Count ~ stage+ camera*observer + (1|image ID)				
b. Camera distance				
Count ~ stage*observer + distance*observer + (1|image ID)	10	54059	5.4998	0.064
Count ~ stage+ distance*observer + (1|image ID)				
Count ~ stage+ distance*observer + (1|image ID)	8	54065	30.573	**< 0.001**
Count ~ stage+ distance + observer + (1|image ID)				

Table S6.5. Results for the effects of stage (adult, chick, or egg), camera distance, observer (citizen science or researcher), and the interaction between camera distance and observer on the number of petrels counted in images. Filename is included as a random term. Minimum adequate model is shown. Note, all categorical variables are compared to the reference levels of adults (for stage), and citizen scientists (for observer). Significant effects ($p < 0.05$) are highlighted in bold. R^{2}m = 43.6% and R^{2}c = 55.2%.

Variable	**Estimate ± SE**	**z value**	**P value**
(Intercept)	-4.013 ± 0.049	-8.14	**< 0.001**
Stage (Chicks)	-1.373 ± 0.020	-68.35	**< 0.001**
Stage (Eggs)	-1.743 ± 0.023	-74.50	**< 0.001**
Distance	0.023 ± 0.009	2.48	**0.013**
Observer (Researchers)	0.295 ± 0.056	5.26	**< 0.001**
Distance:Researchers	0.057 ± 0.010	5.53	**< 0.001**

Table S6.6. Pairwise comparisons of the number of petrels counted in images between citizen scientists and researchers for each of the ten cameras from a zero-inflated generalised linear mixed model. Results are averaged over the categorical variable of stage (adults, chicks, or eggs), and significant effects ($p < 0.05$) are highlighted in bold.

Camera	**Ratio ± SE**	**t ratio**	**P value**
ABC1	0.370 ± 0.016	-22.64	**<.0001**
ABC2	0.616 ± 0.044	-6.85	**<.0001**
ABC3	0.392 ± 0.019	-19.43	**<.0001**
ABC4	0.098 ± 0.014	-16.59	**<.0001**
ABC5	0.549 ± 0.042	-7.92	**<.0001**
SWC1	0.637 ± 0.057	-5.05	**<.0001**
SWC2	0.737 ± 0.023	-9.80	**<.0001**
SWC3	0.666 ± 0.021	-13.11	**<.0001**
SWC4	0.298 ± 0.040	8.95	**<.0001**
SWC5	0.716 ± 0.043	-5.52	**<.0001**

Figure S6.1. Incubating (left) and resting (right) adult Round Island petrels in a time-lapse camera image. Note, the lower wings and hunched posture of the incubating adult. Incubating is only confirmed, and thus is recorded as 'apparently incubating', until an egg has been observed.

Figure S6.2. Two unattended eggs (far left and right) and an advanced chick (centre) in a time-lapse camera image.

Figure S6.3. Adult and (small) chick in the bottom left of time-lapse camera image. The adult must be interacting or sat very close to the chick to be recorded under the 'adult and chick' category.

Figure S6.4. Time-lapse camera image recorded as 'empty'. There are no Round Island petrel adults, eggs, chicks, or any other species, observed in this image.

Figure S6.5. Timelapse camera image recorded as 'unclear'. Vegetation has obscured visibility of petrel nest sites, and moisture has collected on the camera lens after rain.

Figure S6.6. Example camera-trap image showing the most common non-petrel species observed (centre right), a Telfair's skink (*Leiolopisma telfairii*).

Figure S6.7. Example camera-trap image of an Aldabra giant tortoise (*Aldabrachelys gigantea*).

Figure S6.8. Example camera-trap image of a wedge-tailed shearwater (*Ardenna pacifica*).

Figure S6.9. Example camera-trap image with the ‘raw clicks’ of Seabird Watch volunteers overlaid and resulting cluster locations. Each dot represents a single click from a volunteer and are clustered (demonstrated by oval) using the clustering algorithm to generate ‘consensus clicks’. Note, this image shows clicks made for the ‘adult’ stage only.

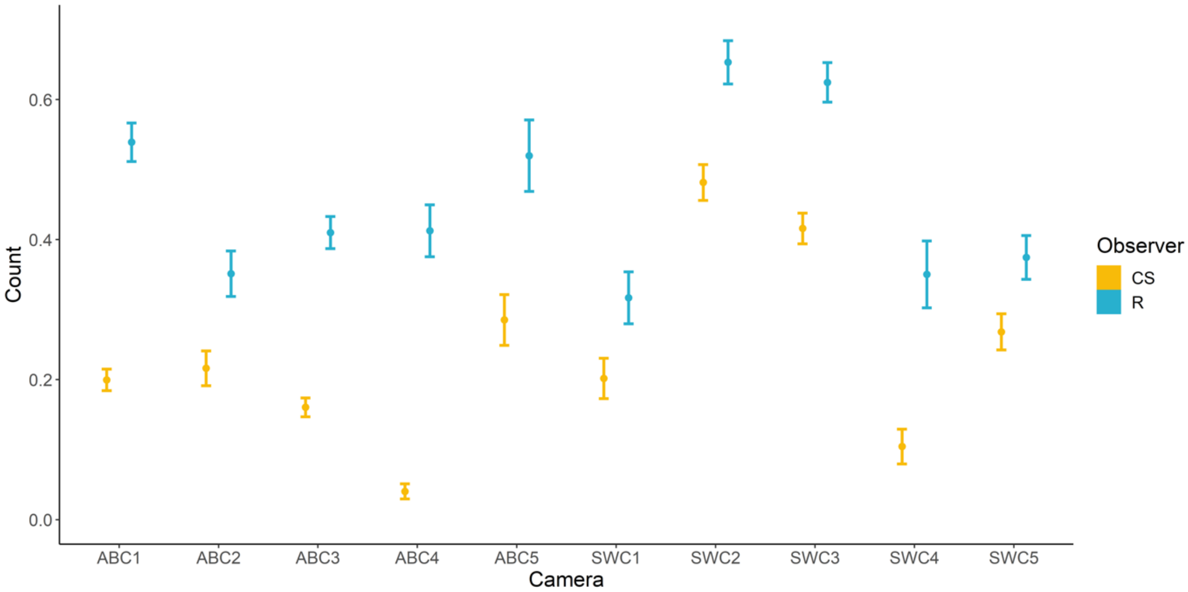

Figure S6.10. Predicted counts of the number of petrels (averaged across adults, chicks, and eggs) in camera images from a zero-inflated generalised linear mixed model (error bars ± 95% confidence intervals) and the differences across camera sites and between citizen scientists (orange) and researchers (blue). Model predictions are based on the population-level mean of the random effect of image name.

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Chapter 7

Concluding Remarks

Photo: Johannes Chambon

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Concluding Remarks

Understanding how species will respond to changing environmental conditions as a result of climate change and other anthropogenic factors has been a key focus for conservationists in recent years. Shifts in phenology and distribution in response to environmental change have been reported in many species (Visser & Both, 2005), yet responses have been species-specific, making predictions between species difficult (Díaz et al., 2019). Migratory species add to this difficulty by relying on multiple locations and conditions across the annual cycle (Robinson et al., 2009), and it has only been recently, with advances in remote tracking technology, that we have been able to follow individuals throughout the annual cycle and across years (e.g., Bogdanova et al., 2017; Ng et al., 2018). These tracking data have started to reveal the extent of within- and between-individual variation in migratory journeys, which is a key aspect of understanding the mechanisms through which shifts in phenology and distribution occur, and thus their consequences for species conservation.

The primary aim of this thesis was to explore levels of within- and between-individual variation in migratory behaviour in a tropical seabird system. Using a large geolocator tracking dataset from the Round Island petrel, studies within this thesis have gained insight into the levels of individual variation in at-sea movement patterns in this wide-ranging seabird across the unpredictable environments of tropical systems. The chapters within this thesis are intended to complement each other and fill in important gaps in these poorly studied regions of the world (Chapter 2). I have demonstrated that, similar to many other migratory species (Chapter 2), Round Island petrels display low levels of within-individual variation in migratory behaviour (Chapter 3) but very high levels of between-individual variation (Chapter 4), and that there could be differences in the conditions experienced depending on the migratory strategy taken by individuals (Chapter 5). I also undertook a breeding period field study to validate the use of time-lapse photography and citizen science as tools for monitoring tropical seabird breeding phenology and nest success (Chapter 6).

Below, I draw together the key findings and implications of these data chapters and suggest future directions to develop research themes from this project.

Repeatability of avian migration

It is increasingly being recognised that consistent individual differences in behaviour are common across the animal kingdom (Bolnick et al., 2003; Dall et al., 2012). In recent years especially, aided by advances in animal tracking technologies, a large number of studies have started repeatedly tracking individuals across multiple annual cycles, often with a focus on variation in migratory behaviours (e.g., Brown et al., 2021; McFarlane Tranquilla et al., 2014), and 'repeatability' is now a widely reported metric in behavioural studies. In **Chapter 2**, I took advantage of these estimates and used a global, multi-species approach to investigate levels of repeatability in avian migratory timings and how this might vary across the annual cycle, with taxonomic group, and with various study designs. This meta-analysis revealed consistent individual differences in migratory timings to be a common feature across migratory systems, with the timing of departure from the non-breeding grounds being more repeatable than timings of arrival at or departure from breeding grounds. However, I feel it is important to reiterate that repeatability estimates have some important limitations which need to be considered, especially in the context of understanding the rate and direction of shifts in migratory timings in response to changing environmental conditions. In particular, repeatability represents the proportion of the total phenotypic variation (sum of between-individual variance, within-individual variance and measurement error) in the sampled population that can be attributed to variation between groups (usually individuals). This means that the same repeatability estimates can arise from very different patterns of these variance components (see Dochtermann & Royauté, 2019). These ratios can therefore differ because of differences in either the numerator or denominator (or both), or ratios can be the same despite differences in both the numerator and denominator. Thus, similar repeatability values could arise from a population in Figure 1.1 quadrant 3 (individuals consistent within and across a population) and from a population in quadrant 2 (individuals vary annually but not consistently across a population), which have potentially opposite responses to changing environmental conditions. Comparisons of repeatability (as a proportion) among groups is therefore largely uninformative, but direct estimates of the within- and between-individual variances in the metric of interest are comparable (Dingemanse et al., 2022). Better interpretation of repeatability and thus what this means for species responses to environmental change will therefore be greatly aided by authors reporting the variance components (and measurement errors) underpinning the reported repeatability estimates (see also Dingemanse & Wright, 2020; Sánchez-Tójar et al., 2022).

In general, our meta-analysis revealed that repeatability in migratory timings is relatively high; however, another important aspect to consider is repeatability in migratory routes and locations, which may influence the potential for migratory species to shift in space. I did not touch upon this aspect of migration in my thesis, despite many studies also reporting high levels of site-fidelity in space-use (e.g., Fayet et al., 2017; Merkel et al., 2020). The main reason for this was that, unlike repeatability estimates which are used largely in the literature for migratory timings, there is not a consistent metric which is used to measure spatial repeatability. The aspects of spatial migration which are estimated also vary, which together make comparisons across studies difficult. Recent attempts have been made (e.g., Stuber et al., 2022), but these authors also suggest trait means and variance components need to be reported before conclusions on which types of spatial behaviours are more or less repeatable can be made. For example, similarity in migratory routes has been measured using average nearest-neighbour distance (NND; e.g., Fayet et al., 2017; Guilford et al., 2011; Merkel et al., 2020), and similarity of non-breeding distributions have been measured using spatial overlap indices (e.g., Delord et al., 2019; McFarlane Tranquilla et al., 2014), and/or mean latitude and longitude of non-breeding destinations (e.g., Grecian et al., 2019), to name a few. However, one problem with quantifying spatial repeatability with some of the more commonly used methods (such as spatial overlap indices) is that the degree of separation of non-overlapping ranges is often not quantified. In **Chapter 3**, I therefore used a recently adapted and underutilised method, the earth mover's distance (EMD; Kranstauber et al., 2017), to quantify spatial dissimilarity. I found this to be particularly valuable for systems with large, non-overlapping variation in individual migratory distributions, such as Round Island petrels, and I hope this method will be used by other researchers as the framework could easily be applied to different species. EMD may also prove to be a suitable, comparable metric for future meta-analyses.

One of the takeaways from Chapter 2 is that there is a lack of studies investigating repeatability of avian migratory timings in the tropics. This general neglect of studies in tropical systems is common across many fields of research (Stroud & Feeley, 2017) and limits our understanding of how these species may respond to environmental change in less strongly seasonal environments. In the field of seabird research, these concerns of having limited availability of tracking data have been previously voiced (Bernard et al., 2021; Ceia & Ramos, 2015; Mott & Clarke, 2018), and I echo that a coordinated ramping-up of effort at tropical latitudes is required to inform conservation requirements for these important populations.

Within- and between-individual variation in petrel migration

The long-term geolocator dataset on the Round Island petrel provided the perfect opportunity to address the knowledge gap identified in Chapter 2 and quantify the levels of within- and between-individual variation (and thus repeatability) in migratory behaviours in a tropical system. Thus, in **Chapter 3**, I used multiple analytical approaches to quantify individual variation in the non-breeding distributions and timings of tropical Round Island petrels. I found striking levels of between-individual variation in at-sea movements and timings, with petrels undertaking non-breeding migrations to different areas across much of the Indian Ocean and throughout the whole year. Yet repeat-tracking of individual petrels revealed remarkably low levels of within-individual variation in these aspects of migration, suggesting they repeatedly follow the same migration strategy. This low within- and high between-individual variation likely places Round Island petrels in quadrant four from Figure 1.1, suggesting that rapid change may be possible (because so many different strategies occur in the population) but that the directionality of change would be very hard to predict, as it would likely depend on changes in the factors influencing the strategies adopted by recruits and/or the relative survival rates across strategies. Thus, changes in at-sea conditions in any part of the non-breeding range would appear to affect only select individuals of the petrel population, depending on where those changes occurred. However, in **Chapter 4**, I built on these findings and, by using a novel Bayesian Mixtures Analysis, quantified the levels of between-individual variation in non-breeding distribution. These analyses revealed nine different strategies to be present in the tracked population, but with highly uneven representation. More than 80% of the tracked petrel population undertook two of the nine migratory strategies (to the Arabian Sea or the Somali Basin), meaning that unfavourable changes in these areas could affect large numbers of the petrel population, if the tracked population is representative of the population as a whole.

Out of all the petrels deployed with geolocators, and with available data, only two individuals were recorded to leave the Indian Ocean (only petrels with complete migrations were included in this thesis, and so these were excluded; see Booth Jones et al., 2017). As geolocators are archival loggers and thus must be recovered for data to be obtained, it remains unclear how frequent and/or successful these strategies might be. These movements might be more frequent than we realise, due to either unrepresentative sampling or because individuals might not come back to Round Island (either because survival was low, or they have switched breeding colonies). Strong philopatry is thought to be common of Procellariform seabirds (Warham, 1990); however, evidence from the Herald petrel ringed on Raine Island (Australia) and subsequently caught breeding on

Round Island, questions these thoughts. These events, although rare, could be telling us something important about how these systems operate and change.

In **Chapter 6**, I moved away from the non-breeding period to focus on the breeding period. After deploying 10 time-lapse cameras on Round Island in 2019, I tested the utility of this method as a tool for monitoring individual petrel breeding phenology and nest success, as well as assessing the role that citizen scientists can play in processing the deluge of images that time-lapse cameras produce. At the time of deployment, it was unclear how well the cameras and stands would withstand the strong winds and rain that Round Island experiences, so it was very encouraging to discover how well these cameras functioned and continued to function for the 2+ years of this project. The potential for cameras, and citizen scientists, to be used to tackle what has been a challenging part of the Round Island petrel story (individual nest-level success) were well demonstrated in Chapter 6. With the camera stands on Round Island still in place, they are still available for future studies. I am currently working on a collaborative project with staff and students at UEA's School of Computing Sciences to explore the use of Artificial Intelligence and machine learning to process the camera images, which would greatly aid the Mauritian Wildlife Foundation and National Parks and Conservation Service in future studies on petrel breeding ecology.

Implications for conservation

Migratory species are exposed to a variety of threats at-sea as they travel through multiple countries' jurisdictions and the open ocean (Miller et al., 2018). Individual countries have resource rights up to 200 nautical miles from their shores, areas known as Exclusive Economic Zones (EEZs; United Nations, 1982). Beyond these zones of national jurisdiction are the 'high seas', which are legally recognised as a global commons. For successful species conservation, identifying the set of national jurisdictions and high seas areas visited by different species across their annual cycles is vital (Beal et al., 2021). My findings on the large levels of between-individual variation of Round Island petrels, with birds migrating to very different areas across the Indian Ocean (Chapters 3 & 4), highlights the challenges of protecting this population, as well as other wide-ranging species. Additional analyses (not included in previous chapters) revealed all tracked Round Island petrels (n = 198), and approximately 59.8% of all non-breeding locations (using all 267 complete tracks), to occur in the high seas. The remaining locations (40.2%) were split across 27 different EEZs, with individual petrels using between one and 12 different EEZs (Fig. 7.1). These results echo the importance of internationally coordinated efforts to conserve the non-breeding areas of wide-ranging species, such as the Round Island petrel (e.g., Davies et al., 2021a).

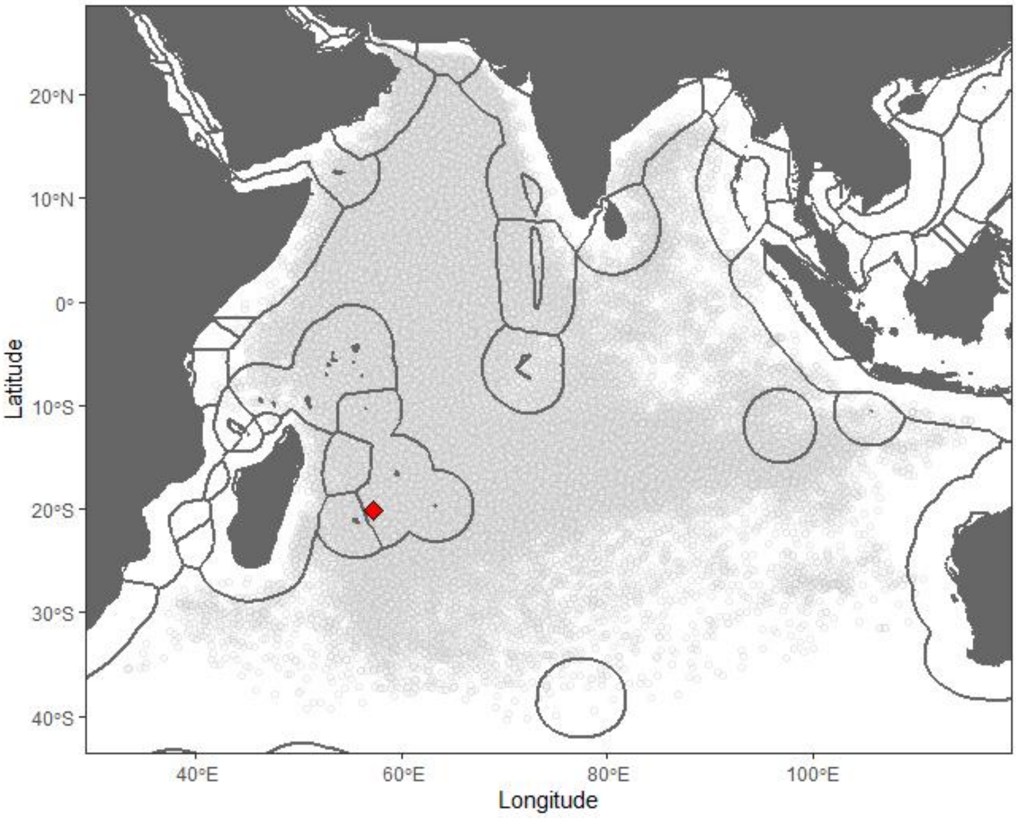

Figure 7.1. Non-breeding locations (grey points) of all tracked Round Island petrels (n = 198, tracks = 267) from Round Island, Mauritius (red diamond) within EEZs and the high seas of the Indian Ocean. Dark grey lines at sea represent borders of national EEZs.

Tracking data, including those presented in this thesis, have demonstrated the importance of the high seas for many migratory species (Beal et al., 2021; Harrison et al., 2018). As a result, important sites away from colonies and shores have been identified, and marine protected areas (MPAs) have been created. For example, tracking data from 21 seabird species in the North Atlantic revealed a seabird hotspot which, after formal designation, is now under year-round protection as the North Atlantic Current and Evlanov Seamount (NACES) MPA (Davies et al., 2021b). In the Indian Ocean, the results from this thesis have highlighted the Arabian Sea and Somali Basin areas to be important areas for Round Island petrels. These areas have been shown to be important for other seabirds and marine animals, yet collaborative studies will be required to inform conservation and policy for protection of these areas. Given that gadfly petrels (genus *Pterodroma*) are among the most threatened of seabird groups (they are members of the order Procellariiformes (albatrosses, petrels, shearwaters, and storm-petrels) for which 74% of the 35 species are classified from near threatened to critically endangered by the IUCN Red List (Croxall et al., 2012; IUCN, 2022)), and given their highly pelagic lives and long journeys over vast oceanic areas, there is an urgent need to improve knowledge of their biology, foraging behaviour, and at-sea distributions (Rodríguez et al., 2019), and to develop international conservation efforts to ensure their continued persistence.

Future directions

Throughout this thesis, research outcomes have prompted new questions and highlighted areas for future work that would further our understanding of the drivers of within- and between-individual variation in migratory behaviour. These include: 1) the need for structured, representative sampling across the full (phenological, spatial, genotypic, and age) range, and 2) a focus on tracking across life stages, particularly the juvenile stage.

Despite the large phenological and genotypic variation within the Round Island petrel population, we found no strong evidence for petrel genetic background or timing of departure influencing the large variation in petrel migratory distributions. However, most of our tracked birds departed Round Island between November and May, and (genetically) were more Trindade-like. Thus, while our large sample of tracked birds may have captured the range of migratory strategies, it is unclear whether the relative distribution of tracked individuals across strategies is representative of the population (Vickers et al., 2021). The focus of this thesis was also on the at-sea movements of adult individuals, and of those that returned to breed (and thus recovery of geolocators). However, the high levels of individual consistency in migratory behaviour means that we need to understand the early-life factors influencing which strategies individuals follow, and their fitness implications.

Tracking of juvenile seabirds has been comparatively limited to date (Hazen et al., 2012; Lane et al., 2021), due to their extended at-sea periods, commonly referred to as the "lost-years" (Reich et al., 2007), before their first return to the colony to breed. It is only with recent advances in tracking technologies, such as the miniaturisation of tags, and improved data storage and transmission capabilities, that we have been able to shed light on the early-life movements of (large) marine species (Frankish et al., 2020; Mansfield et al., 2014; Shillinger et al., 2012). The often-low survival rates in early life (Daunt et al., 2007) also make targeted tracking difficult, especially if recovery of archival tags is required. However, as Round Island petrel juvenile survival is quite high (ranging from 0.79 to 0.92 depending on the monsoon season petrels fledged in; Malcolm Nicoll, unpublished data), this might be a good system in which to explore the conditions experienced in early life. The wider petrel research team has recently started a project focusing on the deployment of geolocators on fledging petrels, and some of these devices have been recovered. Although all geolocator batteries die before juvenile petrels return to the colony (after about 2/3 years maximum, and petrels return to the island to breed at ~ 5 years old; Tatayah, 2010), these data show initial petrel movements to be very wide-ranging and focused near coastlines in the first year of life. A continued focus on accumulating early-life migratory tracks for Round Island petrels, as well as other migratory species, is going to be key if we're to understand the early-life factors influencing how individual migratory strategies develop. While we found little evidence for links between timing of departure from Round Island and migratory strategies of adults, it is possible that timing of departure in the fledging year influences migratory strategy, but that this correlates poorly with adult migration phenology which is likely to be influenced by when they return to island, find a mate, and complete the breeding event. Further advances in technology will hopefully make exploration of these issues possible in the near future.

Conclusion

Results presented throughout this thesis have shown the importance of tracking individuals for understanding individual variation in tropical systems, in these poorly sampled parts of the world. Even in these unpredictable and patchy systems, individuals display low levels of within-individual variation and high levels of between-individual variation, suggesting benefits of repeatedly following the same migration strategy year after year. Collectively, these results highlight the importance of trying to understand the factors influencing which strategies individuals follow (which are likely due to experiences conditions early in life), their fitness implications, with the potential to predict how migratory populations may respond to environmental change.

References

Abrahms, B., Hazen, E.L., Aikens, E.O., Savoca, M.S., Goldbogen, J.A., Bograd, S.J., Jacox, M.G., Irvine, L.M., Palacios, D.M. & Mate, B.R. (2019). Memory and resource tracking drive blue whale migrations. *Proceedings of the National Academy of Sciences*, 116: 5582-5587.

Acker, P., Daunt, F., Wanless, S., Burthe, S.J., Newell, M.A., Harris, M.P., Grist, H., Sturgeon, J., Swann, R.L., Gunn, C. & Payo-Payo, A. (2021). Strong survival selection on seasonal migration versus residence induced by extreme climatic events. *Journal of Animal Ecology*, 90(4): 796-808.

Åkesson, S. & Helm, B. (2020). Endogenous programs and flexibility in bird migration. *Frontiers in Ecology & Evolution*, 8: 78.

Alerstam, T., Hedenstrom, A. & Akesson, S. (2003). Long-distance migration: evolution and determinants. *Oikos,* 103: 247-260.

Alves, J.A., Gunnarsson, T.G., Hayhow, D.B., Appleton, G.F., Potts, P.M., Sutherland, W.J. & Gill, J.A. (2013). Costs, benefits, and fitness consequences of different migratory strategies*. Ecology,* 94: 11–17.

Ambrosini, R., Romano, A. & Saino, N. (2019). Changes in migration, carry-over effects, and migratory connectivity. In P.O. Dunn & A.P. Møller (Eds.), *Effects of climate change on birds*. New York, NY: Oxford University Press.

Anderson, G.Q.A. & Green, R.E. (2009). The value of ringing for bird conservation. *Ringing & Migration*, 24: 205-212.

Ashmole, N. (1971). Seabird ecology and the marine environment. New York: Academic Press.

Au, D.W.K. & Pitman, R.L. (1986). Seabird interactions with dolphins and tuna in the eastern Tropical Pacific. *The Condor*, 88: 304-317.

Austin, R.E., Wynn, R.B., Votier, S.C., Trueman, C., McMinn, M., Rodríguez, A., Suberg, L., Maurice, L., Newton, J., Genovart, M., Péron, C., Grémillet, D. &

Guilford, T. (2019). Patterns of at-sea behaviour at a hybrid zone between two threatened seabirds. *Scientific Reports*, 9: 14720.

Barbosa, M. & Morrissey, M.B. (2021). The distinction between repeatability and correlation in studies of animal behaviour. *Animal Behaviour,* 175: 201-217.

Beal, M., Dias, M.P., Phillips, R.A., Oppel, S., Hazin, C., Pearmain, E.J., Adams, J., Anderson, D.J., Antolos, M., Arata, J.A., Arcos, J.M., Arnould, J., Awkerman, J., Bell, E., Bell, M., Carey, M., Carle, R., Clay, T.A., Cleeland, J., Colodro, V., Conners, M., Cruz-Flores, M., Cuthbert, R., Delord, K., Deppe, L., Dilley, B.J., Dinis, H., Elliott, G., De Felipe, F., Felis, J., Forero, M.G., Freeman, A., Fukuda, A., González-Solís, J., Granadeiro, J.P., Hedd, A., Hodum, P., Igual, J.M., Jaeger, A., Landers, T.J., Le Corre, M., Makhado, A., Metzger, B., Militão, T., Montevecchi, W.A., Morera-Pujol, V., Navarro-Herrero, L., Nel, D., Nicholls, D., Oro, D., Ouni, R., Ozaki, K., Quintana, F., Ramos, R., Reid, T., Reyes-González, J.M., Robertson, C., Robertson, G., Romdhane, M.S., Ryan, P.G., Sagar, P., Sato, F., Schoombie, S., Scofield, R.P., Shaffer, S.A., Shah, N.J., Stevens, K.L., Surman, C., Suryan, R.M., Takahashi, A., Tatayah, V., Taylor, G., Thompson, D.R., Torres, L., Walker, K., Wanless, R., Waugh, S.M., Weimerskirch, H., Yamamoto, T., Zajkova, Z., Zango, L. & Catry, P. (2021). Global political responsibility for the conservation of albatrosses and large petrels. *Science Advances*, 7(10): eabd7225.

Bell, A., Hankison, S. & Laskowski, K. (2009). The repeatability of behaviour: a meta-analysis. *Animal Behaviour*, 77: 771-783.

Benoit-Bird, J.K., Au, W.W. & Wisdom, D.W. (2009). Nocturnal light and lunar cycle effects on diel migration of micronekton. *Limnology and Oceanography*, 54: 1789-1800.

Berg, M., Linnebjerg, J.F., Taylor, G., Ismar-Rebitz, S.M.H., Bell, M., Gaskin, C.P., Åkesson, S. & Rayner, M.J. (2019). Year-round distribution, activity patterns and habitat use of a poorly studied pelagic seabird, the fluttering shearwater *Puffinus gavia*. *PLoS ONE*, 14(8): e0219986.

Bernard, A., Rodrigues, A.S.L., Cazalis, V. & Grémillet, D. (2021). Toward a global strategy for seabird tracking. *Conservation Letters*, 14(3): e12804.

Berthold, P., Kaatz, M. & Querner, U. (2004). Long-term satellite tracking of white stork (*Ciconia ciconia*) migration: constancy versus variability. *Journal of Ornithology*, 145: 356-359.

BirdLife International (2022). Seabird Tracking Database,Tracking Ocean Wanderers. Cambridge. Available at: www.seabirdtracking.org (accessed 01 December 2022).

BirdLife International and Handbook of the Birds of the World. (2022). Bird species distribution maps of the world. Version 2022.1. Available at http://datazone.birdlife.org/species/requestdis.

Black, C., Rey, A.R. & Hart, T. (2017). Peeking into the bleak midwinter: Investigating nonbreeding strategies of Gentoo Penguins using a camera network. *The Auk*, 134(3): 520-529.

Black, C. (2018). Spying on seabirds: a review of time-lapse photography capabilities and limitations. *Seabird*, 31: 1-14.

Black, C., Collen, B., Lunn, D., Filby, D., Winnard, S. & Hart, T. (2018a). Time-lapse cameras reveal latitude and season influence breeding phenology durations in penguins. *Ecology and Evolution*, 8: 8286–8296.

Black, C., Southwell, C., Emmerson, L., Lunn, D. & Hart, T. (2018b). Time-lapse imagery of Adélie Penguins reveals differential winter strategies and breeding site occupation. *PLoS ONE*, 13: e0193532.

Block, B.A., Jonsen, I.D., Jorgensen, S.J., Winship, A.J., Shaffer, S.A., Bograd, S.J., Hazen, E.L., Foley, D.G., Breed, G.A., Harrison, A.L., Ganong, J.E., Swithenbank, A., Caslteton, M., Dewar, H., Mate, B.R., Shillinger, G.L., Schaefer, K.M., Benson, S.R., Weise, M.J., Henry, R.W. & Costa, D.P. (2011). Tracking apex marine predator movements in a dynamic ocean.

Bogdanova, M.I., Butler, A., Wanless, S., Moe, B., Anker-Nilssen, T., Frederiksen, M., Boulinier, T., Chivers, L.S., Christensen-Dalsgaard, S., Descamps, S., Harris, M.P., Newell, M., Olsen, B., Phillips, R.A., Shaw, D., Steen, H., Strøm, H., Thórarinsson, T.L. & Daunt, F. (2017). Multi-colony tracking reveals spatio-temporal variation in carry-over effects between breeding success and winter movements in a pelagic seabird. *Marine Ecology Progress Series*, 578: 167-181.

Bolnick, D.I., Svanbäck, R., Fordyce, J.A., Yang, L.H., Davis, J.M., Hulsey, C.D. & Forister, M.L. (2003). The ecology of individuals: Incidence and implications of individual specialization, *The American Naturalist*, 161(1): 1-28.

Bonnet-Lebrun, A.S., Dias, M.P., Phillips, R.A., Granadeiro, J.P., Brooke, M.D.L., Chastel, O., Clay, T.A., Fayet, A.L., Gilg, O., González-Solís, J., Guilford, T., Hanssen, S.A., Hedd, A., Jaeger, A., Krietsch, J., Lang, J., Le Corre, M., Militão, T., Moe, B., Montevecchi, W.A., Peter, H.U., Pinet, P., Rayner, M.J., Reid, T., Reyes-González, J.M., Ryan, P.G., Sagar, P.M., Schmidt, N.M., Thompson, D.R., van Bemmelen, R., Watanuki, Y., Weimerskirch, H., Yamamoto, T. & Catry, P. (2021). Seabird migration strategies: Flight budgets, diel activity patterns, and lunar influence. *Frontiers in Marine Science*, 8: 683071.

Booth Jones, K.A., Nicoll, M.A.C., Raisin, C., Dawson, D.A., Hipperson, H., Horsburgh, G.J., Groombridge, J.J., Ismar, S.M.H., Sweet, P., Jones, C.G., Tatayah, V., Ruhomaun, K. & Norris, K. (2017). Widespread gene flow between oceans in a pelagic seabird species complex. *Molecular Ecology*, 26: 5716-5728.

Both, C., Bijlsma, R.G. & Ouwehand, J. (2016). Repeatability in spring arrival dates in Pied flycatchers varies among years and sexes. *Ardea*, 104: 3-21.

Bridge, E.S., Thorup, K., Bowlin, M.S., Chilson, P.B., Diehl, R.H., Fléron, R.W., Hartl, P., Kays, R., Kelly, J.F., Robinson, D. & Wikelski, M. (2011). Technology on the move: Recent and forthcoming innovations for tracking migratory birds. *BioScience*, 61: 689-698.

Brodersen, J., Chapman, B.B., Nilsson, P.A., Skov, C., Hansson, L.A. & Brönmark, C. (2014). Fixed and flexible: Coexistence of obligate and facultative migratory strategies in a freshwater fish. *PLoS ONE*, 9: e90294.

Brooke, M.D.L. (2004). Albatrosses and Petrels Across the World (Bird Families of the World), Oxford University Press, Oxford.

Brooke, M.D.L, Imber, M.J. & Rowe, G. (1999). Occurrence of two surface-breeding species of *Pterodroma* on Round Island, Indian Ocean. *Ibis*, 142: 139-158.

Brooks, M.E., Kristensen, K., van Benthem, K.J., Magnusson, A., Berg, C.W., Nielsen, A., Skaug, H.J., Maechler, M. & Bolker, B.M. (2017). glmmTMB Balances Speed and Flexibility Among Packages for Zero inflated Generalized Linear Mixed Modeling. *The R Journal*, 9(2): 378-400.

Brown, R.M., Nichols, R.A., Faulkes, C.G., Jones, C.G., Bugoni, L., Tatayah, V., Gottelli, D. & Jordan, W.C. (2010). Range expansion and hybridization in Round Island petrels (*Pterodroma* spp.): evidence from microsatellite genotypes. *Molecular Ecology*, 19: 3157-3170.

Brown, R.M., Jordan, W.C., Faulkes, C.G., Jones, C.G., Bugoni, L., Tatayah, V., Palma, R.L. & Nichols, R.A. (2011). Phylogenetic relationships in *Pterodroma* petrels are obscured by recent secondary contact and hybridization. *PLoS ONE*, 6: e20350.

Brown, J.M., van Loon, E.E., Bouten, W., Camphuysen, K.C.J., Lens, L., Müller, W., Thaxter, C.B. & Shamoun-Baranes, J. (2021). Long-distance migrants vary migratory behaviour as much as short-distance migrants: An individual-level comparison from a seabird species with diverse migration strategies. *Journal of Animal Ecology,* 90: 1058-1070.

Burgess, M., Castello, J., Davis, T. & Hewson, C. (2022). Loop-migration and non-breeding locations of British breeding wood warblers *Phylloscopus sibilatrix.* Bird Study: 1-11.

Calenge, C. (2006). The package adehabitat for the R software: a tool for the analysis of space and habitat use by animals. *Ecological Modelling,* 197: 516-519.

Camphuysen, K.C.J., Shamoun-Baranes, J., Bouten, W. & Garthe, S. (2012). Identifying ecologically important marine areas for seabirds using behavioural information in combination with distribution patterns. *Biological Conservation*, 156: 22-29.

Campioni, L., Dias, M.P., Granadeiro, J.P. & Catry, P. (2019). An ontogenetic perspective on migratory strategy of a long-lived pelagic seabird: Timings and destinations change progressively during maturation. *Journal of Animal Ecology*, 89: 29-43.

Carey, M.J. (2009). The effects of investigator disturbance on procellariform seabirds: a review. *New Zealand Journal of Zoology*, 36: 367-377.

Carneiro, C., Gunnarsson, T.G. & Alves, J.A. (2019). Why are Whimbrels not advancing their arrival dates into Iceland? Exploring seasonal and sex-specific variation in consistency of individual timing during the annual cycle. *Frontiers in Ecology and Evolution*, 7: 248.

Carr, P., Votier, S., Koldewey, H., Godley, B., Wood, H. & Nicoll, M.A.C. (2021). Status and phenology of breeding seabirds and a review of Important Bird and Biodiversity Areas in the British Indian Ocean Territory. *Bird Conservation International*, 31: 14-34.

Carreiro, A.R., Paiva, V.H., Medeiros, R., Franklin, K.A., Oliveria, N., Fagundes, A.I. & Ramos, J.A. (2020). Metabarcoding, stables isotopes, and tracking: unraveling the trophic ecology of a winter-breeding storm petrel (*Hydrobates castro*) with a multimethod approach. *Marine Biology*, 167: 14.

Catry, T., Ramos, J.A., Le Corre, M. & Phillips, R.A. (2009). Movements, at-sea distribution and behaviour of a tropical pelagic seabird: the wedge-tailed shearwater in the western Indian Ocean. *Marine Ecology Progress Series*, 391, 231-242.

Catry, P., Ruxton, G.D., Ratcliffe, N., Hamer, K.C. & Furness, R.W. (1999). Short-lived repeatabilities in long-lived great skuas: implications for the study of individual quality. *Oikos*, 84: 473–479.

Catry, P., Dias, M.P., Phillips, R.A. & Granadeiro, J.P. (2013). Carry-over effects from breeding modulate the annual cycle of a long-distance migrant: an experimental demonstration. *Ecology*, 94(6): 1230-1235.

Ceia, F.R. & Ramos, J.A. (2015). Individual specialization in the foraging and feeding strategies of seabirds: a review. *Marine Biology*, 162: 1923-1938.

Cerveira, L.R., Ramos, J.A., Rodrigues, I., Almeida, N., Araújo, P.M., dos Santos, I., Vieira, C., Pereira, J.M., Ceia, F.R., Geraldes, P., Melo, T. & Paiva, V.H. (2020). Inter-annual changes in oceanic conditions drives spatial and trophic consistency of a tropical marine predator. *Marine Environmental Research*, 162: 105165.

Chapman, B.B., Brönmark, C., Nilsson, J.Å. & Hansson, L.A. (2011). The ecology and evolution of partial migration. *Oikos,* 120: 1764-1775.

Charmantier, A. & Gienapp, P. (2014). Climate change and timing of avian breeding and migration: evolutionary versus plastic changes. *Evolutionary Applications*, 7: 15-28.

Cheke, A. & Hume, J.P. (2008). Lost Land of the Dodo: The Ecological history of Mauritius, Reunion and Rodrigues, United Kingdom, A&C Black.

Cherel, Y. & Bocher, P. (2022). Diet of the soft-plumaged petrel (*Pterodroma mollis*) at Kerguelen Islands and a review of the food of gadfly petrels (*Pterodroma* spp.) worldwide. *Marine Biology*, 169: 31.

Cinar, O., Nakagawa, S. & Viechtbauer, W. (2022). Phylogenetic multilevel meta-analysis: a simulation study on the importance of modelling the phylogeny. *Methods in Ecology and Evolution*, 13: 383– 395.

Cleasby, I.R., Nakagawa, S. & Schielzeth, H. (2015). Quantifying the predictability of behaviour: statistical approaches for the study of between-individual variation in the within-individual variance. *Methods in Ecology and Evolution*, 6: 27-37.

Collins, P.M., Green, J.A., Dodd, S., Shaw, P.J.A. & Halsey, L.G. (2014). Predation of Black-legged Kittiwake Chicks *Rissa tridactyla* by a Peregrine Falcon *Falco peregrinus*: insights from time-lapse cameras. *The Wilson Journal of Ornithology*, 126: 158–161.

Conklin, J.R., Battley, P.F. & Potter, M.A. (2013). Absolute consistency: Individual versus population variation in annual-cycle schedules of a long-distance migrant bird. *PLoS ONE*, 8: e54535.

Conklin, J.R., Lisovski, S. & Battley, P.F. (2021). Advancement in long-distance bird migration through individual plasticity in departure. *Nature Communications*, 12: 4780.

Cribari-Neto, F. & Zeileis, A. (2010). Beta Regression in R. *Journal of Statistical Software,* 34(2): 1-24.

Croxall, J.P., Butchart, S.H.M., Lascelles, B., Stattersfield, A.J., Sullivan, B., Symes, A. & Taylor, P. (2012). Seabird conservation status, threats and priority actions: a global assessment. *Bird Conservation International*, 22: 1–34.

Croxall, J.P., Silk, J.R.D., Phillips, R.A., Afanasyev, V. & Briggs, D.R. (2005). Global circumnavigations: Tracking year-round ranges of nonbreeding albatrosses. *Science*, 307: 249-250.

Cruz, S.M., Hooten, M., Huyvaert, K.P., Proaño, C.BB., Anderson, D.J., Afanasyev, V. & Wikelski, M. (2013). At-sea behavior varies with lunar phase in a nocturnal pelagic seabird, the swallow-tailed gull. *PLoS ONE*, 8(2): e56889.

Dalabehara, H.B. & Sarma, V.V.S.S. (2021). Physical forcing controls spatial variability in primary production in the Indian Ocean. *Deep Sea Research Part II: Topical Studies in Oceanography*, 183: 104906.

Dall, S.R.X., Bell, A.M., Bolnick, D.I., Ratnieks, F.L.W. & Sih, A. (2012). An evolutionary ecology of individual differences. *Ecology Letters*, 15: 1189-1198.

Dalpadado, P., Arrigo, K.R., van Dijken, G.L., Gunasekara, S.S., Ostrowski, M., Bianchi, G. & Sperfeld, E. (2021). Warming of the Indian Ocean and its impact on the temporal and spatial dynamics of primary production. *Progress in Oceanography*, 198: 102688.

Daunt, F., Afanasyev, V., Adam, A., Croxall, J. P. & Wanless, S. (2007). From cradle to early grave: juvenile mortality in European shags *Phalacrocorax aristotelis* results from inadequate development of foraging proficiency. *Biology Letters*, 3(4): 371-374.

Davies, T.E., Carneiro, A.P.B., Campos, B., Hazin, C., Dunn, D.C., Gjerde, K.M., Johnson, D.E. & Dias, M.P. (2021a). Tracking data and the conservation of the high seas: Opportunities and challenges. *Journal of Applied Ecology*, 58: 2703-2710.

Davies, T.E., Carneiro, A.P.B., Tarzia, M., Wakefield, E., Hennicke, J.C., Frederiksen, M., Hansen, E.S., Campos, B., Hazin, C., Lascelles, B., Anker-Nilssen, T., Arnardóttir, H., Barrett, R.T., Biscoito, M., Bollache, L., Boulinier, T., Catry, P., Ceia, F.R., Chastel, O., Christensen-Dalsgaard, S., Cruz-Flores, M., Danielsen, J., Daunt, F., Dunn, E., Egevang, C., Fagundes, A.I., Fayet, A.L., Fort, J., Furness, R.W., Gilg, O., González-Solís, J., Granadeiro, J.P., Grémillet, D., Guilford, T., Hanssen, S.A., Harris, M.P., Hedd, A., Huffeldt, N.P., Jessopp, M., Kolbeinsson, Y., Krietsch, J., Lang, J., Linnebjerg, J.F., Lorentsen, S.H., Madeiros, J., Magnusdottir, E., Mallory, M.L., McFarlane Tranquilla, L., Merkel, F.R., Militão, T., Moe, B., Montevecchi, W.A., Morera-Pujol, V., Mosbech, A., Neves, V., Newell, M.A., Olsen, B., Paiva, V.H., Peter, H.U., Petersen, A., Phillips, R.A., Ramírez, I., Ramos, J.A., Ramos, R., Ronconi, R.A., Ryan, P.G., Schmidt, N.M., Sigurðsson, I.A., Sittler, B., Steen, H., Stenhouse, I.J., Strøm, H., Systad, G.H.R., Thompson, P., Thórarinsson, T.L., van Bemmelen, R.S.A., Wanless, S., Zino, F. & Dias, M.P. (2021b). Multispecies tracking reveals a major seabird hotspot in the North Atlantic. *Conservation Letters*, 14(5): e12824.

del Hoyo, J., Elliott, A. & Sargatal, J. (1992). Handbook of the Birds of the World - Volume 1. Barcelona: Lynx Edicions.

Delmore, K.E. & Irwin, D.E. (2014). Hybrid songbirds employ intermediate routes in a migratory divide. *Ecology Letters*, 17(10): 1211-1218.

De Pascalis, F., Collins, P.M. & Green, J.A. (2018) Utility of time-lapse photography in studies of seabird ecology. *PLoS ONE*, 13(12): e0208995.

Dell'Ariccia, G., Benhamou, S., Dias, M.P., Granadeiro, J.P., Sudre, J., Catry, P. & Bonadonna, F. (2018). Flexible migratory choices of Cory's shearwaters are not driven by shifts in prevailing air currents. *Scientific Reports*, 8: 3376.

Delord, K., Barbraud, C., Pinaud, D., Ruault, S., Patrick, S.C. & Weimerskirch, H. (2019). Individual consistency in the non-breeding behaviour of a long-distance migrant seabird, the Grey petrel *Procellaria cinerea. Marine Ornithology*, 47: 93-103.

Dias, M.P., Alho, M., Granadeiro, J.P. & Catry, P. (2015). Wanderer of the deepest seas: migratory behaviour and distribution of the highly pelagic Bulwer's petrel. *Journal of Ornithology*, 156: 955-962.

Dias, M.P., Granadeiro, J.P. & Catry, P. (2012a). Do seabirds differ from other migrants in their travel arrangements? On route strategies of Cory's shearwater during its trans-equatorial journey. *PLoS ONE*, 7(11): e49376.

Dias, M.P., Granadeiro, J.P. & Catry, P. (2012b). Working the day or the night shift? Foraging schedules of Cory's shearwaters vary according to marine habitat. *Marine Ecology Progress Series*, 467: 245–252.

Dias, M.P., Granadeiro, J.P., Phillips, R.A., Alonso, H. & Catry, P. (2011). Breaking the routine: individual Cory's shearwaters shift winter destinations between hemispheres and across ocean basins. *Proceedings of the Royal Society B: Biological Sciences*, 278: 1786-1793.

Dias, M.P., Granadeiro, J.P. & Catry, P. (2013). Individual variability in the migratory path and stopovers of a long-distance pelagic migrant. *Animal Behaviour*, 86: 359-364.

Dias, M.P., Martin, R., Pearmain, E.J., Burfield, I.J., Small, C., Phillips, R.A., Yates, O., Lascelles, B., Borboroglu, P.G. & Croxall, J.P. (2019). Threats to seabirds: A global assessment. *Biological Conservation*, 237: 525-537.

Dias, M.P., Romero, J., Granadeiro, J.P., Catry, T., Pollet, I.L. & Catry, P. (2016). Distribution and at-sea activity of a nocturnal seabird, the Bulwer's petrel *Bulweria bulwerii*, during the incubation period. *Deep-Sea Research I*, 113: 49-56.

Díaz, S.M., Settele, J., Brondízio, E., Ngo, H., Guèze, M., Agard, J., Arneth, A., Balvanera, P., Brauman, K., Butchart, S. & Chan, K., 2019. The global assessment report on biodiversity and ecosystem services: Summary for policy makers. https://zenodo.org/record/3553579#.YkFxei8w1B0

Dingemanse, N.J. & Dochtermann, N.A. (2013). Quantifying individual variation in behaviour: mixed-effect modelling approaches. *Journal of Animal Ecology*, 82: 39-54.

Dingemanse, N.J. & Wright, J. (2020). Criteria for acceptable studies of animal personality and behavioural syndromes. *Ethology*, 126: 865-869.

Dingemanse, N.J., Hertel, A.R. & Royauté, R. (2022). Moving away from repeatability: a comment on Stuber et al. *Behavioral Ecology*, 33(3): 488-489.

Dochtermann, N.A. & Royauté, R. (2019). The mean matters: going beyond repeatability to interpret behavioural variation. *Animal behaviour*, 153: 147-150.

Dodino, S., Hart, T., Harris, S. & Rey, A.R. (2018). Year-round colony attendance patterns for the Gentoo Penguin (*Pygoscelis papua*) at Martillo Island, Tierra del Fuego, Argentina. *The Wilson Journal of Ornithology*, 130: 493–501.

Drake, A., Rock, C.A., Quinlan, S.P., Martin, M. & Green, D.J. (2014). Wind speed during migration influences the survival, timing of breeding, and productivity of a Neotropical migrant, *Setophaga petechia. PLoS ONE*, 9(5): e97152.

Edney, A.J. & Wood, M.J. (2020). Applications of digital imaging and analysis in seabird monitoring and research. *Ibis*, 163(2): 317–337.

Egevang, C., Stenhouse, I.J., Phillips, R.A., Petersen, A., Fox, J.W. & Silk, J.R.D. (2010). Arctic terns *Sterna paradisaea* reveals longest animal migration. *Proceedings of the National Academy of Sciences,* 107(5): 2078–2081.

Embling, C.B., Illian, J., Armstrong, E., van der Kooij, J., Sharples, J., Camphuysen, K.C.J. & Scott, B.E. (2012). Investigating fine-scale spatio-temporal predator–prey patterns in dynamic marine ecosystems: a functional data analysis approach. *Journal of Applied Ecology*, 49: 481-492.

Falush, D., Stephens, M. & Pritchard, J. (2003). Inference of population structure using multilocus genotype data: linked loci and correlated allele frequencies. *Genetics*, 164: 1567-87.

Fayet, A.L. (2020). Exploration and refinement of migratory routes in long-lived birds. *Journal of Animal Ecology,* 89: 16-19.

Fayet, A.L., Freeman, R., Anker-Nilssen, T., Diamond, A., Erikstad, K.E., Fifield, D., Fitzsimmons, M.G., Hansen, E.S., Harris, M.P., Jessopp, M., Kouwenberg, A.L., Kress, S., Mowat, S., Perrins, C.M., Petersen, A., Petersen, I.K., Reiertsen, T.K., Robertson, G.J., Shannon, P., Sigurðsson, I.A., Shoji, A., Wanless, S. & Guilford, T. (2017). Ocean-wide drivers of migration strategies and their influence on population breeding performance in a declining seabird. *Current Biology*, 27: 3871-3878.

Fayet, A.L., Freeman, R., Shoji, A., Boyle, D., Kirk, H.L., Dean, B.J., Perrins, C.M. & Guilford, T. (2016). Drivers and fitness consequences of dispersive migration in a pelagic seabird. *Behavioural Ecology*, 27: 1061-1072.

Fieberg, J. & Kochanny, C.O. (2015). Quantifying home- range overlap: The importance of the utilization distribution. *Journal of Wildlife Management*, 69: 1346-1359.

Frankish, C.K., Phillips, R.A., Clay, T.A., Somveille, M. & Manica, A. (2020). Environmental drivers of movement in a threatened seabird: insights from a mechanistic model and implications for conservation. *Diversity and Distributions*, 26: 1315-1329.

Franklin, K.A., Nicoll, M.A.C., Butler, S.J., Norris, K., Nakagawa, S. & Gill, J.A. (2022). Individual repeatability of avian migratory phenology: a systematic review and meta-analysis. *Journal of Animal Ecology*, 91: 1416-1430.

Franklin, K.A., Norris, K., Gill, J.A., Ratcliffe, N., Bonnet-Lebrun, A.S., Butler, S.J., Cole, N.C., Jones, C.G., Lisovski, S., Ruhomaun, K., Tatayah, V. & Nicoll, M.A.C. (2022). Individual consistency in migration strategies of a tropical seabird, the Round Island petrel. *Movement Ecology,* 10: 13.

Fraser, K.C., Shave, A., de Greef, E., Siegrist, J. & Garroway, C.J. (2019). Individual variability in migration timing can explain long-term, population-level advances in a songbird. *Frontiers in Ecology & Evolution*, 7: 324.

Friesen, V. (2015). Speciation in seabirds: why are there so many species… and why aren't there more? *Journal of Ornithology*, 156: 1-13.

Geen, G.R., Robinson, R.A. & Baillie, S.R. (2019). Effects of tracking devices on individual birds – a review of the evidence. *Journal of Avian Biology*, 50: e01823.

Gjerdrum, C. & Bolduc, F. (2016). Non-breeding distribution of Herring Gull (*Larus argentatus)* and Great Black-backed Gull (*Larus marinus*) in eastern Canada from ship-based surveys. *Waterbirds*, 39: 202-219.

Gill, J.A., Alves, J.S., Sutherland, W.J., Appleton, G.F., Potts, P.M. & Gunnarsson, T.G. (2014). Why is timing of bird migration advancing when individuals are not? *Proceedings of the Royal Society B: Biological Sciences*, 281: 20132161.

Gill, J.A., Alves, J.A. & Gunnarsson, T.G. (2019). Mechanisms driving phenological and range change in migratory species. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 374: 20180047.

Gill, R.E., Tibbitts, T.L., Douglas, D.C., Handel, C.M., Mulcahy, D.M., Gottschalck, J.C., Warnock, N., McCaffery, B.J., Battley, P.F. & Piersma, T. (2009). Extreme endurance flights by landbirds crossing the Pacific Ocean: Ecological corridor rather than barrier? *Proceedings of the Royal Society B: Biological Sciences*, 276: 447-457.

Gilroy, J.J., Gill, J.A., Butchart, S.H.M., Jones, V.R. & Franco, A.M.A. (2016). Migratory diversity predicts population declines in birds. *Ecology Letters,* 19: 308-317.

Gilsenan, C., Valcu, M. & Kempenaers, B. (2019). Timing of arrival in the breeding area is repeatable and affects reproductive success in a non-migratory population of blue tits. *Journal of Animal Ecology*, 89: 1017-1031.

Gordo, O. (2007). Why are bird migration dates shifting? A review of weather and climate effects on avian migratory phenology. *Climate Research*, 35: 37–58.

Grafen, A. (1989). The phylogenetic regression. *Philosophical Transactions of the Royal Society B: Biological Sciences,* 326: 119–157.

Grist, H., Daunt, F., Wanless, S., Nelson, E.J., Harris, M.P., Newell, M., Burthe, S. & Reid, J.M. (2014). Site fidelity and individual variation in winter location in partially migratory European shags. *PLoS ONE*, 9: e98562.

Green, S.E., Stephens, P.A., Whittingham, M.J. & Hill, R.A. (2022). Camera trapping with photos and videos: implications for ecology and citizen science. *Remote Sensing in Ecology and Conservation.*

Grecian, W.J., Williams, H.J., Votier, S.C., Bearhop, S., Cleasby, I.R., Grémillet, D., Hamer, K.C., Le Nuz, M., Lescroël, A., Newton, J., Patrick, S.C., Phillips, R.A., Wakefield, E.D. & Bodey, T.W. (2019). Individual spatial consistency and dietary flexibility in the migratory behavior of northern gannets wintering in the northeast Atlantic. *Frontiers in Ecology and Evolution*, 7: 214.

Guilford, T., Freeman, R., Boyle, D., Dean, B., Kirk, H., Phillips, R. & Perrins, C. (2011). A dispersive migration in the Atlantic puffin and its implications for migratory navigation. *PLoS ONE*, 6: e21336.

Gunnarsson, T.G., Gill, J.A., Sigurbjörnsson, T. & Sutherland, W.J. (2004). Pair bonds: Arrival synchrony in migratory birds. *Nature*, 431: 646.

Gunnarsson, T.G. & Tómasson, G. (2011). Flexibility in spring arrival of migratory birds at northern latitudes under rapid temperature changes. *Bird Study*, 58(1): 1-12.

Hackett, S.J., Kimball, R.T., Reddy, S., Bowie, R.C.K., Braun, E.L., Braun, M.J., Chojnowski, J.L., Cox, W.A., Han, K.L., Harshman, J., Huddleston, C.J., Marks, B.D., Miglia, K.J., Moore, W.S., Sheldon, F.H., Steadman, D.W. & Witt, C.C. (2008). A phylogenomic study of birds reveals their evolutionary history. *Science*, 320: 1763–1768.

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

Hanson, J.O., Rhodes, J.R., Butchart, S.H.M., Buchanan, G.M., Rondinini, C., Ficetola, G.F. & Fuller, R.A. (2020). Global conservation of species' niches. *Nature*, 580: 232–234.

Harley, C.D.G., Hughes, A.R., Hultgren, K.M., Miner, B.G., Sorte, C.J.B., Thornber, C.S., Rodriguez, L.F., Tomanek, L. & Williams, S.L. (2006). The impacts of climate change in coastal marine systems. *Ecology letters*, 9: 228-241.

Harrison, AL., Costa, D.P., Winship, A.J., Benson, S.R., Bograd, S.J., Antolos, M., Carlisle, A.B., Dewar, H., Dutton, P.H., Jorgensen, S.J., Kohin, S., Mate, B.R., Robinson, P.W., Schaefer, K.M., Shaffer, S.A., Shilinger, G.L., Simmons, S.E., Weng, K.C., Gjerde, K.M. & Block, B.A. (2018). The political biogeography of migratory marine predators. *Nature Ecology & Evolution*, 2: 1571-1578.

Hart, L.A., Downs, C.T. & Brown, M. (2016). Sitting in the sun: Nest microhabitat affects incubation temperatures in seabirds. *Journal of Thermal Biology*, 60: 149-154.

Hasselquist, D., Montràs-Janer, T., Tarka, M. & Hansson, B. (2017). Individual consistency of long-distance migration in a songbird: significant repeatability of autumn route, stopovers and wintering sites but not timing of migration. *Journal of Avian Biology,* 48: 91-102.

Hatzinger, R., Hornik, K., Nagel, H., & Maier, M. J. (2014). R: Einführung durch angewandte Statistik (2nd ed.). München: Pearson Studium.

Hazen, E., Maxwell, S., Bailey, H., Bograd, S., Hamann, M., Gaspar, P., Godley, B.J. & Shillinger, G. (2012). Ontogeny in marine tagging and tracking science: Technologies and data gaps. *Marine Ecology Progress Series*, 457: 221-240.

Helbig, A.J. (1991). Inheritance of migratory direction in a bird species: a cross-breeding experiment with SE-and SW-migrating Blackcaps (*Sylvia atricapilla*). *Behavioral Ecology and Sociobiology*, 28: 9-12.

Higgins, J.P. & Thompson, S.G. (2002). Quantifying heterogeneity in a meta-analysis. *Statistics in medicine*, 21(11): 1539-58.

Hijmans, R.J., Williams, E. & Vennes, C. (2019). Geosphere: Spherical Trigonometry. R package version 1.5-10.

Hill, R.D. (1994). Theory of geolocation by light levels. Pages 227–236 In B.J. Le Boeuf & R.M. Laws, eds., Elephant seals: population ecology, behavior, and physiology. University of California Press, Berkley.

Hinke, J.T., Barbosa, A., Emmerson, L.M., Hart, T., Juáres, M.A., Korczak-Abshire, M., Milinevsky, G., Santos, M., Trathan, P.N., Watters, G.M. & Southwell, C. (2018). Estimating nest-level phenology and reproductive success of colonial seabirds using time-lapse cameras. *Methods in Ecology and Evolution*, 9: 1853-1863.

Hobson, K.A., Norris, D.R., Kardynal, K.J. & Yohannes, E. (2019). Animal migration: a context for using new techniques and approaches. In K.A. Hobson & L.I. Wassenaar (Eds.), *Tracking animal migration with stable isotopes* (2nd ed.). UK: Academic Press.

Holloway, G.J., Jones, C.G., Ratcliffe, N., Ruhomaun, K., Tatayah, V., Norris, K. & Nicoll, M.A.C. (in review). Finite exchangeability, finite mixtures, statistical partitioning. *Bayesian Analysis*.

Holtmann, B., Lagisz, M. & Nakagawa, S. (2017). Metabolic rates, and not hormone levels, are a likely mediatory of between-individual differences in behaviour: a meta-analysis. *Functional Ecology*, 31: 685-696.

Hsing, P.Y., Bradley, S., Kent, V.T., Hill, R.A., Smith, G.C., Whittingham, M.J., Cokill, J., Crawley, D. & Stephens, P.A. (2018). Economical crowdsourcing for camera trap image classification. *Remote Sensing in Ecology and Conservation*, 4: 361-374.

Huffeldt, N.P. & Merkel, F.R. (2013). Remote time-lapse photography as a monitoring tool for colonial breeding seabirds: A case study using thick-billed murres (*Uria lomvia*). *Waterbirds*, 36: 330–341.

Hunt, G.L., Mehlum, F., Russell, R.W., Irons, D., Decker, M.B. & Becker, P.H. (1999). Physical processes, prey abundance, and the foraging ecology of seabirds. Pages 2040– 2056 in N.J. Adams and R.H. Slotow, eds. Proceedings of the

22nd International Ornithological Congress, Durban, South Africa. BirdLife South Africa, Johannesburg, South Africa.

Imber, M.J. (1975). Behaviour of petrels in relation to the moon and artificial lights. *Notornis*, 22(4): 302-306.

Imber, M.J. (2004). Kermadec petrels (*Pterodroma neglecta*) at Ilha da Trindade, South Atlantic Ocean and in the North Atlantic. *Notornis*, 51: 33-40.

Imber, M.J. (2005). A response to M. Tove's rebuttal of Imber (2004). *Notornis*, 52: 58-59.

Imber, M.J. (2008). Kermadec Petrels (*Pterodroma neglecta*) off the Azores, North Atlantic Ocean. *Notornis,* 55: 106-108.

IPCC. (2022). Climate Change 2022: Impacts, Adaptation, and Vulnerability. Contribution of Working Group II to the Sixth Assessment Report of the Intergovernmental Panel on Climate Change [Pörtner, H.O., Roberts, D.C., Tignor, M., Poloczanska, E.S., Mintenbeck, K., Alegría, A., Craig, M., Langsdorf, S., Löschke, S., Möller, V., Okem, A.,& Rama, B. (eds.)]. Cambridge University Press. In Press.

Jaeger, A., Feare, C.J., Summers, R.W., Lebarbenchon, C., Larose, C.S. & Le Corre, M. (2017). Geolocation reveals year round at-sea distribution and activity of a superabundant tropical seabird, the Sooty tern *Onychoprion fuscatus. Frontiers in Marine Science*, 4: 394.

Jahn, A.E., Lerman, S.B., Phillips, L.M., Ryder, T.B. & Williams, E.J. (2019). First tracking of individual American Robins (*Turdus migratorius*) across seasons. *The Wilson Journal of Ornithology*, 131(2): 356-359.

Jaquemet, S., Le Corre, M., Weimerskirch, H. (2004). Seabird community structure in a coastal tropical environment: importance of natural factors and fish aggregating devices (FADs). *Marine Ecology Progress Series*, 268: 281-292.

Jaquemet, S., Le Corre, M. & Quartly, G.D. (2007). Ocean control of the breeding regime of the sooty tern in the southwest Indian Ocean. *Deep Sea Research Part I: Oceanographic Research Papers*, 54(1): 130-142.

Jetz, W., Thomas, G.H., Joy, J.B., Hartmann, K. & Mooers, A.O. (2012) The global diversity of birds in space and time. *Nature*, 491: 444–448.

Jones, F.M., Allen, C., Arteta, C., Arthur, J., Black, C., Emmerson, L.M., Freeman, R., Hines, G., Lintott, C.J., Macháčková, Z., Miller, G., Simpson, R., Southwell, C., Torsey, H.R., Zisserman, A. & Hart, T. (2018). Time-lapse imagery and volunteer classifications from the Zooniverse Penguin Watch project. *Scientific Data*, 5: 180124.

Jones, F.M., Arteta, C., Zisserman, A., Lempitsky, V., Lintott, C.J. & Hart, T. (2020). Processing citizen science- and machine-annotated time-lapse imagery for biologically meaningful metrics. *Scientific Data*, 7: 1–15.

Kent, J.W. & Rankin, M.A. (2001). Heritability and physiological correlates of migratory tendency in the grasshopper *Melanoplus sanguinipes. Physiological Entomology*, 26: 371-380.

Kentie, R., Marquez-Ferrando, R., Figuerola, J., Gangoso, L., Hooijmeijer, J.C.E.W., Loonstra, A.H.J., Robin, F., Sarasa, M., Senner, N., Valkema, H., Verhoeven, M.A. & Piersma, T. (2017). Does wintering north or south of the Sahara correlated with timing and breeding performance in black-tailed godwits? *Ecology and Evolution*, 7: 2812-2820.

Kikuchi, D.W. & Reinhold, K. (2021). Modelling migration in birds: competition's role in maintaining individual variation. *Proceedings of the Royal Society B: Biological Sciences,* 288: 20210323.

Kliska, K., Southwell, C., Salton, M., Williams, R. & Emmerson, L. (2022). Phenology-based adjustments improve population estimates of Antarctic breeding seabirds: the case of Cape petrels in East Antarctica. *Royal Society Open Science*, 9: 211659.

Knudsen, E., Lindén, A., Both, C., Jonzén, N., Pulido, F., Saino, N., Sutherland, W.J., Bach, L.A., Coppack, T., Ergon, T., Gienapp, P., Gill, J.A., Gordo, O., Hedenström, A., Lehikoinen, E., Marra, P.P., Møller, A.P., Nilsson, A.L.K., Péron, G., Ranta, E., Rubolini, D., Sparks, T.H., Spina, F., Studds, C.E., Sæther, S.A., Tryjanowski, P. & Stenseth, N. C. (2011). Challenging claims in the study of migratory birds and climate change. *Biological Reviews*, 86(4): 928-946.

Kopp, M., Peter, H.U., Mustafa, O., Lisovski, S., Ritz, M.S., Phillips, R.A. & Hahn, S. (2011). South polar skuas from a single breeding population overwinter in different oceans though show similar migration patterns. *Marine Ecology Progress Series,* 435: 263-267.

Korner-Nievergelt, F., Jenni, L., Tøttrup, A.P. & Pasinelli, G. (2012). Departure directions, migratory timing and non-breeding distribution of the Red-backed shrike *Lanius collurio*: do ring re-encounters and light-based geolocator data tell the same story? *Ringing & Migration*, 27: 83-93.

Kosmidis, I. (2021). brglm2: Bias Reduction in Generalized Linear Models. R package version 0.8.2 https://CRAN.R-project.org/package=brglm2

Kosmidis, I. & Firth, D. (2021). Jeffreys-prior penalty, finiteness and shrinkage in binomial-response generalized linear models. *Biometrika*, 108(1): 71-82.

Kranstauber, B., Smolla, M. & Safi, K. (2017). Similarity in spatial utilization distributions measured by the earth mover's distance. *Methods in Ecology and Evolution*, 8: 155-160.

Kranstauber, B., Smolla, M. & Scharf, A.K. (2020). move: Visualising and analysing animal track data. R package version 4.0.6. https://CRAN.R-project.org/package=move

Krietsch, J., Hahn, S., Kopp, M., Phillips, R.A., Peter, H.A. & Lisovski, S. (2017). Consistent variation in individual migration strategies of brown skuas. *Marine Ecology Progress Series*, 578: 213-225.

Krüger, L., Paiva, V.H., Colabuono, F.I., Petry, M.V., Montone, R.C. & Ramos, J.A. (2016). Year-round spatial movements and trophic ecology of Trindade petrels (*Pterodroma arminjoniana*). *Journal of Field Ornithology*, 87(4): 404-416.

Kumar, S.P., Narvekar, J., Nuncio, M., Gauns, M., Sardesai, S. (2009). What drives the biological productivity of the Northern Indian Ocean? In: Wiggert, J.D., Hood, R.R., Naqvi, S.W.A., Brink, K.H., Smith, S.L., editors. Indian Ocean Biogeochemical Processes and Ecological Variability. San Francisco: American Geophysical Union, p. 33-56.

Kürten, N., Schmalijohann, H., Bichet, C., Haest, B., Vedder, O., González-Solís, J. & Bouwhuis, S. (2022). High individual repeatability of the migratory behaviour of a long-distance migratory seabird. *Movement Ecology*, 10: 5.

Laforge, M.P., Webber, Q.M.R. & Vander Wal, R. (2021). Plasticity and repeatability in spring migration and parturition dates with implications for annual reproductive success. *bioRxiv,* 2021.08.24.457438.

Lambert, C. & Fort, J. (2022). No evidence that seasonal changes in large-scale environmental conditions drive migration in seabirds*. Journal of Animal Ecology*, 91(9): 1813-1825.

Lane, J.V., Pollock, C.J., Jeavons, R., Sheddan, M., Furness, R.W. & Hamer, K.C. (2021). Post-fledgling movements, mortality and migration of juvenile northern gannets. *Marine Ecology Progress Series*, 671: 207-218.

Lawrence, K.B., Barlow, C.R., Bensusan, K., Perez, C. & Willis, S.G. (2022). Phenological trends in the pre- and post-breeding migration of long-distance migratory birds. *Global Change Biology*, 28: 375-389.

Leal, G.R. & Bugoni, L. (2021). Individual variability in habitat, migration routes and niche used by Trindade petrels. *Pterodroma arminjoniana. Marine Biology*, 168: 134.

Le Corre, M., Jaeger, A., Pinet, P., Kappes, M.A., Weimerskirch, H., Catry, T., Ramos, J.A., Russell, J.C., Shah, N. & Jaquemet, S. (2012). Tracking seabirds to identify potential Marine Protected Areas in the tropical Western Indian Ocean. *Biological Conservation,* 156: 83-93.

Le Corre, M., Manoury, M., Orlowski, S., Bignon, F. & Dicque, G. (2020). Camera trapping reveals cooperative breeding in the red-footed booby *Sula sula*. *Marine Ornithology*, 48: 175-178.

Lehnert, L.S., Kramer-Schadt, S., Teige, T., Hoffmeister, U., Popa-Lisseanu, A., Bontadina, F., Ciechanowski, M., Dechmann, D.K.N., Kravchenko, K., Presetnik, P., Starrach, M., Straube, M., Zoephel, U. & Voigt, C.C. (2018). Variability and repeatability of noctule bat migration in Central Europe: evidence for partial and differential migration. *Proceedings of the Royal Society B: Biological Sciences*, 285: 20182174.

Lenth, R.V. (2021). emmeans: Estimated Marginal Means, aka Least-Squares Means. R package version 1.6.1. https://CRAN.R-project.org/package=emmeans

Lessells, C.M. & Boag, P.T. (1987). Unrepeatable repeatabilities: A common mistake. *The Auk*, 104: 116-121.

Lévy, M., Shankar, D., André, J., Shenoi, S., Durand, F. & de Boyer Montégut, C. (2007). Basin-wide seasonal evolution of the Indian Ocean's phytoplankton blooms. *Journal of Geophysical Research*, 112.

Lewison, R., Oro, D., Godley, B.J., Underhill, L., Bearhop, S., Wilson, R.P., Ainley, D., Arcos, J.M., Boersma, P.D., Borboroglu, P.G., Boulinier, T., Frederiksen, M., Genovart, M., González-Solís, J., Green, J.A., Grémillet, D., Hamer, K.C., Hilton, G.M., Hyrenbach, K.D., Martínez-Abraín, A., Montevecchi, W.A., Phillips, R.A., Ryan, P.G., Sagar, P., Sydeman, W.J., Wanless, S., Watanuki, Y., Weimerskirch, H. & Yorio, P. (2012). Research priorities for seabirds: Improving conservation and management in the 21st century. *Endangered Species Research*, 17: 93-121.

Lindström, Å., Alerstam, T., Andersson, A., Bäckman, J., Bahlenberg, P., Bom, R., Ekblom, R., Klaassen, R.H.G, Korniluk, M., Sjöberg, S. & Weber, J.K.M.

(2021). Extreme altitude changes between night and day during marathon flights of great snipes. *Current Biology*, 31(15): 3433-3439.

Lisovski S., Bauer S., Briedis M., Davidson S. C., Dhanjal-Adams K. L., Hallworth M. T., Karagicheva, J., Meier, C.M., Merkel, B., Ouwehand, J., Pedersen, L., Rakhimberdiev, E., Roberto-Charron, A., Seavy, N.E., Sumner, M.D., Taylor, C.M., Wotherspoon, S.J. & Bridge, E.S. (2020). Light-level geolocator analyses: A user's guide. *Journal of Animal Ecology,* 89 (1): 221-236.

Lisovski, S. & Hahn, S. (2012). GeoLight - processing and analysing light-based geolocator data in R. *Methods in Ecology and Evolution*, 3(6): 1055-1059.

Lisovski, S., Hewson, C.M., Klaassen, R.H., Korner-Nievergelt, F., Kristensen, M.W. & Hahn, S. (2012). Geolocation by light: accuracy and precision affected by environmental factors. *Methods in Ecology and Evolution*, 3: 603-612.

Lisovski, S., Wotherspoon, S., Sumner, M. (2016). TwGeos: Basic data processing for light-level geolocation archival tags. R package version 0.1.2. https://github.com/slisovski/TwGeos/

López-López, P., García-Ripollés, C. & Urios, V. (2014). Individual repeatability in timing and spatial flexibility of migration routes of trans-Saharan migratory raptors. *Current Zoology*, 60(5): 642-652.

López-López, P. (2016). Individual-based tracking systems in ornithology: welcome to the era of big data. *Ardeola*, 63(1): 103-136.

Luigi, G. (1995). Aspectos da biologia reprodutiva de *Pterodroma arminjoniana* (Giglioli & Salvadori, 1869) (Aves: Procellariidae) na Ilha da Trindade, Atlantico Sul. Rio de Janeiro, Brazil: Federal University Rio de Janeiro.

Luigi, G., Bugoni, L., Fonseca-Neto, F.P. & Teixeira, D.M. (2009). Biologia e conservação do petrel-de-trindade, *Pterodroma arminjoniana*, na ilha da Trindade, Atlântico sul. In: Mohr, L.V., Castro, J.W.A., Costa, P.M.S., Alves, R.J.V. (eds) Ilhas oceânicas brasileiras: da pes- quisa ao manejo, vol 2. Ministério do Meio Ambiente, Brasília, pp 223–263.

Mackley, E.K., Phillips, R.A., Silk, J.R.D., Wakefield, E.D., Afanasyev, V., Fox, J.W. & Furness, R.W. (2010). Free as a bird? Activity patterns of albatrosses during the non-breeding period. *Marine Ecology Progress Series*, 406: 291-303.

Maier, M.J. (2022). Companion Package to the Book ``R: Einführung durch angewandte Statistik''. R package version 0.9.4, URL: https://CRAN.R-project.org/package=REdaS

Mansfield, K.L., Wyneken, J., Porter, W.P. & Luo, J. (2014). First satellite tracks of neonate sea turtles redefine the 'lost years' oceanic niche. *Proceedings of the Royal Society B: Biological Sciences*, 281(1781): 20133039.

Mayfield, H.F. (1961) Nesting success calculated from exposure. *Wilson Bulletin*, 73: 255–261.

Mayfield, H.F. (1975) Suggestions for calculating nest success. *Wilson Bulletin*, 87: 456–466.

McFarlane Tranquilla, L.A., Montevecchi, W.A., Fifield, D.A., Hedd, A., Gaston, A.J., Roberston, G.J. & Phillips, R.A. (2014). Individual winter movement strategies in two species of murre (*Uria* spp.) in the Northwest Atlantic. *PLoS ONE*, 9: e90583.

McGraw, K.O. & Wong, S.P. (1996). Forming inferences about some intraclass correlation coefficients. *Psychological Methods*, 1: 30–46.

McNamara, J.M., Welham, R.K. & Houston, A.I. (1998). The timing of migration within the context of an annual routine. *Journal of Avian Biology*, 29: 416-423.

McNamara, J.M. & Dall, S.R.X. (2010). Information is a fitness enhancing resource. *Oikos*, 119: 231-236.

Mellone, U., López-López, P., Limiñana, R. & Urios, V. (2011). Weather conditions promote route flexibility during open ocean crossing in a long-distance migratory raptor. *International Journal of Biometeorology*, 55: 463-468.

Méndez, V., Gill, J.A., Alves, J.A., Burton, N.H.K. & Davies, R.G. (2017). Consequences of population change for local abundance and site occupancy of wintering waterbirds. *Diversity and Distributions*, 24: 24-35.

Mendez, L., Prudor, A. & Weimerskirch, H. (2017). Ontogeny of foraging behaviour in juvenile red-footed boobies (*Sula sula*). *Scientific Reports*, 7: 13886.

Merkel, B., Descamps, S., Yoccoz, N.G., Grémillet, D., Daunt, F., Erikstad, K.E., Ezhov, A.V., Harris, M.P., Gavrilo, M., Lorentsen, S.H., Reiertsen, T.K., Steen, H., Systad, G.H., Þórarinsson, P.L., Wanless, S. & Strøm, H. (2020). Individual migration strategy fidelity but no habitat specialization in two congeneric seabirds. *Journal of Biogeography,* 48: 263-275.

Merlin, C. & Liedvogel, M. (2019). The genetics and epigenetics of animal migration and orientation: birds, butterflies and beyond. *The Journal of Experimental Biology*, 222: jeb191890.

Militão, T., Sanz-Aguilar, A., Rotger, A. & Ramos, R. (2022). Non-breeding distribution and at-sea activity patterns of the smallest European seabird, the European Storm Petrel (*Hydrobates pelagicus*). *Ibis*, 164: 1160-1179.

Mill, A.M. (2008). Latitudinal gradients of biologically useful semi-darkness. Ecography, 31: 578-582.

Miller, R. L., Marsh, H., Cottrell, A. & Hamann, M. (2018). Protecting migratory species in the Australian marine environment: a cross-jurisdictional analysis of policy and management plans. *Frontiers in Marine Science*, 5: 229.

Moher, D., Liberati, A., Tetzlaff, J., Altman, D.G. & The PRISMA Group. (2009). Preferred reporting items for systematic reviews and meta-analyses: the PRISMA statement. *PLoS Medicine*, 6: e1000097.

Møller, A.P. (2001). Heritability of arrival date in a migratory bird. *Proceedings of the Royal Society B: Biological Sciences*, 268: 203-206.

Møller, A.P., Rubolini, D. & Lehikoinen, E. (2008). Populations of migratory bird species that did not show a phenological response to climate change are declining. *Proceedings of the National Academy of Sciences*, 105: 16195-16200.

Morrison, C.A., Alves, J.A., Gunnarsson, T.G., Þórisson, B. & Gill, J.A. (2019). Why do earlier-arriving migratory birds have better breeding success? *Ecology and Evolution*, 9(15): 8856-8864.

Morrison, C.A., Butler, S.J., Clark, J.A., Arizaga, J., Baltà, O., Cepák, J, Nebot, A.L., Piha, M., Thorup, K., Wenninger, T., Robinson, R.A. & Gill, J.A. (2022). Demographic variation in space and time: implications for conservation targeting. *Royal Society Open Science*, 9(3): 211671.

Mott, R. & Clarke, R.H. (2018). Systematic review of geographic biases in the collection of at-sea distribution data for seabirds. *Emu - Austral Ornithology*, 118: 235-246.

Mouritsen, H. & Larsen, O.N. (1998). Migrating young Pied Flycatchers *Ficedula hypoleuca* do not compensate for geographical displacements. *The Journal of Experimental Biology*, 201: 2927–2934.

Murphy, R.C. & Pennoyer, J.M. (1952). Larger petrels of the genus *Pterodroma*. American Museum novitates; no. 1580.

Nakagawa, S. & Schielzeth, H. (2010). Repeatability for Gaussian and non-Gaussian data: a practical guide for biologists. *Biological Reviews*, 85: 935-956.

Nakagawa, S. & Santos, E.S. (2012). Methodological issues and advances in biological meta-analysis. *Evolutionary Ecology*, 26(5): 1253-74.

Nakagawa, S. & Schielzeth, H. (2013) A general and simple method for obtaining R2 from generalized linear mixed-effects models. *Methods in Ecology and Evolution*, 4: 133–142.

Nakagawa, S., Lagisz, M., O'Dea, R.E., Rutkowska, J., Yang, Y., Noble, D.W.A. & Senior, A.M. (2021). The orchard plot: cultivating a forest plot for use in ecology, evolution, and beyond. *Research Synthesis Methods*, 12(1): 4-12.

Nakagawa, S., Lagisz, M., Jennions, M.D., Koricheva, J., Noble, D.W.A., Parker, T. H., Sánchez-Tójar, A., Yang, Y. & O'Dea, R. E. (2022). Methods for testing publication bias in ecological and evolutionary meta-analyses. *Methods in Ecology and Evolution,* 13: 4-21.

Newbery, K.B. & Southwell, C. (2009). An automated camera system for remote monitoring in polar environments. *Cold Regions Science and Technology*, 55: 47-51.

Newton, I. (2004). Population limitation in migrants. *Ibis*, 146: 197-226.

Newton, I. (2006). Advances in the study of irruptive migration. *Ardea*, 94(3): 433-460.

Newton, I. (2008). The migration ecology of birds. London, UK: Academic Press.

Newton, I. (2010). The migration ecology of birds. Elsevier.

Newton, I. & Dale, L. (1996). Relationship between migration and latitude among west European birds. *Journal of Animal Ecology*, 65: 137-146.

Ng, J.W., Knight, E.C., Scarpignato, A.L., Harrison, A.L., Bayne, E.M. & Marra, P.P. (2018). First full annual cycle tracking of a declining aerial insectivorous bird, the Common Nighthawk (*Chordeiles minor*), identifies migration routes, nonbreeding habitat, and breeding site fidelity. *Canadian Journal of Zoology*, 96(8): 869-875.

Nicoll, M.A.C., Nevoux, M., Jones, C.G., Ratcliffe, N., Ruhomaun, K., Tatayah, V. & Norris, K. (2017). Contrasting effects of tropical cyclones on the annual survival of a pelagic seabird in the Indian Ocean. *Global Change Biology*, 23: 550-565.

Nicoll, M.A.C., Cole, N.C., Horswill, C., Jones, C.G., Ratcliffe, N., Ruhomaun, K., Tatayah, V. & Norris, K. (2022), No detectable effect of geolocator deployment on the short- or long-term apparent survival of a tropical seabird. *Ibis*, 164: 1201-1212.

Noble, D.W.A., Lagisz, M., O'Dea, R.E. & Nakagawa, S. (2017). Nonindependence and sensitivity analyses in ecological and evolutionary meta-analyses. *Molecular Ecology*, 26: 2410-2425.

O'Brien, J. (2020). exiftoolr: ExifTool Functionality from R. R package version 0.1.5. https://CRAN.R-project.org/package=exiftoolr

O'Dea, R.E., Lagisz, M., Jennions, M.D., Koricheva, J., Noble, D.W.A., Parker, T.H., Gurevitch, J., Page, M.J., Stewart, G., Moher, D. & Nakagawa, S. (2021). Preferred reporting items for systematic reviews and meta-analyses in ecology and evolutionary biology: a PRISMA extension. *Biological Reviews*, 96: 1695-1722.

Oestreich, W.K., Aiu, K.M., Crowder, L.B., McKenna, M.F., Berdahl, A.M. & Abrahms, B. (2022). The influence of social cues on timing of animal migrations*. Nature Ecology & Evolution*, 6: 1617-1625.

Oppel, S., Bolton, M., Carneiro, A.P.B., Dias, M.P., Green, J.A., Masello, J.F., Phillips, R.A., Owen, E., Quillfeldt, P., Beard, A., Bertrand, S., Blackburn, J., Boersma, P.D., Borges, A., Broderick, A.C., Catry, P., Cleasby, I., Clingham, E., Creuwels, J., Crofts, S., Cuthbert, R.J., Dallmeijer, H., Davies, D., Davies, R., Dilley, B.J., Dinis, H.A., Dossa, J., Dunn, M.J., Efe, M.A., Fayet, A.L., Figueiredo, L., Frederico, A.P., Gjerdrum, C., Godley, B.J., Granadeiro, J.P., Guilford, T., Hamer, K.C., Hazin, C., Hedd, A., Henry, L., Hernández-Montero, M., Hinke, J., Kokubun, N., Leat, E., McFarlane Tranquilla, L., Metzger, B., Militão, T., Montrond, G., Mullié, W., Padget, O., Pearmain, E.J., Pollet, I.L., Pütz, K., Quintana, F., Ratcliffe, N., Ronconi, R.A., Ryan, P.G., Saldanha, S., Shoji, A., Sim, J., Small, C., Soanes, L., Takahashi, A., Trathan, P., Trivelpiece, W., Veen, J., Wakefield, E., Weber, N., Weber, S., Zango, L., Daunt, F., Ito, M., Harris, M.P., Newell, M.A., Wanless, S., González-Solís, J. & Croxall, J. (2018). Spatial scales of marine conservation management for breeding seabirds. *Marine Policy*, 98: 37-46.

Oppel, S., Weber, S., Weber, N., Fox, D., Leat, E., Sim, J., Sommerfeld, J., Bolton, M., Broderick, A.C. & Godley, B.J. (2017). Seasonal shifts in foraging distribution due to individual flexibility in a tropical pelagic forager, the Ascension frigatebird. *Marine Ecology Progress Series,* 585: 199-212.

Orben, R.A., Paredes, R., Roby, D.D., Irons, D.B. & Shaffer, S.A. (2015) Wintering North Pacific black-legged kittiwakes balance spatial flexibility and consistency. *Movement Ecology*, 3: 36.

Otsubo, J. & Higuchi, H. (2022). Time-lapse camera photographs reveal arrival and breeding timing of short-tailed albatrosses *Phoebastria albatrus*. *Endangered Species Research*, 47: 49-59.

Ouzzani, M., Hammady, H., Fedorowicz, Z. & Elmagarmid, A. (2016). Rayyan—a web and mobile app for systematic reviews. *Systematic Reviews*, 5(1): 210.

Paleczny, M., Hammill, E., Karpouzi, V. & Pauly, D. (2015). Population trend of the world’s monitored seabirds, 1950-2010. *PLoS ONE*, 10: 1–11.

Panuccio, M., Martín, B., Morganti, M., Onrubia, A. & Ferrer, M. (2016). Long-term changes in autumn migration dates at the Strait of Gibraltar reflect population trends of soaring birds. *Ibis*, 159(1): 55-65.

Paradis, E. & Schliep, K. (2019). ape 5.0: An environment for modern phylogenetics and evolutionary analyses in R. *Bioinformatics*, 35(3): 526–528.

Pastor-Prieto, M., Ramos, R., Zajková, Z., Reyes-González, J.M., Rivas, M.L., Ryan, P.G. & González-Solís, J. (2019). Spatial ecology, phenological variability and moulting patterns of the Endangered Atlantic petrel *Pterodroma incerta*. *Endangered Species Research*, 40: 189-206.

Payo-Payo, A., Acker, P., Bocedi, G., Travis, J.M., Burthe, S.J., Harris, M.P., Wanless, S., Newell, M., Daunt, F. & Reid, J.M. (2022). Modelling the responses of partially-migratory metapopulations to changing seasonal migration rates: from theory to data. *Journal of Animal Ecology*.

Pebsworth, P.A. & LaFleur, M. (2014). Advancing primate research and conservation through the use of camera traps: Introduction to the special issue. *International Journal of Primatology*, 35: 825-840.

Phalan, B., Phillips, R.A., Silk, J.R.D, Afanasyev, V., Fukuda, A., Fox, J., Catry, P., Higuchi, H. & Croxall, J.P. (2007). Foraging behaviour of four albatross species by night and day. *Marine Ecology Progress Series*, 340: 271–28.

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

Phillips, R.A., Silk, J.R.D., Croxall, J.P., Afanasyev, V. & Bennett, V.J. (2005). Summer distribution and migration of nonbreeding albatrosses: individual consistencies and implications for conservation. *Ecology*, 86: 2386-2396.

Phillips, E.M., Horne, J.K., Zamon, J.E., Felis, J.J. & Adams, J. (2019). Does perspective matter? A case study comparing Eulerian and Lagrangian estimates of common murre (*Uria aalge*) distributions. *Ecology and Evolution*, 9: 4805–4819.

Pick, J.L., Khwaja, N., Spence, M.A., Ihle, M. & Nakagawa, S. (2019). Counter culture: Causes, extent and solutions of systematic bias in the analysis of behavioural counts. [EcoEvoRxiv]

Pinet, P., Salamolard, M., Probst, J., Russell, J., Jaquemet, S. & Le Corre, M. (2009). Barau's Petrel *Pterodroma baraui*: history, biology and conservation of an endangered endemic petrel. *Marine Ornithology*, 37: 107-113.

Pinet, P., Jaeger, A., Cordier, E., Potin, G. & Le Corre, M. (2011). Celestial moderation of tropical seabird behaviour. *PLoS ONE*, 6(11): e27663.

Pinet, P., Jaquemet, S., Pinaud, D., Weimerskirch, H., Phillips, R.A. & Le Corre, M. (2011). Migration, wintering distribution and habitat use of an endangered tropical seabird, Barau's petrel *Pterodroma baraui. Marine Ecology Progress Series*, 423: 291-302.

Potti, J. (1998). Arrival time from spring migration in male Pied flycatchers: individual consistency and familial resemblance. *The Condor*, 100(4): 702-708.

Prasanna Kumar, S., Muraleedharan, P.M., Prasad, T.G., Gauns, M., Ramaiah, N., de Souza, S.N., Sardesai, S. & Madhupratap, M. (2002). Why is the Bay of Bengal less productive during summer monsoon compared to the Arabian Sea? *Geophysical Research Letters*, 29(24): 88-1.

Pritchard, J., Stephens, M. & Donnelly, P. (2000). Inference of population structure using multilocus genotype data. *Genetics*, 155: 945-959.

Raine, A.F., Driskill, S., Vynne, M., Harvey, D. & Pias, K. (2020). Managing the effects of introduced predators on Hawaiian endangered seabirds. *The Journal of Wildlife Management*, 84(3): 425-435.

Ramírez, I., Paiva, V.H., Fagundes, I., Menezes, D., Silva, I., Ceia, F.R., Phillips, R.A., Ramos, J.A. & Garthe, S. (2016). Conservation implications of consistent foraging and trophic ecology in a rare petrel species. *Animal Conservation,* 19(2): 139-152.

Ramírez, I., Paiva, V.H., Menezes, D., Silva, I., Phillips, R.A., Ramos, J.A. & Garthe, S. (2013). Year-round distribution and habitat preferences of the Bugio petrel. *Marine Ecology Progress Series*, 476: 269–284.

Ramos, R., Ramírez, I., Paiva, V.H., Militão, T., Biscoito, M., Menezes, D., Phillips, R.A., Zino, F. & González-Solís, J. (2016). Global spatial ecology of three closely-related gadfly petrels. *Scientific Reports*, 6:23447.

Ravache, A., Bourgeois, K., Thibault, M., Dromzée, S., Weimerskirch, H., de Grissac, S., Prudor, A., Lorrain, A., Menkes, C., Allain, V., Bustamante, P., Letourneur, Y. & Vidal, É. (2020). Flying to the moon: Lunar cycle influences trip duration and nocturnal foraging behavior of the wedge-tailed shearwater *Ardenna pacifica*. *Journal of Experimental Marine Biology and Ecology*, 525: 151322.

Rees, E.C. (1989). Consistency in the timing of migration for individual Bewick's swans. *Animal Behaviour*, 38(3): 384-393.

Regular, P.M., Hedd, A. & Montevecchi, W.A. (2011). Fishing in the dark: A pursuit-diving seabird modifies foraging behaviour in response to nocturnal light levels. *PLoS ONE*, 6(10): e26763.

Reich, K.J., Bjorndal, K.A. & Bolten, A.B. (2007). The 'lost years' of green turtles: using stable isotopes to study cryptic lifestages. *Biology Letters,* 3: 712-714.

Robinson, R.A., Crick, H.Q., Learmonth, J.A., Maclean, I., Thomas, C.D., Bairlein, F., Forchhammer, M.C., Franics, C.M., Gill, J.A., Godley, B.J., Harwood, J., Hays, G.C., Huntley, B., Hutson, A.M., Pierce, G.J., Rehfisch, M.M., Sims, D.W., Sanots, M.B., Sparks, T.H., Stroud, D.A. & Visser, M.E. (2009). Travelling through a warming world: climate change and migratory species. *Endangered Species Research*, 7: 87-99.

Rohatgi, A. (2015). WebPlotDigitizer (Version 4.2) [Computer software]. Retrieved from http://arohatgi.info/WebPlotDigitizer

Rotics, S., Kaatz, M., Resheff, Y.S., Turjeman, S.F., Zurell, D., Sapir, N., Eggers, U., Flack, A., Fiedler, W., Jeltsch, F., Wikelski, M. & Nathan, R. (2016). The challenges of the first migration: movement and behaviour of juveniles vs. adult white storks with insights regarding juvenile mortality*. Journal of Animal Ecology*, 85: 938-947.

Royauté, R. & Dochtermann, N.A. (2021). Comparing ecological and evolutionary variability within datasets. *Behavioral Ecology and Sociobiology*, 75: 127.

Rubner, Y., Tomasi, C. & Guibas, L.J. (2000). The earth mover's distance as a metric for image retrieval. *International Journal of Computer Vision*, 40: 99-121.

Runge, C.A., Watson, J.E., Butchart, S.H., Hanson, J.O., Possingham, H.P. & Fuller, R.A. (2015). Protected areas and global conservation of migratory birds. *Science*, 350(6265): 1255-1258.

Ryan, P.G. & Cooper, J. (1989). Observer precision and bird conspicuousness during counts of birds at sea. *South African Journal of Marine Science*, 8: 271-276.

R Core Team (2019). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL https://www.R-project.org/

Sánchez-Tójar, A., Moiron, M. & Niemelä, P.T. (2022). Terminology use in animal personality research: a self-report questionnaire and a systematic review. *Proceedings of the Royal Society B: Biological Sciences*, 289: 20212259.

Schacter, C.R. & Jones, I.L. (2018). Confirmed year-round residence and land roosting of Whiskered Auklets (*Aethia pygmaea*) at Buldir Island, Alaska. *The Auk*, 135(3): 706-715.

Schofield, G., Hobson, V.J., Fossette, S., Lilley, M.K.S., Katselidis, K.A. & Hays, G.C. (2010). Fidelity to foraging sites, consistency of migration routes and habitat modulation of home range by sea turtles. *Diversity and Distributions*, 16(5): 840-853.

Schott, F.A. & McCreary, J.P. (2001). The monsoon circulation of the Indian Ocean. *Progress in Oceanography*, 51: 1-123.

Semlitsch, R.D., Scott, D.E., Pechmann, J.H.K. & Gibbons, J.W. (1993). Phenotypic variation in the arrival time of breeding salamanders: individual repeatability and environmental influences. *Journal of Animal Ecology,* 62(2): 334-340.

Senapathi, D., Underwood, F., Black, E., Nicoll, M.A.C. & Norris, K. (2009). Evidence for long-term regional changes in precipitation on the East Coast Mountains in Mauritius*. International Journal of Climatology*, 30: 1164-1177.

Senior, A.M., Grueber, C.E., Kamiya, T., Lagisz, M., O'Dwyer, K., Santos, E.S.A. & Nakagawa, S. (2016). Heterogeneity in ecological and evolutionary meta-analyses: its magnitude and implications. *Ecology*, 97(12): 3293-3299.

Senner, N.R., Verhoeven, M.A., Abad-Gómez, J.M., Alves, J.A., Hooijmeijer, J.C.E.W., Howison, R.A., Kentie, R., Loonstra, A.H.J., Masero, J.A., Rocha, A., Stager, M. & Piersma, T. (2019) High migratory survival and highly variable migratory behaviour in black-tailed godwits. *Frontiers in Ecology and Evolution*, 7: 96.

Sergio, F., Tanferna, A., De Stephanis, R., Jiménez, L. L., Blas, J., Tavecchia, G., Preatoni, D. & Hiraldo, F. (2014). Individual improvements and selective mortality shape lifelong migratory performance. *Nature*: 515, 410–413.

Shaffer, S.A., Tremblay, Y., Weimerskirch, H., Scott, D., Thompson, D.R., Sagar, P.M., Moller, H., Taylor, G.S., Foley, D.G., Block, B.A. & Costa, D.P. (2006). Migratory shearwaters integrate oceanic resources across the Pacific Ocean in an endless summer. *Proceedings of the National Academy of Sciences*, 103(34): 12799-12802.

Shillinger, G., Bailey, H., Bograd, S. J., Hazen, E. L. & Hamann, M. (2012). Tagging through the stages: Technical and ecological challenges in observing life histories through biologging. *Marine Ecology Progress Series*, 457: 165–170.

Shimada, T., Limpus, C.J., Hamann, M., Bell, I., Esteban, N., Groom, R. & Hays, G.C. (2019). Fidelity to foraging sites after long migrations. *Journal of Animal Ecology*, 89: 1008-1016.

Soanes, L.M., Green, J.A., Bolton, M., Milligan, G., Mukhida, F. & Halsey, L.G. (2021). Linking foraging and breeding strategies in tropical seabirds. *Journal of Avian Biology*, 52(7): e02670.

Southwell, C. & Emmerson, L. (2015). Remotely-operating camera network expands Antarctic seabird observations of key breeding parameters for ecosystem monitoring and management. *Journal for Nature Conservation*, 23: 1–8.

Spear, L.B., Balance, L.T. & Ainley, D.G. (2001). Response of seabirds to thermal boundaries in the tropical Pacific: the thermocline versus the Equatorial Front. *Marine Ecology Progress Series*, 219: 275-289.

Spear, L.B. & Ainley, D.G. (1997). Flight behaviour of seabirds in relation to wind direction and wing morphology. *Ibis*, 139: 221-233.

Stanley, C.Q., MacPherson, M., Fraser, K.C., McKinnon, E.A. & Stutchbury, B.J.M. (2012). Repeat tracking of individual songbirds reveals consistent migration timing but flexibility in route. *PLoS ONE*, 7: e40688.

Stoffel, M.A., Nakagawa, S. & Schielzeth, H. (2017). rptR: repeatability estimation and variance decomposition by generalized linear mixed-effects models. *Methods in Ecology and Evolution*, 8: 1639-1644.

Strandberg, R., Klaassen, R.H.G. & Thorup, K. (2009). Spatio-temporal distribution of migrating raptors: A comparison of ringing and satellite tracking. *Journal of Avian Biology*, 40(5): 500-510.

Stroud, J.T. & Feeley, K.J. (2017). Neglect of the tropics is widespread in ecology and evolution: A comment on Clarke et al. *Trends in Ecology & Evolution*, 32(9): 626-628.

Stuber, E.F., Carlson, B.S. & Jesmer, B.R. (2022). Spatial personalities: a meta-analysis of consistent individual differences in spatial behavior. *Behavioral Ecology*, 33(3): 477-486.

Stutchbury, B.J.M., Gow, E.A., Done, T., MacPherson, M., Fox, J.W. & Afanasyev, V. (2011). Effects of post-breeding moult and energetic condition on timing of songbird migration into the tropics. *Proceedings of the Royal Society B: Biological Sciences*, 278: 131-137.

Sumner, M.D., Wotherspoon, S.J. & Hindell, M.A. (2009). Bayesian estimation of animal movement from archival and satellite tags. *PLoS ONE*, 4(10).

Sutherland, W.J. (1998). Evidence for flexibility and constraint in migratory systems. *Journal of Avian Biology*, 29: 441-446.

Tatayah, V. (2007). The breeding biology of the Round Island Petrel (*Pterodroma arminjoniana*) and the factors determining breeding success. MPhil Thesis, University of Mauritius.

Tatayah, V. (2010). The breeding biology of the Round Island petrel. PhD Thesis, University of Mauritius.

Teitelbaum, C.S., Converse, S.J., Fagan, W.F., Böhning-Gaese, K., O'Hara, R.B., Lacy, A.E. & Mueller, T. (2016). Experience drives innovation of new migration patterns of whooping cranes in response to global change. *Nature communications*, 7(1): 1-7.

Thackery, S.J., Sparks, T.H., Frederiksen, M., Burthe, S., Bacon, P.J., Bell, J.R., Botham, M.S., Brereton, T.M., Bright, P.W., Carvalho, L., Clutton-Brock, T., Dawson, A., Edwards, M., Elliott, J.M., Harrington, R., Johns, D., Jones, I.D., Jones, J.T., Leech, D.I., Roy, D.B., Scott, W.A., Smith, M., Smithers, R.J., Winfield, I.J. & Wanless, S. (2010). Trophic level asynchrony in rates of phenological change for marine, freshwater and terrestrial environments. *Global Change Biology*, 16: 3304-3313.

Thieurmel, B. & Elmarhraoui, A. (2019). suncalc: Compute Sun Position, Sunlight Phases, Moon Position and Lunar Phase. R package version 0.5.0.

Thorsteinsson, V., Pálsson, O.K., Tómasson, G.G., Jónsdóttir, I.G. & Pampoulie, C. (2012). Consistency in the behaviour types of the Atlantic cod: repeatability, timing of migration and geo-location. *Marine Ecology Press Series*, 462: 251-260.

Thorup, K., Korner-Nievergelt, F., Choen, E.B. & Baillie, S.R. (2014). Large-scale spatial analysis of ringing and re-encounter data to infer movement patterns: A review including methodological perspectives. *Methods in Ecology and Evolution*, 5: 1337-1350.

Thorup, K., Vega, M.L., Snell, K.R.S., Lubkovskaia, R., Willemoes, M., Sjöberg, S., Sokolov, L.V. & Bulyuk, V. (2020). Flying on their own wings: young and adult cuckoos respond similarly to long-distance displacement during migration. *Scientific Reports*, 10: 7698.

Trevail, A.M., Green, J.A., Sharples, J., Polton, J.A., Arnould, J.P.Y. & Patrick, S.C. (2018). Environmental heterogeneity amplifies behavioural response to a temporal cycle. *Oikos*, 128(4): 517-528.

Tove, M.H. (2005). Kermadec Petrels (*Pterodroma neglecta*) in the Atlantic Ocean–a rebuttal. *Notornis*, 52: 56-58.

United Nations Convention on the Law of the Sea (United Nations, 1982).

Väli, Ü., Mirski, P., Sellis, U., Dagys, M. & Maciorowski, G. (2018). Genetic determination of migration strategies in large soaring birds: evidence from hybrid eagles. *Proceedings of the Royal Society B: Biological Sciences*, 285: 20180855.

van Bemmelen, R.S.A., Kolbeinsson, Y., Ramos, R., Gilg, O., Alves, J.A., Smith, M., Schekkerman, H., Lehikoinen, A., Petersen, I.K., Þórisson, B., Sokolov, A.A., Välimäki, K., van der Meer, T., Okill, J.D., Bolton, M., Moe, B., Hanssen, S.A., Bollache, L., Petersen, A., Thorstensen, S., González-Solís, J., Klaassen, R.H.G. & Tulp, I. (2019). A migratory divide among red-necked phalaropes in the Western Palearctic reveals constrasting migration and wintering movement strategies. *Frontiers in Ecology and Evolution*, 7: 86.

van Bemmelen, R., Moe, B., Hansen, S.A., Schmidt, N.M., Hansen, J., Lang, J., Sittler, B., Bollache, L., Tulp, I., Klaassen, R. & Gilg, O. (2017). Flexibility in otherwise consistent non-breeding movements of a long-distance migratory seabird, the long-tailed skua. *Marine Ecology Progress Series*, 578: 197-211.

van Vliet, J.V., Musters, C.J.M. & Ter Keurs, W.J. (2009). Changes in migration behaviour of blackbirds *Terdus merula* from the Netherlands. *Bird Study*, 56: 276-281.

Vansteelant, W.M.G., Kekkonen, J. & Byholm, P. (2017). Wind conditions and geography shape the first outbound migration of juvenile honey buzzards and their distribution across sub-Saharan Africa. *Proceedings of the Royal Society B: Biological Sciences*, 284: 20170387.

VanderWerf, E.A. & Young, L.C. (2018). U.S. Tropical Pacific seabird surveying guide. Report prepared for the U.S. Fish and Wildlife Service, Region 1, Portland, OR. Honolulu, HI: Pacific Rim Conservation.

Vardanis, Y., Nilsson, J.A., Klaassen, R.H.G., Strandberg, R. & Alerstam, T. (2016). Consistency in long-distance bird migration: contrasting patterns in time and space for two raptors. *Animal Behaviour*, 113: 117-187.

Veen, T., Hjernquist, M.B., Van Wilgenburg, S.L., Hobson, K.A., Font, L. & Klaassen, M. (2014). Identifying the African wintering grounds of hybrid flycatchers using a multi-isotope (δ2H, δ13C, δ15N) assignment approach. *PLoS ONE*, 9(5): e98075.

Veitch, C.R. (1997). Breeding season of Kermadec petrels (*Pterodorma negelcta neglecta*) at Meyer Islands, Kermadec group, New Zealand. *Notornis*, 45: 67-69.

Ventura, F., Granadeiro, J.P., Padget, O. & Catry, P. (2020). Gadfly petrels use knowledge of the windscape, not memorized foraging patches, to optimize foraging trips on ocean-wide scales. *Proceedings of the Royal Society B: Biological Sciences,* 287: 20191775.

Verhoeven, M.A., Loonstra, A.J., Hooijmeijer, J.C., Masero, J.A., Piersma, T. & Senner, N.R. (2018). Generational shift in spring staging site use by a long-distance migratory bird. *Biology letters*, 14: 20170663.

Vickers, S.H., Franco, A. & Gilroy, J.J. (2021). Sensitivity of migratory connectivity estimates to spatial sampling design. *Movement ecology*, 9(1): 1-12.

Viechtbauer, W. (2010). Conducting meta-analyses in R with the metaphor package. *Journal of Statistical Software*, 36(3): 1–48.

Villegas-Ríos, D., Réale, D., Freitas, C., Moland, E. & Olsen, E.M. (2017). Individual-level consistency and correlations of fish spatial behaviour assessed from aquatic animal telemetry. *Animal Behaviour*, 124: 83-94.

Visser, M.E. & Both, C. (2005). Shifts in phenology due to global climate change: the need for a yardstick. *Proceedings of the Royal Society B: Biological Sciences*, 272: 2561-2569.

Visser, I. & Speekenbrink, M. (2010). depmixS4: An R Package for Hidden Markov Models. *Journal of Statistical Software*, 36: 1-21. http://www.jstatsoft.org/v36/i07/

Wakefield, E.D., Phillips, R.A. & Matthiopoulos, J. (2009). Quantifying habitat use and preferences of pelagic seabirds using individual movement data: a review. *Marine Ecology Progress Series*, 391: 165-182.

Walther, G.R., Post, E., Convey, P., Menzel, A., Parmesan, C., Beebee, T.J.C., Fromentin, J.M., Hoegh-Guldberg, O. & Bairlein, F. (2002). Ecological responses to recent climate change. *Nature,* 416: 389-395.

Warham, J. (1990). The Petrels: Their Ecology and Breeding Systems. Academic Press: New York.

Wehrmann, J., de Boer, F., Benjumea, R., Cavaillès, S., Engelen, D., Jansen, J., Verhelst, B. & Vansteelant W.M.G. (2019) Batumi Raptor Count: autumn raptor migration count data from the Batumi bottleneck, Republic of Georgia. *Zookeys*, 836: 135-157.

Weimerskirch, H. (2007). Are seabird foraging for unpredictable resources? *Deep-Sea Research II*, 54: 211-223.

Weimerskirch, H., Borsa, P., Cruz, S., de Grissac, S., Gardes, L., Lallemand, J., Le Corre, M. & Prudor, A. (2017). Diversity of migration strategies among great frigatebirds populations. *Journal of Avian Biology*, 48:103-113.

Weimerskirch, H., Gault, A. & Cherel, Y. (2005). Prey distribution and patchiness: factors in foraging success and efficiency of wandering albatrosses. *Ecology*, 86(10): 2611-2622.

Weinstein, B.G. (2017). A computer vision for animal ecology. *Journal of Animal Ecology*, 87(3): 533-545.

Wellbrock, A.H.J., Bauch, C., Rozman, J. & Witte, K. (2017). 'Same procedure as last year?' Repeatedly tracked swifts show individual consistency in migration pattern in successive years. *Journal of Avian Biology,* 48: 897-903.

Wiggert, J.D., Jones, B.H., Dickey, T.D., Brink, K.H., Weller, R.A., Marra, J. & Codispoti, L.A. (2000). The Northeast Monsoon's impact on mixing, phytoplankton biomass and nutrient cycling in the Arabian Sea. *Deep Sea Research Part II: Topical Studies in Oceanography*, 47: 1353-1385.

Winger, B.M., Auteri, G.G., Pegan, T.M. & Weeks, B.C. (2018). A long winter for the Red Queen: rethinking the evolution of seasonal migration. *Biological Reviews*, 94: 737-752.

Wolak, M.E., Fairbairn, D.J. & Paulsen, Y.R. (2012). Guidelines for estimating repeatability. *Methods in Ecology and Evolution*, 3: 129-137.

Wood, S.N. (2011) Fast stable restricted maximum likelihood and marginal likelihood estimation of semiparametric generalized linear models. *Journal of the Royal Statistical Society (B),* 73(1):3-36.

Wotherspoon, S.J., Sumner, M.D. & Lisovski, S. (2013). R package SGAT: solar/satellite geolocation for animal tracking. GitHub Repository. http://github.com/swotherspoon/sgat

Wotherspoon, S., Sumner, M. & Lisovski, S. (2016). TwGeos: Basic data processing for light-level geolocation archival tags. R package version 0.0-1.

Wright, D.E., Lintott, C.J., Smartt, S.J., Smith, K.W., Fortson, L., Trouille, L., Allen, C.R., Beck, M., Bouslog, M.C., Boyer, A., Chambers, K.C., Flewelling, H., Granger, W., Magnier, E.A., McMaster, A., Miller, G.R.M., O'Donnell, J.E., Simmons, B., Spiers, H., Tonry, J.L., Veldthuis, M., Wainscoat, R.J., Waters, C., Willman, M., Wolfenbarger, Z. & Young, D.R. (2017). A transient search using combined human and machine classifications. *Monthly Notices of the Royal Astronomical Society*, 472(2): 1315–1323.

Yamamoto, T., Takahashi, A., Sato, K., Oka, N., Yamamoto, M. & Trathan, P.N. (2014). Individual consistency in migratory behaviour of a pelagic seabird. *Behaviour*, 151: 683-701.

Yamamoto, T., Takahashi, A., Yoda, K., Katsumata, N., Watanabe, S., Sato, K. & Trathan, P.N. (2008). The lunar cycle affects at-sea behaviour in a pelagic seabird, the streaked shearwater, *Calonectris leucomelas. Animal Behaviour*, 76: 1647-1652.

Yoda, K., Yamamoto, T., Suzuki, H., Matsumoto, S., Muller, M. & Yamamoto, M. (2017). Compass orientation drives naive pelagic seabirds to cross mountain ranges. *Current Biology*, 27: 1152–1153.

Yong, D.L., Jain, A., Liu, Y., Iqbal, M., Choi, C.Y., Crockford, N.J., Millington, S. & Provencher, J. (2018). Challenges and opportunities for transboundary conservation of migratory birds in the East Asian-Australasian flyway. *Conservation Biology*, 32(3): 740-743.

Zhou, X., Duchamp-Alphonse, S., Kageyama, M., Bassinot, F., Doressoundiram, F., & Kissel, C. (2022). Variations of primary productivity in the northwest Arabian Sea during the last 23,000 years and their paleoclimatological implications. *Paleoceanography and Paleoclimatology*, 37(10): e2022PA004453.