Understanding seabird behaviour through long term tracking data

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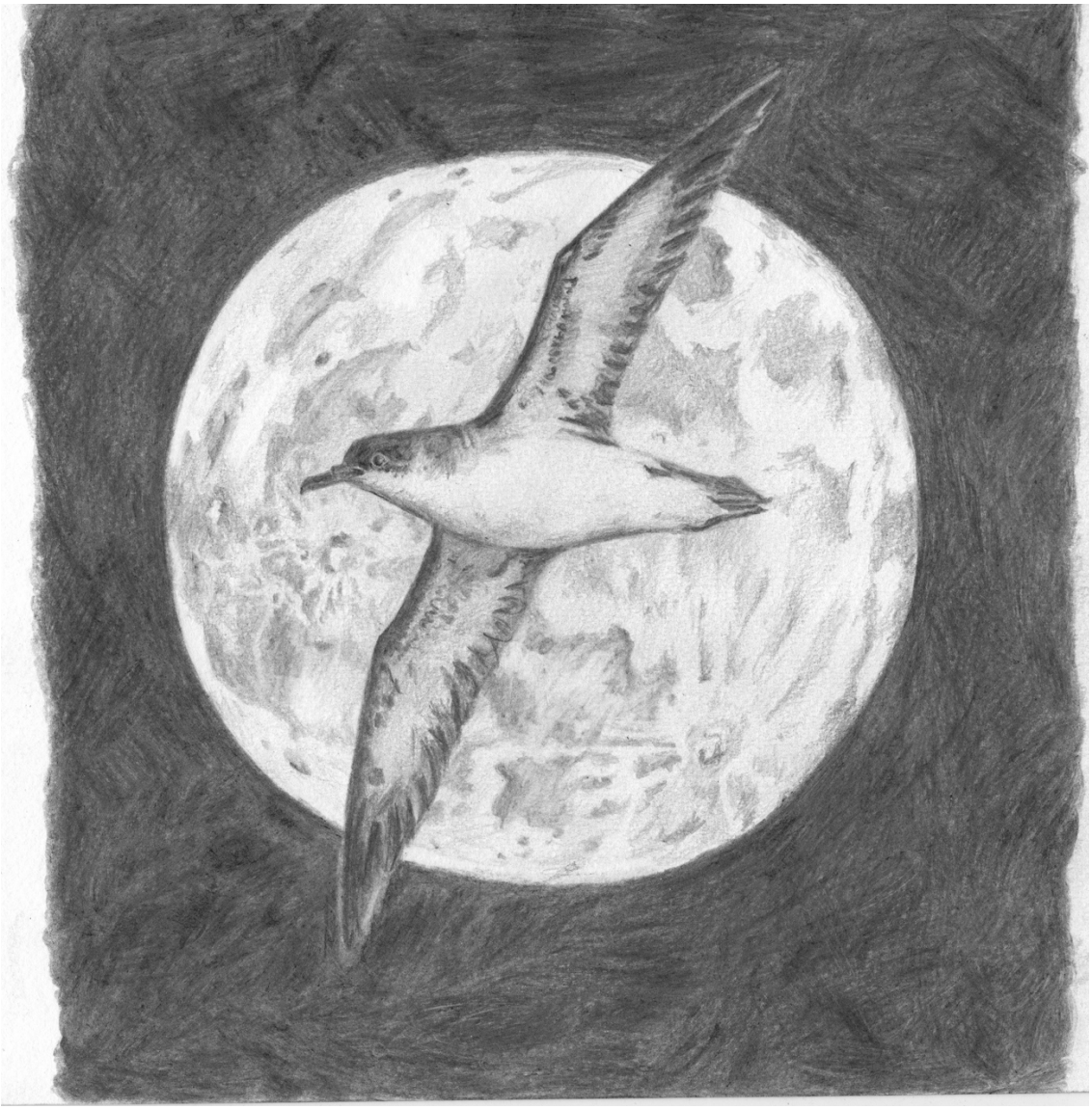

Illustration by Ceris Aston: Assistant Warden of Skomer

Abstract

Comprehending how organisms maximise their reproductive success in an ever-changing environment lies at the core of animal behaviour studies. However, animals that inhabit highly dynamic habitats often pose challenges for direct observation. Biologging deployments facilitate remote monitoring of animals in otherwise inaccessible environments, particularly pelagic species. In this thesis, I harnessed an extensive geolocator dataset spanning multiple colonies to extract novel behavioural insights concerning the Manx Shearwater (*Puffinus puffinus*), a procellariform seabird known for its extreme life history strategy. Their remarkable migration across hemispheres to synchronize with seasonal food availability presents a unique array of challenges. Firstly, I unveil the ability of individual shearwaters to plastically adjust their over-wintering distribution in response to the El Niño Southern Oscillation. However, decreased foraging activity during El Niño years initiates carry-over effects on subsequent breeding, resulting in a reduction of chick provisioning efforts. Additionally, I elucidate how shearwaters adjust their southbound migratory patterns based on breeding phenology. Birds that breed later and subsequently postpone their post-breeding migration take shorter duration migrations with fewer foraging stopovers. Notably, these late-departing birds optimize their flight with lunar cycles, strategically utilizing moonlit nights for visually guided flight. Next, I investigate how seasonal fluctuations in photoperiod influence light-limited chick provisioning behaviours. I find that extended daylight promotes increased foraging and provisioning efforts, albeit accompanied by shorter nights, diminishing adults' ability to mitigate predation risks through moonlight avoidance. Lastly, I delve into how sex-specific reproductive roles influence diving behaviour during pre-laying using dive logger deployments. I discern that males exhibit increased diving efforts during pre-laying, and are less able to exploit evening foraging opportunities due to heightened colony attendance for nest defence. I also employed a pioneering DNA metabarcoding analysis of Manx shearwater diet, identifying six distinct fish species consumed by breeding adults. This thesis exemplifies the application of advanced analytical techniques to long-term biotelemetry data, providing valuable insights into individual animal behaviour.

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Declaration and Author Contributions

The work in this thesis is primarily my own effort. However, it's important to acknowledge the contributions of 17 other authors, which are detailed below.

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

Joe Wynn and Oliver Padget contributed fieldwork, analysis, conception and ideas in all chapters.

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"Skomer, where everyone is welcome but leave your drama on the mainland"

- Leighton Newman, Skomer Warden.

"On the crest of the wave, in the deepest dark cave. Everywhere and always at once. In the wind touching you and the seas turquoise blue, and the fish who swam safely away"

- Iona Boat Song (traditional), shared by Eve at Skomer Farmfest

"No more words. In the name of this place we drink in with our breathing, stay quiet like a flower. So, the night birds will start singing."

- Rumi

This thesis is dedicated to my sisters, Lisha and Roxy.

Contents

Introduction

The behaviour of an animal determines how an organism lives in and interacts with its surrounding environment (Kappeler, 2010). Studies of animal behaviour are therefore an important part of biology. In 1963 Niko Tinbergen laid out the 4 major problems in biology, urging behavioural biologists to consider questions at the level of causation, survival, evolution and ontogeny (Tinbergen, 1963). Although he highlighted the importance of all four levels of analysis, his paper focused heavily on questions of survival value, an area that he believed was lacking in behavioural studies at that time (Barrett *et al.*, 2013). He emphasised that understanding how a behaviour allows an individual to survive should be the starting part of any behavioural study. Following Tinbergen's lead, this thesis is a study on how behaviour is optimised for survival under different environmental constraints, with a specific focus on the life-history of a highly pelagic migratory marine predator, the Manx shearwater.

The drivers that underpin the behaviour of an individual animal are widely understood through the lens of natural selection (McFarland, 1977). We expect individuals to behave in a way that maximises fitness (Acerenza, 2016). The optimal way to behave will vary depending

on the environment an animal lives in and individual factors such as condition, sex and age (McNamara and Houston, 2008). Therefore, we can expect a diversity of behaviour to evolve between populations and to be expressed by individuals within them. For example, consider two individuals that each forage in different areas: one where prey availability is high and one where resources are limited. Even if both individuals are behaving in a way that maximises survival, we would expect them to differ in their foraging behaviour (Lemon, 1991; Navarro, González-Solís and Viscor, 2007; Pyke, 2009). Similarly, we might expect an individual living in a high population density area to engage in different territorial behaviour to an individual living in an area where competition for breeding sites is low (Pajunen, 1996; Mayer *et al.*, 2020). Woodchucks residing in high latitude regions with prolonged winters engage in lengthier hibernation periods compared to their counterparts in areas where temperatures warm up and food becomes abundant sooner (Zervanos *et al.*, 2010). Barnacle geese that are in poor condition might forage for longer over winter to regain body fat, and then return later to the breeding grounds (Prop, Black and Shimmings, 2003).

Since Tinbergen first called on biologists to focus more on how behaviour affects survival value, numerous studies have explored how animals maximise survival in different environments (McNamara and Houston, 2008; Barrett *et al.*, 2013). However, environmental conditions create constraints on how well individuals can optimise opposing life history traits (Roff and Fairbairn, 2007). This creates trade-offs for individuals to contend with, where the maximisation of one life history trait can cause a reduction in another (Ou *et al.*, 2020). For example, deer in Norway forage in areas of high predation risk, creating a trade-off between foraging and offspring survival (Panzacchi *et al.*, 2010). Anti-predation behaviour (for example hiding) varies in different environments dependent on the number of predators. This then leaves less time for foraging when predators are nearby. As a result, deer adjust their behaviour to maximise different components of fitness dependent on what pressures are present. In

order to persist, individuals must find ways to optimise their behaviour to compensate for trade-offs (Acerenza, 2016).

Traditionally, the study of natural animal behaviour was conducted by means of field observation (Tinbergen, 1963). Whilst field observations are still an important component of behavioural studies, technological advances have produced bio-logging devices that can be attached to individual animals, allowing the study of behaviour to happen remotely (Evans, Lea and Patterson, 2013). As long-term studies develop, behavioural ecologists can now observe natural behavioural patterns using a dataset of remotely gathered activity. This allows us to gain insights into how animals behave when they are away from direct physical observation. Bio-logging opens up the potential to ask questions at a finer scale resolution, such as how animals move, allocate their time, expend energy, navigate and interact with one another (Whitford and Klimley, 2019; Isaksson *et al.*, 2021). In this thesis I aim to understand how individual behaviour adjusts with shifting conditions in order to maximise fitness. This thesis will draw on a long-term bio-logging dataset of a migratory seabird species, the Manx shearwater (*Puffinus puffinus*), to find novel ways to observe behaviour without physical observation. In the remainder of this introduction, I will introduce the central themes of my subsequent chapters and set out the questions I seek to address.

Shifting Environments: To Stay or To Go

Animals living in seasonal environments can experience extreme intra-annual variation in environmental factors such as temperature, food availability, precipitation, wind speeds and day length (Yoder *et al.*, 1993; Hill *et al.*, 2004). This is especially true at high latitudes where differences between winter and summer conditions are prominent. Some animals remain sedentary despite seasonal changes, either remaining through physiological adaptations such as thermal tolerance, or behavioural adaptations such as hibernation or torpor (Bujan *et al.*, 2020; Geiser, 2020). One alternative strategy is to leave in search of better conditions. Migration, the synchronised movement of populations between two habitats, can be considered as an evolved behavioural response to shifting seasons (Brönmark *et al.*, 2008). Migratory animals can travel great distances, sometimes ranging thousands of kilometres each year. Avian migrations can traverse particularly long distances given that flight allows for increased mobility (Vincze *et al.*, 2019). The longest migration of any animal is in the arctic tern, a seabird that breeds and winters at opposite poles (Egevang *et al.*, 2010). Seabirds, being pelagic and wide ranging, often take some of the longest and most extreme animal migrations, representing a useful study system for understanding migratory behaviour and fitness (Weimerskirch *et al.*, 2015; Bonnet-Lebrun *et al.*, 2021). Therefore, many of the examples included in this introduction will be of avian species, especially seabirds. Since few studies have addressed seabird migratory behaviour in much detail, this thesis aims to provide a detailed exploration of the behaviour of a trans-Atlantic seabird migrant. (Dias, Granadeiro and Catry, 2012).

Migration is risky, especially for those travelling long-distances (Franke *et al.*, 2011). When migratory individuals travel long distances, they are exposed to increased risks from effects such as predation, extreme weather, injury and starvation (Alerstam and Hedenstrom, 1998). Therefore, survival is often reduced during migration itself, yet one of the fundamental principles of migration theory is that the benefit of migration must somewhere outweigh the

cost (McNamara and Houston, 2008; Buechley *et al.*, 2021). For example, the migratory destination must have a significantly higher seasonal abundance than the breeding grounds to make moving more beneficial than staying (Winger *et al.*, 2019). There are a number of ways animals can behave to optimise migration, and in doing so reduce survival risks. Given that journeys can be long, and often over areas of low food availability, one strategy is to set off on migration with sufficient fat reserves (Vincze *et al.*, 2019). However, fuel loading can reduce migration efficiency via increased wing loading (Klaassen, 1996; Hedenström and Alerstam, 1997). Another strategy is to stop en-route and exploit productive areas for re-fuelling, known as stop-over sites (Newton, 2008). These sites allow organisms to avoid starvation but at the cost of potentially lengthening migratory journey times (Domer *et al.*, 2021; Schmaljohann, Eikenaar and Sapir, 2022). This could delay arrival at the over-wintering grounds, resulting in missed foraging opportunities and increased competition for resources (Thorup *et al.*, 2017). However, stopping might facilitate migratory stints co-occurring with favourable environmental conditions for travelling (Liechti, 2006).

For avian species, optimal environmental conditions for migration are often discussed in terms of wind direction and speed (Butler *et al.*, 1997). Favourable wind conditions can reduce the costs of migration by allowing birds to preserve energy whilst travelling (Muñoz Arroyo and Mateos-Rodríguez, 2022). For example, albatrosses require wind conditions of at least 5 m/s in order to travel via dynamic soaring (Sachs, 2005). Radar studies indicate that birds time their migratory stints to coincide with favourable winds (Richardson, 1978; Alerstam, 2011). Migration can happen both during the day or night–about two thirds of European passerines migrate at night (Michalik, Brust and Hüppop, 2020). As well as reducing the risk of over-heating, migrating in the dark allows birds to avoid predation by visual hunters over land (Newton, 2008; Sparks *et al.*, 2022). In seabirds, migratory flight at night is also observed, yet most seabirds have few at-sea predators (Dias, Granadeiro and Catry, 2012; Dias *et al.*, 2016). Alternatively, across seabird species, night flight has been shown to increase with moonlight,

suggesting that seabirds are seeking the reverse conditions of many nocturnal passerines, migrating instead when light is present (Bonnet-Lebrun *et al.*, 2021). This is likely due to seabirds having complex flight behaviour such as dynamic soaring that is largely visually guided (Paiva *et al.*, 2010; Kempton *et al.*, 2022). Therefore, seabirds may benefit from timing migratory stints with lunar conditions to reduce their total migration duration. This has not yet been investigated in any seabird and is a phenomenon I will explore in chapter 3 as part of this thesis.

When animals experience adverse environmental conditions over-winter, this can reduce both adult survival, and the success of their next breeding attempt (McNamara and Houston, 2008; O'connor *et al.*, 2014). Environmental oscillations can increase extreme weather events (Ballance, Pitman and Fiedler, 2006). For example, peregrine falcons showed increased migration mortality during positive North Atlantic Oscillation phases (Franke *et al.*, 2011). Environmental variability can also change the distribution of prey, which might lead to a reduction in foraging opportunities (Grémillet and Boulinier, 2009; Machado, Barreiro and Calliari, 2013). This can have carry over effects, where events in one season affect the next (O'connor *et al.*, 2014; Fayet *et al.*, 2016). For example, black-browed albatross that foraged less over-winter had lower breeding success in the next season (Salton *et al.*, 2015). Foraging site fidelity can be a useful tool when resources are predictable (Weimerskirch, 2007). However, individuals that show high site fidelity and are more fixed in their behaviour may be more vulnerable to climatic variation (Grémillet *et al.*, 2008; Léandri-Breton *et al.*, 2021). For example, albatrosses are predicted to make little adjustment to their current migratory behaviour under high greenhouse emission climate scenarios (Somveille *et al.*, 2020). Climatic changes due to anthropogenic warming are projected to cause a spatial mismatch between current bird distributions and their over-wintering resources (Thorup *et al.*, 2017; Rodríguez *et al.*, 2019). Whether individuals can adjust their behaviour with climatic conditions will ultimately determine their survival and fitness (Sauve, Divoky and Friesen, 2019). Species with

flexible foraging behaviour appear to be more resistant to current environmental oscillations (Chambers *et al.*, 2011; Brown *et al.*, 2021). However, few studies have examined whether environmentally induced variation in over-wintering behaviour might carry over and impact fitness in later seasonal stages. To begin to understand the migratory behaviour of individuals with environmental change, we first require sufficiently long-term data (Moe *et al.*, 2017). Therefore, as part of this thesis, in chapter 2 I aim to explore using long-term data whether shearwaters adjust their over-wintering behaviour with climatic conditions, and whether this carries over into future breeding behaviour.

Shifting Environments: Timing is Everything

In the section above, I briefly discussed how outward avian migrations should be optimally timed so as to reach the over-wintering foraging grounds at the point at which they outcompete seasonal food availability at the breeding grounds. Meanwhile, the return migration should be timed to commence breeding when peak resources are available for both rearing offspring and self-provisioning (Gordo, 2007; Duijns *et al.*, 2019). Therefore, for migratory individuals, annual routines are scheduled to maximise seasonal abundance (McNamara and Houston, 2008). When describing seasonal resources, we are mainly referring to food abundance, which is the major determinant of survival and fitness (White, 2008). There is a general rule across avian species, that the earlier breeding individuals have higher fledging success (Arnold, Hatch and Nisbet, 2006; Reed, Jenouvrier and Visser, 2013; Rotics *et al.*, 2018). This is often attributed to declines in food abundance as the season progresses (Moe *et al.*, 2009; Monticelli and Ramos, 2012). There are other ecological factors that may contribute to the success of earlier laying birds such as the benefits of obtaining higher quality nesting territories and breeding partners (Werner, Paiva and Ramos, 2014; Rotics *et al.*, 2018).

Given that seasonal weather determines food abundance, breeding is often initiated by environmental conditions at the breeding grounds (Burant *et al.*, 2022). Peaks in food

abundance are driven largely by seasonal changes in temperature and photoperiod, both of which are cues across avian taxa to initiate breeding at the appropriate time (Dawson *et al.*, 2001; Kappeler, 2010). Therefore, as temperatures increase with anthropogenic warming, we have seen an advancement in lay date in many avian species (Gordo, 2007; Moller, Fielder and Berthold, 2011). Where individuals show phenotypic plasticity, this could be seen as a positive behavioural adjustment to realign breeding birds with their prey (Callery *et al.*, 2022). However, although temperature has historically been a cue associated with successful breeding, shifts in phenology are now causing mismatches between breeding and prey abundance in cases where prey respond differently to temperature changes (Shipley *et al.*, 2020). Long-distance migrants may be less able to adjust their phenology with local conditions, given they are not receiving environmental cues at the breeding grounds (Both *et al.*, 2010). For example, when spring conditions in the arctic advanced by 2 weeks, Brent geese, which are long distance migrants from temperate regions, arrived too late to time breeding with optimal conditions (Clausen and Clausen, 2013). In a changing climate, individuals that are able to plastically adjust their phenology have a greater chance of survival (Conklin, Lisovski and Battley, 2021). For example, selection for individuals with phenotypic plasticity in the timing of reproduction has been demonstrated in great tit populations following warming (Nussey *et al.*, 2005). In chapter 2 of this thesis I will explore whether phenological shifts have been observed in shearwaters as a result of large-scale environmental oscillations.

Given that we expect animals to maximise fitness, and given that there are clear advantages to laying earlier, why do some individuals lay later? Birds that are in better physical condition have been found to lay earlier (Descamps *et al.*, 2011). Poor individual condition may occur as a result of carry over effects from previous life history events in a bird's annual cycle (Fayet *et al.*, 2016). Breeding is energetically expensive due to the costs of egg production, incubating and chick provisioning (Hunter, 1984; Kim, Priddel and Carlile, 2017; Gatt *et al.*, 2020). Previous breeding can reduce condition, which may delay the return migration. For example,

successfully breeding shearwaters have been found to return later to the colony than birds that did not reproduce successfully in the previous year (A. Shoji *et al.*, 2015; Gatt *et al.*, 2020). Additionally, as discussed earlier in this thesis, adverse over-wintering environments can reduce individual condition (Salton *et al.*, 2015; Desprez *et al.*, 2018) For example, barnacle geese with lower fat reserves remained longer at the over-wintering grounds to forage, resulting in a later arrival at the breeding grounds (Prop, Black and Shimmings, 2003). Common terns laid later following winters with warmer temperatures where resources were limited (Dobson *et al.*, 2017). Birds are therefore constrained in their phenology by their physical condition, and individuals must contend with a trade-off between current reproduction and self-maintenance (Acerenza, 2016). In chapter 3 I will investigate how shearwaters that lay later catch up on their post-breeding migration, so as to still arrive at the over-wintering grounds on time.

Shifting seasonal conditions affect breeding success via the timing of peak food abundance, but also through more direct environmental effects. Cold conditions, where temperatures are low and precipitation is high, additionally causes breeding failure (Bordjan and Tome, 2014). Therefore, reproduction should be timed for when temperatures are warm enough for chicks to survive (Cox, Thompson and Reidy, 2013). Photoperiod also affects the timing of breeding onset in avian species (Dawson *et al.*, 2001; Gordo, 2007). Day length is a reliable cue for seasonal food abundance given the correlation between increased light and primary production. However, day length is not often considered as a direct seasonal constraint (Hill *et al.*, 2004). Many behaviours such as foraging and flight require light. As large quantities of food are often required for chick provisioning, extended forage time via extended day lengths may be beneficial (Fort *et al.*, 2013; Boom *et al.*, 2023). Therefore, it is reasonable to assume that birds might time reproduction to coincide with longer day lengths. In chapter 4 of this thesis, I will explore the role of photoperiod as an ecological constraint for light restricted behaviours in shearwaters.

Individual Factors: Born this Way

The ability of an individual to adjust its behaviour is largely influenced by inherited factors. Avian species with larger brains have increased survival in adverse environments, due to their increased ability to learn and make decisions (Krebs, 1990; Sol *et al.*, 2007). For example, gulls have been able to thrive in urban environments by learning how to obtain food from human waste (Goumas, Boogert and Kelley, 2020). On an individual level, behavioural flexibility can be dictated by an individual's cognitive ability (Baldwin, Garcia-Porta and Botero, 2022). It has also been shown that behavioural plasticity is in itself a heritable trait (Nussey *et al.*, 2005; Baldwin, Garcia-Porta and Botero, 2022). Therefore, some individuals may have a greater capacity to adapt to shifting environments than others. Plasticity may additionally be limited by morphological constraints. Body size can determine the ability of an animal to exist in certain environments (Zimova *et al.*, 2022). Larger individuals of a species are typically found at the colder limit of its range. According to Bergman's rule, body size increases with latitude because organisms with a higher surface to volume area ratio can more efficiently conserve heat (Olson *et al.*, 2009). Anthropogenic warming has led to an observed shrinking across multiple avian species via selection for smaller individuals (Van Buskirk, Mulvihill and Leberman, 2010). Body size may not only affect an individual's foraging range, but also its competitive abilities and migratory strategy (Smith and Brown, 1986; Hedenström and Alerstam, 1997; Quillfeldt *et al.*, 2011).

Sex specific characteristics may also limit an individual's ability to adjust its behaviour. This may be due to morphological differences, such as differences in body or appendage sizes (Phillips *et al.*, 2011; De Pascalis *et al.*, 2020). For example, sexes with dimorphic feeding apparatus might be adapted to forage for different prey (Ligon, 1968). Additionally, differences in wing loading have been argued to affect flight performance causing differing foraging distribution between sexes (Shaffer, Weimerskirch and Costa, 2001; De Pascalis *et al.*,

2020). There is also the potential for competitive exclusion of the smaller sex from foraging areas (Catry, Phillips and Croxall, 2006). However, sex differences in behaviour still arise in monomorphic avian species (Lewis *et al.*, 2002; Pinet *et al.*, 2012; Bennison *et al.*, 2022). This may occur as a result of differential reproductive roles (Burke, Montevecchi and Regular, 2015). For example, only females can synthesise and lay an egg (Perrins, 1996). One sex might have greater parental responsibilities. For instance, male guillemots are responsible for provisioning for chicks after fledging (Burke, Montevecchi and Regular, 2015). To understand how individuals are constrained by heritable factors, in chapter 5 of this thesis I will investigate how foraging behaviour differs with reproductive role in shearwaters.

Why Study the Manx Shearwater (*Puffinus puffinus*)?

The Manx shearwater is a procellariform seabird that breeds predominantly in Western Europe and over-winters off Patagonia (Storey and Brooke, 1991). Characteristic of the procellariforms is the ability to traverse long distances through taking highly pelagic and far-ranging foraging trips (Paiva *et al.*, 2010; Weimerskirch *et al.*, 2015; Dehnhard *et al.*, 2020). Much like other procellariforms, Manx shearwaters are able to exploit favourable winds for shear soaring flight, allowing them to travel far with reduced energetic demands and migrate across hemispheres on an annual basis (Gibb *et al.*, 2017; Kempton *et al.*, 2022). Prior to biotelemetry, ringing recoveries provided limited insight into this trans-Atlantic migration (Storey and Brooke, 1991). In 2009, though, the first 12 migrations of geolocator-tagged shearwaters revealed their complex migratory behaviour in more detail (Guilford *et al.*, 2009). Despite migrating thousands of kilometres each year, all 12 shearwaters over-wintered in a relatively restricted area off the Patagonian shelf (figure 1). Additionally, the tracked shearwaters took a series of marine stopovers, a phenomenon that was previously unobserved in this species.

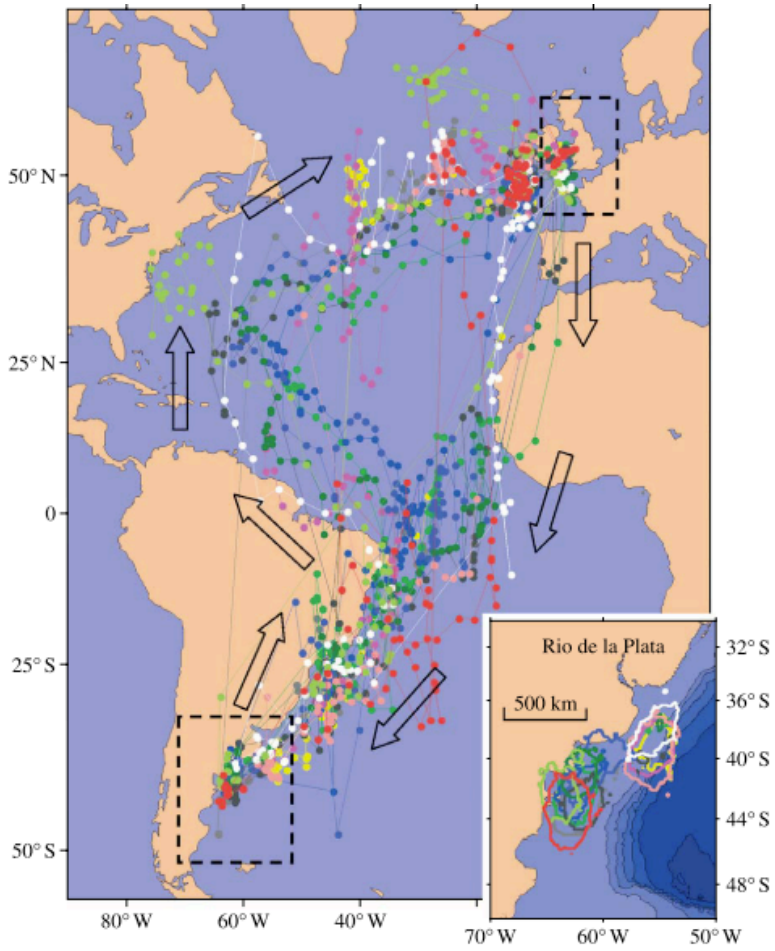

Figure 1. The migration of the first geolocator-tracked 12 shearwaters from Guilford *et al.*, 2009. Black boxes indicate the areas where shearwaters bred and over-wintered during non-migratory periods. The inset shows the 50% occupancy contours for each individual within the over-wintering box for all daily positions within that box. Tracks and contours are coloured per individual.

Alongside having long migrations, the shearwaters additionally have intensive breeding periods which last 5-6 months. With rare exceptions, they lay only one egg per year and invest large amounts of parental care into rearing their chick to fledging. Whilst they can travel at a mean speed of 40 km/hour at sea, when on land they are slow moving and cannot quickly take off (Guilford *et al.*, 2008). Therefore, to avoid predation at the colony, the shearwaters nest in burrows underground and are nocturnal in their colony visitation behaviour (Riou and

Hamer, 2008). Unlike during the winter, whilst breeding, the shearwaters are constrained in their movement by central place foraging. They must return frequently to the breeding colony for parental care and nest defence. Nonetheless, Global Positioning System (GPS) deployment has revealed that shearwaters are still highly mobile during breeding and are capable of varying their at-sea behaviour with changing circumstances (Dean *et al.*, 2015). For example, during incubation, when partners alternate between stints on the egg, shearwaters often take trips as long as 10 days, feeding at far away productive areas such as tidal front systems or the continental shelf edge (Guilford *et al.*, 2008). When the chick hatches, provisioning adults then forage closer to the colony so as to return more frequently to provide food. Shearwaters are also able to adjust their foraging trip length depending on the condition of their partner, with chick-rearing breeding pairs alternating between self and chick-provisioning trips (Akiko Shoji *et al.*, 2015; Tyson *et al.*, 2017).

Since the initial 12 tracked birds, many researchers have taken an interest in the annual movement behaviour of Manx shearwaters. Shoji et al., 2015 studied how shearwater migratory behaviour carried over to affect breeding performance. They found that birds with higher over-wintering foraging effort were more likely to skip breeding the following season, and consequently had higher breeding performance the following year. Therefore, the conditions shearwaters experience during winter appear to affect further breeding. Fayet et al., 2016 found that breeding conditions also affect future behaviour: birds with extended breeding seasons had lower breeding success in the following year. The PhD thesis of Kirk, 2016 investigated shearwater migratory behaviour. Kirk detected little difference between colonies of shearwaters in their migratory behaviour, but did find significant differences between individuals. With a larger, long-term dataset that includes data from a higher number of shearwater colonies, this thesis aims to expand on this work. Specifically, I hope to investigate how environmental and heritable constraints might cause behavioural variation between individuals. With longer term data, I will be able to explore variation in behaviour

between years. Additionally, with a larger dataset I will be able to ask detailed questions about specific life cycle stages.

General Methodology

Biotelemetry: How to Study Seabird Behaviour

In the 1700s, Linnaeus maintained that swallows over-wintered at the bottom of lakes (Alerstam, 1991). We have since come a long way in understanding avian migration. This is largely due to data collected from ringing (Calvo and Furness, 1992). Ringing involves fixing small metal bands to a bird's tarsus. The recovery of identifiable birds at their over-wintering sites has long provided evidence for migratory destinations, revealing the great distances birds are traversing (Newton, 2008). The pelagic distributions of seabirds have meant that ringing recoveries at over-wintering sites are less common. Although ringing efforts provide approximate descriptions of seabird migrations, it has only been with recent advances in biotelemetry that we have been able to track seabird migrations in detail (Ramos *et al.*, 2015; Austin *et al.*, 2019; Léandri-Breton *et al.*, 2021). Biotelemetry involves fixing devices to an individual animal in order to record its behaviour (Whitford and Klimley, 2019).

One device that has been instrumental in recording seabird migrations is the Global Location Sensor (GLS) (Navarro, González-Solís and Viscor, 2007; Guilford *et al.*, 2009; Bonnet-Lebrun *et al.*, 2021). These devices are relatively cost effective, lightweight and have low power requirements. They are therefore suitable for recording long range migration with less modification to natural behaviour than most affordable GPS devices (Gillies *et al.*, 2020). Geolocators measure light intensity to calculate position, where longitude is estimated from the timing of midday/midnight and latitude from day length (Lisovski and Hahn, 2012). There is therefore a large amount of associated error in light determined positions, with the margin of error typically being on scale of 300 to 400 kilometres (Phillips *et al.*, 2004). This is largely

due to error in the calculation of latitude, which is difficult to determine around the spring and autumn equinoxes where day and night lengths are equal at all latitudes. Light measurements might additionally be obscured by the device being covered by the bird or by artificial light at night. An alternate way to track movement is via Global Positioning System (GPS), which makes use of satellites to establish location. These devices can locate animals to a relatively high degree of precision and provide high resolution tracks (Tremblay *et al.*, 2006). However, a study by Gillies et al., 2020 found that the deployment of i-gotU GPS devices extended the length of shearwater foraging trips, most likely due to the additional weight of these devices. Recent developments in GPS have resulted in small, lightweight devices which could be suitable for tracking migration (Whitford and Klimley, 2019). However, when the tracking data for this thesis was gathered, these smaller GPS devices were not a viable option.

Despite the error in position estimates, geolocators have proven to be useful tools. Although tools are usually developed for a specific purpose, they often have additional uses. Geolocators were developed mainly as animal movement trackers, yet record a multitude of information about an animal's behaviour. Modern geolocator models are also capable of recording temperature and saltwater immersion. Recording immersion can allow the determination of a seabird's at-sea behaviour. For example, when the device is completely dry the bird is most likely in flight. Similarly, when the device is completely wet, the bird is either sitting on the sea surface or diving. Typically, the device records immersion to create a score to summarise the degree of immersion over 5- or 10-minute intervals. In Manx shearwaters, intermediate immersion scores have been demonstrated through co-deployment with dive loggers to accurately predict foraging activity (Dean *et al.*, 2013; Freeman *et al.*, 2013; Shoji *et al.*, 2016). Additionally, given that Manx shearwaters are burrow nesting, breeding in dark and dry conditions, light and immersion loggers can potentially be used in combination to determine colony visitation behaviour for this species (Guilford *et al.*, 2012). As well as being useful in understanding seabird spatial behaviour, geolocators have the potential to provide complex

behavioural information, facilitating an understanding of the life history of the species in question. In this thesis, I aim to utilise the strengths of geolocator data to draw out patterns of behaviour from a large long-term dataset.

How to Study Shearwaters: Methods in the Field

Although biotelemetry can allow researchers to observe animal behaviour without being present, these devices must still be physically attached. Additionally, in order to obtain information on breeding success and phenology, daily monitoring is required at the breeding site. Therefore, there is a significant fieldwork component to any seabird project that aims to study life-history questions using biotelemetry. This thesis mainly uses the data from the deployment of geolocator devices. However, both GPS and Time Depth Recorder (TDR) devices were also deployed to provide higher resolution foraging data for chapter 5.

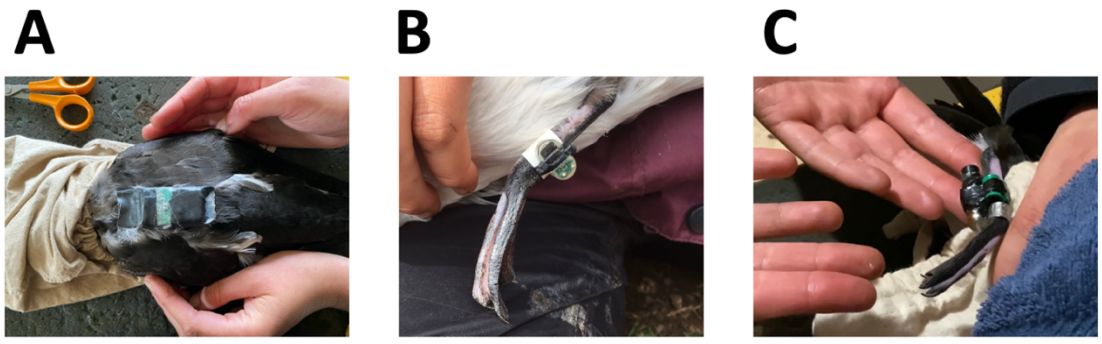

Figure 2. Photographs demonstrating deployments of **A)** Global Positioning System (GPS) devices, **B)** Geolocator (GLS) devices and **C)** Time Depth Recorder (TDR) devices on Manx shearwaters.

Given that Manx shearwaters are nocturnal colony attenders, device attachment often occurs at night. In order to tag birds that are returning to the colony, two knockdown sticks are positioned upright inside the burrow entrance. The knockdown sticks are checked every 20-

30 minutes for disturbance by birds entering the burrow. If the sticks are disturbed and a breeding bird is present, the bird can then be extracted for deployment. During incubation, device deployment can also occur during the day when adults remain in the burrow incubating the egg. GPS devices are attached onto the feathers on the shearwater's back using weatherproof tesa tape. The device is carefully positioned over the spine so as not to cover the uropygial gland. GLS devices, being smaller are attached onto a custom-built plastic leg ring, adjusted for the Manx shearwater's flattened leg shape. The devices are positioned with the immersion pins pointing downwards, so as to record immersion when the bird is sitting on the sea surface. The geolocator is tightened on to the plastic leg ring using 2 cable ties around the centre of the device. A small amount of super glue is added at the ends of the cable ties to hold them in place. Meanwhile, the TDR devices are pre-attached to custom built plastic leg rings with strong duct tape, which is then simply fastened and secured to the bird's leg. Given that this thesis draws on a long-term biotelemetry data-set, the technology of which is constantly evolving, several models of devices have been used as part of this project, details of which are included in table 1. To obtain information on individual shearwater breeding behaviour, all birds in study burrows are individually marked with a BTO metal leg ring. Study burrows are checked on a daily basis to obtain the lay date, defined as the first day on which an egg was present in the burrow. Additionally, following hatching, chicks are weighed on a (usually) daily basis to obtain measurements of chick mass.

Device Type	**Company**	**Model Name**	**Device Weight (g)**
Geolocator	BAS	Mk12	2.5
	Migratetech	C330	3.3

	Migratetech	C250	3.3
	Migratetech	C65	1
	Migratetech	C65-Super	1
Global Position System (GPS)	Oxford University	SnapperGPS	10
	Technosmart	Gipsy	10
Time Depth Recorder (TDR)	CEFAS	G5	2.7

Table 1. A table representing all devices and models of biotelemetry used in this thesis.

The last dietary work conducted on Manx shearwaters was on Rum in the 1980s using traditional stomach flushing methods (Thompson, 1987). Recent developments in DNA metabarcoding have allowed prey species to be identified from faecal samples (Miya *et al.*, 2015; McInnes *et al.*, 2017). This method also shows promise in providing quantitative information about the relative abundance of each prey species present (Deagle *et al.*, 2019). Given that collecting faecal samples is non-invasive and may provide additional information on shearwater foraging, as part of this thesis I additionally conducted a novel dietary analysis using DNA metabarcoding.

Aims and Objectives

Over a decade on from when the first 12 tracked birds were recovered, we now have over 400 complete geolocator tracks of shearwater migration for analysis, with data spanning from 2006 to 2021 at 5 geographically distinct colonies of shearwaters (Guilford *et al.*, 2009). This multi-year dataset allows us to answer novel questions about how individuals might respond to different environments and constraints. Specifically, this thesis aims to address the following questions:

1. Does environmental variability via the Southern Oscillation Index determine shearwater over-wintering and subsequent breeding behaviour? (**Chapter 2**)
2. Does south-bound migratory behaviour vary as a result of individual breeding phenology? (**Chapter 3**)
3. Does variation in photoperiod length impose constraints to foraging and colony visitation behaviour? (**Chapter 4**)
4. Are there differences in foraging behaviour imposed by reproductive role variation between sexes? (**Chapter 5**)

In **chapter 2** I will investigate whether individuals are able to plastically adjust their over-wintering behaviour with changing environmental conditions and consequently whether over-wintering environments constrain later breeding success. This chapter will draw on the strengths of long-term data through providing a multi-year analysis of individual behaviour and linking events in the annual cycle together. I aim to determine migratory phenology, over-wintering position, foraging intensity and chick provisioning rates from the geolocator data, and calibrate chick provisioning rates with measurements taken at the breeding colony.

If birds that lay later are to rear their chicks successfully through to fledging they may have to delay their autumn migration departure date. Therefore, to understand how later laying

individuals compensate for a later migratory departure and catch up, in **chapter 3** I will investigate how variation in phenology might cause optimal migratory behaviour to differ between individuals. To explore this, I will extract diurnal schedules and stopover behaviour from combined light and immersion data.

Whilst chapter 2 explores the constraints of large-scale environmental oscillations, in **chapter 4** I will consider how seasonal variation in photoperiod might additionally constrain breeding behaviour. Photoperiod is not often considered as an environmental constraint, yet most shearwater breeding behaviour occurs under specific light conditions. Shearwaters forage during daylight hours and return to the colony at night to avoid predation. Shearwaters additionally breed at high latitudes with large variation in photoperiod. Therefore, in the peak of summer there are longer days in which to forage but shorter nights in which to return to feed the chick in safety. This may create constraints on anti-predation and chick provisioning behaviour. This study will therefore utilise the immersion logger geolocator data to extract foraging and colony visitation behaviour and explore this phenomenon.

In **chapter 5** I will investigate how reproductive roles might constrain behaviour. This study will focus specifically on pre-laying, given that during this period reproductive roles differ between sexes. Females are required to synthesise an egg, whilst males engage more in nest defence. Therefore, we might expect differences in foraging and colony visitation behaviour. In order to explore foraging behaviour in detail, this chapter will combine biotelemetry utilising TDR, GPS and GLS logger data. I will additionally conduct a novel analysis of shearwater pre-laying diet through collecting faecal samples for DNA metabarcoding.

Ethical Statement

All work in this thesis was ethically approved by the Animal Welfare and Ethical Review Body (AWERB) and Islands Conservation Advisory Committee (ICAC) Additionally, all birds were handled under appropriate British Trust for Ornithology (BTO) Special Methods licencing.

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How environmental variability via the El Niño-Southern Oscillation impacts shearwater over-wintering distribution and subsequent breeding behaviour

2

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Abstract

Far from observation, procellariform seabirds' over-winter at sea: a dynamic environment subject to great variability. Large scale oceanographic phenomena such as the El Niño-Southern Oscillation impact winds and temperatures globally, which can change the location of productive foraging areas. Over-winter foraging is important in determining breeding success in the coming season. To investigate how long-lived seabirds may respond across their annual cycle to such periodic environmental change we analysed a 13-year geolocator/immersion logger dataset. This consisted of 400 tracks of Manx shearwater movements and behaviour throughout their annual trans-equatorial migration. In El Niño years, birds were found to over-winter at significantly more northerly latitudes than in La Niña years, a response attributable to individual flexibility in migratory destination. This latitudinal shift correlated with the daily time birds spent foraging over winter, with birds foraging less in El Niño years. In subsequent breeding, a hemisphere away, El Niño years saw a reduction in foraging and chick provisioning rates: effects that could not be attributed to the North Atlantic Oscillation (NAO). Meanwhile, we detected no convincing effects of El Niño on phenology. We suggest that in a highly migratory animal, environmental conditions experienced during one season may have cascading carry over effects into subsequent behaviour.

Introduction

Migration can be a mechanism to escape the extremes of seasonal climate variation through long-distance, trans-hemispheric migration (Pelletier *et al.*, 2020). How these movements respond to, or are affected by, longer-phased climate fluctuations that affect productivity at migratory destinations is nonetheless still poorly understood. One of the major drivers of climate is the El Niño Southern Oscillation (ENSO), a climatic pattern that alternates between an El Niño state, where Pacific trade winds weaken, and the reverse, La Niña, both of which alter winds and temperatures globally (Philander, 1983; Ayarzagüena *et al.*, 2018). With a periodicity of 3-7 years, both ENSO phases can influence the distribution of food resources at foraging grounds (Quillfeldt and Masello, 2013). Long lived species such as seabirds often migrate long distances to over-winter in productive regions, far from their high latitude or temperate breeding grounds. Breeding is energetically demanding for seabirds, which invest large amounts of parental care into rearing a small number of chicks, with breeding periods as long as 5 to 6 months (Hunter, 1984; Kim, Priddel and Carlile, 2017; Gatt *et al.*, 2020). Therefore, over-winter foraging is important for restoring condition, and preparing for the following breeding season (Alerstam and Hedenstrom, 1998; Fayet *et al.*, 2016). Both Southern Oscillation phases have been shown to affect seabirds adversely, reducing survival in Cory's shearwaters during La Niña (Brichetti et al., 2000), causing an increase in birds skipping breeding in El Niño years for red-footed boobies (Cubaynes *et al.*, 2011) and changing the at-sea breeding distribution of multiple species of tropical petrel (Ballance, Pitman and Fiedler, 2006). However, it is not well understood how oscillations in over-wintering environments might impact subsequent breeding across hemispheres where a different set of environmental conditions are encountered.

Events in one season that impact subsequent behaviour in the next are termed carry-over effects (O'connor *et al.*, 2014), and can occur at any stage of the annual cycle. There are many documented cases of carry-over effects in seabirds; stemming from both costly breeding and

over-wintering seasons. For example, breeding success affected over-wintering phenology in kittiwakes, with birds with failed breeding attempts departing earlier on migration (Bogdanova *et al.*, 2011). Male little penguins with a higher over-winter mass (Salton *et al.*, 2015) and black browed albatross with increased over-wintering foraging had greater breeding success in the following season (Desprez *et al.*, 2018). The Manx shearwater, a small (400-gram) Procellariform seabird breeding mainly in northern Europe, is a system particularly suited to studying over-wintering induced carry-over effects owing to its high breeding site philopatry, high year-to-year survival and tolerance of bird and nest-borne instrumentation (Storey and Brooke, 1991). Further, carry-over effects are thought to be especially important for migratory species such as Manx shearwaters that undergo a long, and potentially costly trans-equatorial migration to the Patagonian shelf (Norris and Taylor, 2006; Guilford *et al.*, 2009), and link pelagic ecology at a global scale. Additionally, Manx shearwaters are long-lived with protracted breeding seasons, so must balance reproductive and survival decisions from year to year (Storey and Brooke, 1991). In work led by (Shoji *et al.*, 2015) shearwaters that foraged more over winter were found to be more likely to skip breeding. This increased the likelihood of rearing a chick successfully in the following breeding season. Breeding season conditions are additionally known to carry-over to winter behaviour and future breeding success in this species, with experimentally extended breeding seasons in Manx shearwaters having knock-on consequences that can be measured using geolocators (Fayet *et al.*, 2016). Extended breeding seasons resulted in less over-winter foraging and lighter fledging mass of chicks in the following breeding season. However, carry-over effects due to environmental variation at the over-wintering grounds is not well understood for this, or any seabird species.

To understand individual response to changing conditions, and whether these responses carry over into future seasons, long-term datasets of annual movements are essential (Moe *et al.*, 2017). Here, we use a 13-year dataset of geolocation-derived migratory positions and immersion log-derived behaviours of Manx shearwaters to explore how over-wintering and

breeding behaviour is affected by ENSO conditions. We predict that variation between ENSO phases will predict over-wintering location. We also predict that the effects of ENSO on shearwater over-wintering location and behaviour will themselves carry-over into the subsequent breeding season's foraging, chick provisioning behaviour and phenology. To explore how ENSO affects shearwater north- and south-bound migration and breeding behaviour we employ path analysis, allowing us to simultaneously assess multiple temporally linked correlations (Shipley, 2016). Further, we take advantage of long-term tracking of individuals, parsing out within-individual effects to investigate whether individuals are flexibly adjusting their location between years with ENSO (van de Pol and Wright, 2009). We further explore over-wintering environmental effects through using a mixed effects model to determine whether birds are shifting position with chlorophyll, an indicator of resource distribution. Lastly, to distinguish carry-over effects from correlations between local conditions at the wintering and breeding sites, we construct a mixed effects model to investigate variation in breeding season foraging with the North Atlantic Oscillation, the major determinant of local conditions in the northern hemisphere (Forchhammer *et al.*, 2019). To summarise a set of environmental predictors (e.g. sea surface temperature, precipitation, sea surface level etc) attributable to oscillations, we use large-scale climate indexes; the Southern Oscillation Index (SOI) and the North Atlantic Oscillation Index (NAO; Forchhammer and Post, 2004; NOAA, 2023).

Methods

Fieldwork

To determine the migratory timing, routes and destinations of individual breeding birds, from 2007 to 2021, 770 geolocator (GLS) devices were deployed and retrieved from Manx shearwaters breeding at multiple colonies across the core breeding range of the species: Rum (57.01, -6.33); Skomer (51.74, -5.29); Ramsey (51.74, 5.29); Copeland (54.68, -5.53); Nólsoy (Faroes) (61.98, -6.65), and Lundy (51.18, -4.67). To estimate daily foraging, resting and flight behaviour, we used devices that incorporated a salt-water immersion logging facility. Models of GLS included BAS mk15 (2.5g) and Migratetech intigeo C330 (3.3g), C250(3.3g) C65 (1g) and C65-Super (1g) combined immersion and light loggers. With average bird mass being 400g (Storey and Brooke, 1991), all Migratetech models weighed 0.25% of the birds' total body weight, whilst older BAS models weighed 0.6%. GLS devices were attached to a custom made darvic leg ring, using cable ties and a small amount of super glue. Handling time was typically 5 to 10 minutes per deployment. Although GLS devices typically can record 3 years of data, most devices were retrieved, downloaded and redeployed each year to maximise data collection. For a subset of Skomer birds, chick peak masses were obtained by daily chick weighing (n=63 chicks).

Processing Position Data

All processing and statistical analyses were carried out in RStudio version 4.0.2 (R Core Team, 2021). Light data were processed using the "geolight" package to calculate position from twilight events defined by a light intensity threshold of 10 (Lisovski and Hahn, 2012). Day length was used to estimate latitude and the timing of midday/midnight was used for longitude. The sun elevation angle used to define twilight was -4.5. A rolling 3-day mean was applied to both longitude and latitude to smooth out error (Phillips *et al.*, 2004). Following the filtering of data to include only those that had complete tracks of north and south-bound

migration there were 423 bird-years available. Mean January position was used to represent over-wintering foraging ground location, as it is a mid-point month where position is least likely to be affected by birds arriving from or departing on southbound and northbound migration, respectively. Given the noise associated with GLS position estimates, latitude and longitude outliers were removed using the interquartile range method, retaining the lower and upper bounds of data (Liechti *et al.*, 2018). Migration phenology was determined using changes in longitude, rather than changes in overall position, as it is not subject to equinox error. Migration dates were determined from visual inspection of longitude, as in supplementary figure 1.

Processing Immersion Data

Saltwater immersion data recorded at 10-minute intervals were retained. Geolocator models that recorded immersion at alternate bin frequencies were excluded from analysis of behaviours due to concerns over differences in observed sensitivity between devices leaving 229 complete immersion tracks, 89 of which had a consecutive year in which to assess carry over effects in foraging. Saltwater immersion was recorded every 3 seconds and summarised to form an immersion score from 0 (completely dry) to 200 (completely immersed). For the times when the bird was at sea, immersion bins were classified into three states; a dry state where immersion score equalled zero, a wet state where immersion score equalled its maximum and an intermediate score which represented all values in-between. These three behavioural states have previously been identified for Manx shearwaters using immersion data in a number of different studies with the intermediate state representing foraging (Guilford *et al.*, 2009; Freeman *et al.*, 2013; Fayet *et al.*, 2016). This method has been previously validated using simultaneously deployed dive logger, GPS and GLS devices to check that assigned states from immersion data do indeed contain diving (Dean *et al.*, 2013). Foraging effort was obtained for over-wintering birds during January and breeding birds during August. Manx shearwaters are known to forage only during daylight hours (Shoji *et al.*, 2016; Darby *et al.*, 2022). To standardise for variation in day length, the number of hours at sea spent foraging were divided by day length at each bird's mean monthly position for January foraging, and per the mean number of daylight hours at each breeding colony in August.

Colony visitation during August was obtained from the immersion data to indicate chick provisioning rates. Manx shearwaters only arrive at or depart from the colony during the night, when it is dark enough to avoid predation (Brooke 1990). If they remain present in their burrow during daylight hours, they are unlikely to depart until it is night. Therefore, during the day if there was a continuous dry period for 6 hours or more, it was assumed that the bird was in its burrow. Days and nights were determined from one another using sunrise and sunset

times derived from the R suncalc package (Teets, 2003). Determining night visits to the colony required a different approach, as dark and dry periods at night could be easily confused with night flight. For each night, immersion bins were defined as 'wet' if any immersion was recorded and summed to calculate the number of wet events per night. A normal Expectation Maximisation (EM) mixture model, a model used to identify the distribution to which observations belong, was applied to distinguish nights with colony visits from nights at sea using the mixtools package (Benaglia *et al.*, 2009). Two distinct distributions were identified and hence used to identify colony visitation by assigning colony visits to nights that had higher probability of belonging to the drier peak.

Environmental Variables

Over-wintering conditions were described using the Southern Oscillation Index (SOI), whilst breeding conditions were described via the North Atlantic Oscillation (NAO) index, both provided by NOAA (NOAA, 2023). The SOI describes a standardised difference between the barometric pressures at observation sites in Darwin (Australia) and Tahiti. When the pressure difference weakens, El Niño conditions occur, indicated by negative index values. For this analysis, the SOI index was taken as a mean for the months of October, November and December. These months coincide with the peak of an El Niño/ La Niña event and phytoplankton blooms in the Southwestern Atlantic that dictate over-wintering conditions (Machado, Barreiro and Calliari, 2013). The NOA index describes the pressure difference between the Azores and Iceland. NAO is most pronounced in winter and can have effects in subsequent seasons (Stenseth *et al.*, 2003). Summer NAO has an effect on European climate but it is less understood (Barnagaud *et al.*, 2011). Therefore, in this analysis, winter NAO (December-March) and summer NAO (June-August) were both considered as drivers of climate around the breeding colony. We used aqua modis derived chlorophyll a data provided by NASA to determine which latitude in the Patagonian shelf area (-35°N, 63°W : -45°N, 59°W) had the maximum chlorophyll per each year (NASA, 2023).

Statistical analysis

We implemented a path analysis model to allow us to link behavioural responses from one season to the next via a path of correlated events (Lleras, 2005; Shipley, 2016). Path analysis was conducted via the r package Lavaan to investigate links between the SOI and previous breeding season behaviour to over-wintering latitude, phenology and foraging effort (Roseel, 2012). These variables were then linked to the coming breeding season's behaviour via colony visitation and foraging effort during August (figure 1). Significance levels were Bonferroni adjusted for structural equation modelling following the recommendations of Smith and Cribbie (2013); $\alpha(per\ test) = \frac{0.05}{k^{1-\sqrt{[r]}}}$, where k is equal to the number of tests and r to the correlation coefficient. Colony location was not included in the model due to varying sample size between years. However, as this analysis considers two subsequent years of an individual bird; it can be assumed variation between years is being measured on a within-individual level. As we were interested in determining the environmental factors causing latitudinal variation between years, and these are confounded with time, the year itself was not included in the path analysis model.

Path analysis relies on several, rather than a single statistical test to assess model fit to the data. As chi squared ($\chi 2$) p values are known to be uninterpretable with large sample sizes, we instead used the relative/normed chi-square ($\chi 2/df$) recommended by (Wheaton et al, 1977) to assess fit. The $\chi 2/df$ value was 2.76, which was suitably below the recommended maximum ratio of 5. Both the comparative fit index (CFI) and the Tucker-Lewis Index (TLI) of the path analysis were 0.9. The Root Mean Square Error of Approximation (RMSEA) and the Standardized Root Mean Square Residual (SRMR) which both relate to model residuals, were

0.05 and 0.07 respectively. All of the above statistics were, therefore, well within the accepted thresholds for suitable model fit (Hu and Bentler, 2009).

Separate to our path analysis, the relationship between August colony visits and chick peak mass was tested. This was to validate whether GLS derived colony visits are indicative of chick provisioning rates in this study, following previous validation in a study using mixture models to indicate chick provisioning by Padget, 2017. Chick peak mass data were available only for a subset of Skomer geolocator birds over the years of this study (n=63), so all available August data on Skomer were pooled to increase the sample size and analysed separately using a mixed effects model in the r package lme4 with burrow as a random effect (Bates *et al.*, 2015). The date the peak mass was taken was included as a fixed effect to assure that any correlations between colony visitation and peak mass were not occurring as a function of peak mass occurring at a later date in some birds. Additionally, to test for local environmental conditions during breeding, the relationship between the North Atlantic Oscillation (NAO) and August foraging was tested in 2 mixed effects models; one for winter and one for summer NAO, with individual as a random effect. A mixed effects model was also used to test whether any variation in mean January latitude with changing ENSO conditions occurred as a result of individual adjustment. Between-individual and within-individual responses to ENSO conditions were separated using the Subject Centring Method from Van de Pol and Wright, exact details of which can be found in (van de Pol and Wright, 2009). Finally, we implemented a mixed effects model to assess whether birds adjusted their latitude to the latitude with the maximum chlorophyll in that year, with individual as a random effect. Significance was assessed in mixed effects models using Likelihood Ratio Estimation and confidence intervals and effect sizes were obtained through bootstrapping methods; where 1000 simulations of random and fixed effects were implemented using the arm package (Gelman and Hill, 2006).

Figures

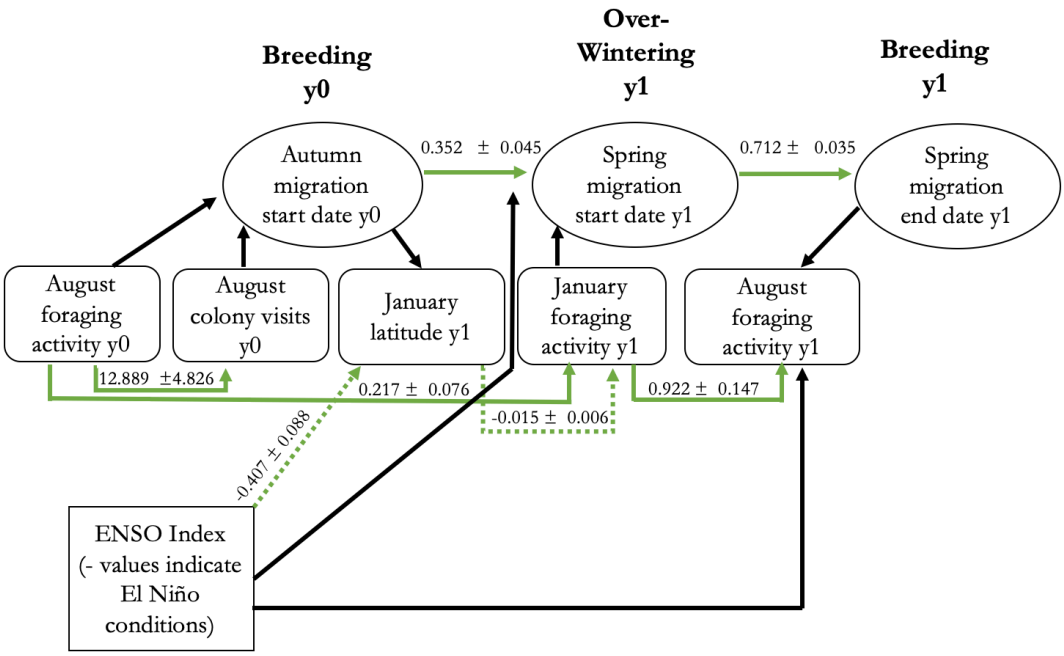

Figure 1. A diagram illustrating path analysis correlations between environmental, behavioural and phenological factors. Significant effects are represented in green and non-significant paths in black. Dotted lines indicate negative relationships and path estimates (ß ± SE) are given for each significant path.

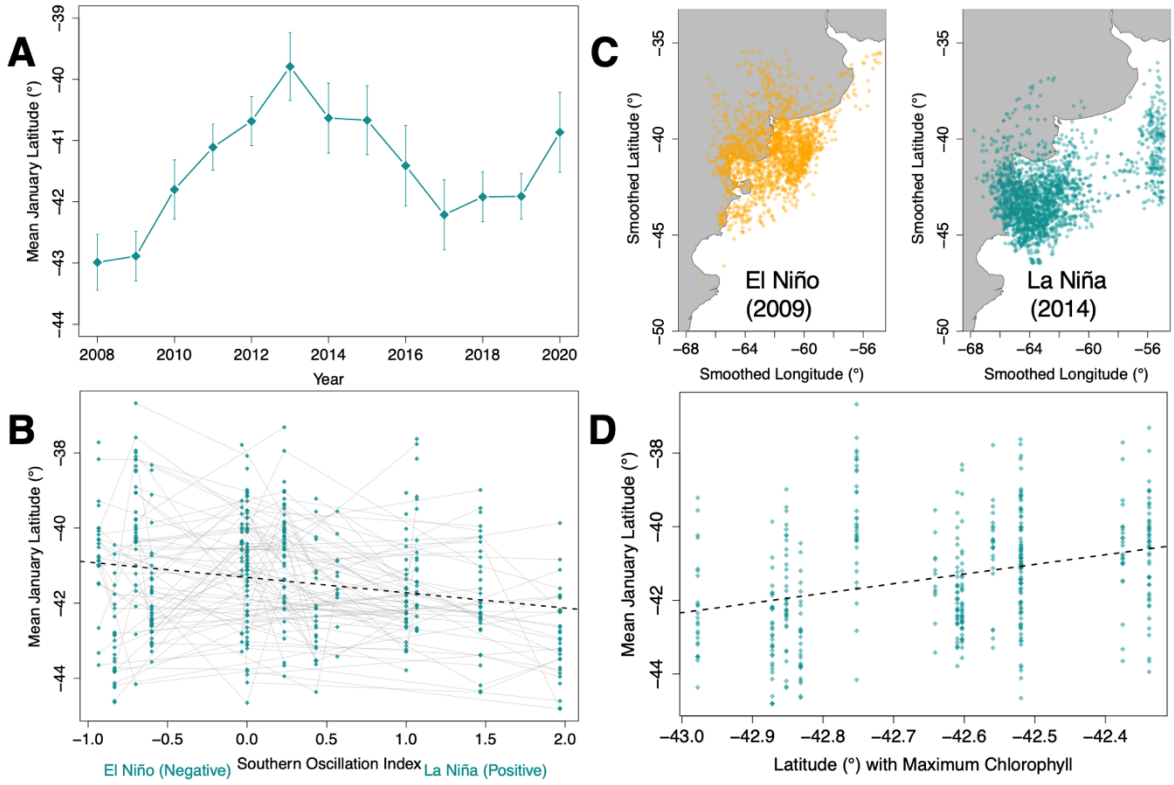

Figure 2. The effect of the El Niño Southern Oscillation index on over-wintering latitude. **A)** Variation in mean over-wintering latitude (n=422) between years with 95% confidence intervals, where each point represents a mean of all individuals. **B)** Variation in mean over-wintering latitude with the SOI index (NOAA, 2023). Grey lines connect individuals tracked in multiple years to visualize individual adaptation to varying ENSO conditions. The regression line is derived from the path analysis model. **C)** Smoothed latitude (°) and longitude (°) for all individuals are plotted for a strong El Niño year in orange (2009) (n=36) and a strong La Niña year in blue (2014) (n=37). **D)** The relationship between the latitude at which the maximum chlorophyll was centred at for a given year against mean January latitude. Chlorophyll data was taken from the aqua-modis project (NASA, 2023). The regression line is derived from the mixed effects model

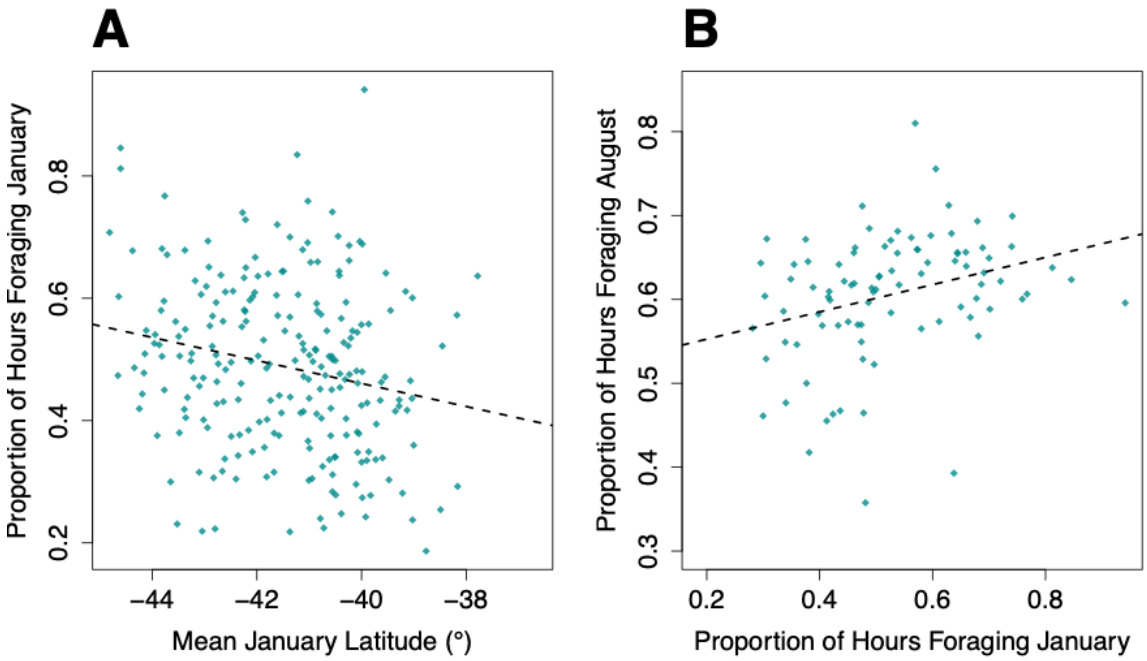

Figure 3. The correlative effects of January latitude on over-wintering and breeding foraging activity. **A)** Mean January latitude plotted against the proportion of the day spent foraging in January) (n =229). **B)** The proportion of the day spent foraging in August during chick rearing plotted against January foraging time (n=91). For both, proportions are derived from foraging hours divided by the available daylight hours at the foraging site

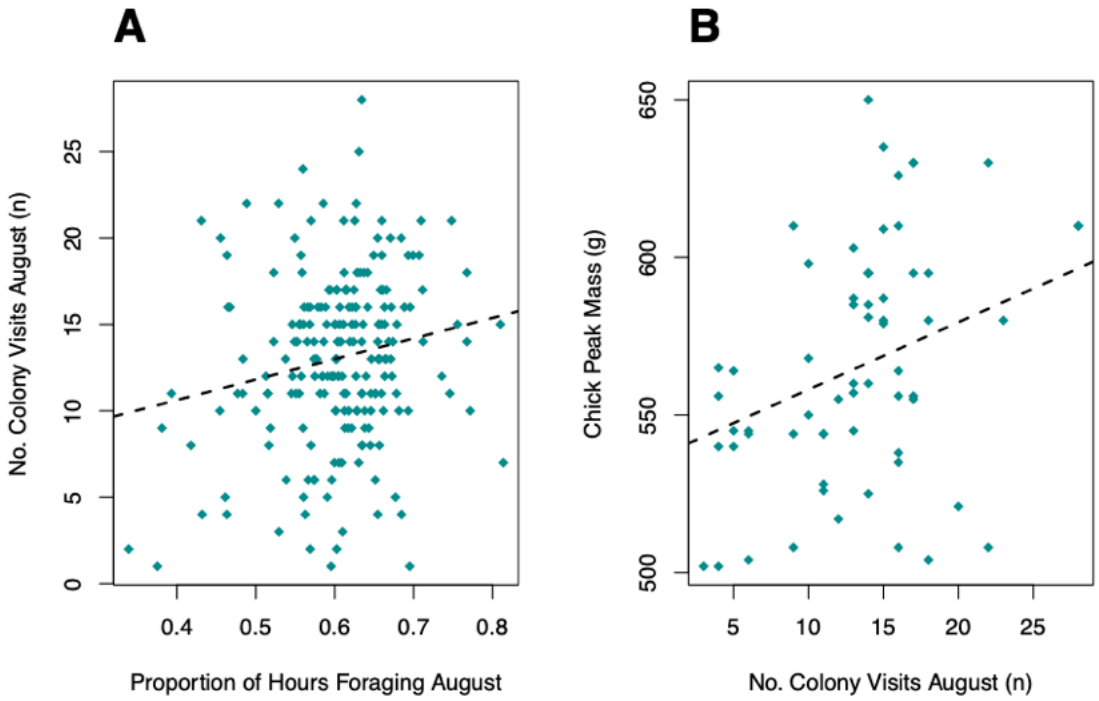

Figure 4. The correlative effects of foraging activity on colony visitation and chick peak mass. **A)** The proportion of the day spent foraging in August (foraging hours divided by the available daylight hours at the foraging site) plotted against the number of colony visits in year 0 (n =213). **B)** The number of colony visits plotted against chick peak mass for Skomer birds only (n=63). Regression lines are derived from A) path analysis and B) a mixed effects model.

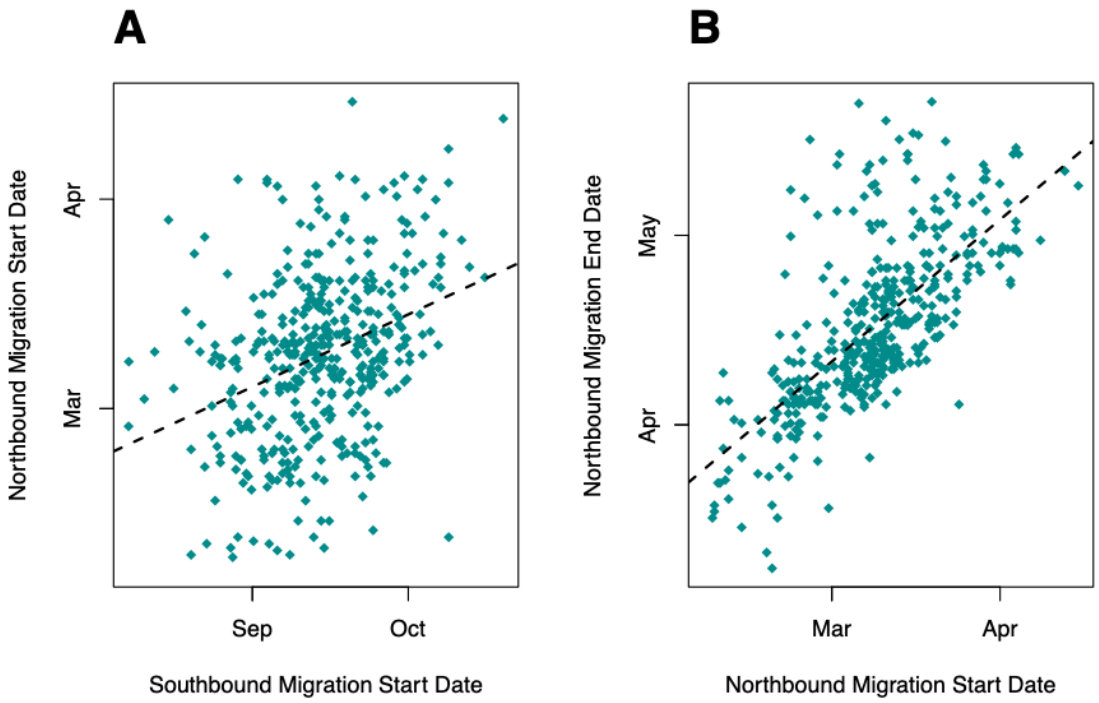

Figure 5. Correlations between Southbound (Autumn) and Northbound migration (Spring). **A)** Northbound/spring migration start date plotted against southbound/autumn migration start date (n=421). **B)** Northbound/spring migration start date plotted against northbound/spring migration end date (n=419). Regression lines are derived from the path analysis model.

Results

The mean January latitude for over-wintering birds showed non-linear variation between 2008 to 2020, oscillating in a wave-like pattern (figure 2). Consecutive years were more similar, with overlap between 95% confidence intervals. This suggests that latitudinal shifts occur relative to the previous year, and birds are responding to a periodic environmental variable. Path analysis (figure 1) suggested this pattern may exist as a result of changes in ENSO; where a significant correlation existed between the SOI and over-wintering latitude (β=-0.407, se=0.088, z=-4.650, p<0.001). Birds in El Niño years were observed to be further north (figure 2). To determine whether shifts occurred via individual flexibility in foraging latitude with ENSO, we implemented a mixed effects model via the Subject Centring Method, to find both significant between (β= -0.91, 95%CI [-1.45, -0.36], $\chi^2$1=10.96, p<0.001) and within individual effects (β= -0.34, 95%CI[-0.52, -0.16], $\chi^2$1=12.90, p< 0.001) (van de Pol and Wright, 2009). There was, however, no difference in the within- and between-individual latitudinal change, suggesting that the effect of El Niño on wintering latitude is best explained by within-individual plasticity than between-individual turnover. We also implemented a separate mixed effects model that indicated birds adjust their over-wintering latitude to where the maximum chlorophyll that year was centred (β =2.62, $\chi^2$1=3.24, 95% CI[1.98, 3.25], p < 0.0001). Therefore, birds appear to adjust their over-wintering latitude in response to shifting resource distributions.

Variation in over-wintering latitude had a significant effect on the proportion of daylight hours spent foraging; with foraging effort decreasing at lower latitudes (β=-0.015, se=0.006, z=-2.776, p<0.01). Therefore, ENSO-induced changes in January latitude appear to cause foraging effort to vary. When January foraging effort was higher, it correlated with an increase in the proportion of time spent foraging in the following August (β=0.217, se=0.075, z=2.848, p<0.01, figure 3). Foraging during August in year 0 had a positive relationship with the following January's foraging (β=0.922, se=0.147, z= 6.265, p<0.001). To summarise,

northward shifts in foraging latitude as a result of El Niño conditions correlated with a reduction in over-wintering and subsequent breeding foraging. We found no evidence of environmental conditions directly affecting foraging during breeding. No significant effects of ENSO on August foraging were detected via path analysis, and separately in mixed effects for local environmental effects via NAO variability, no significant effects of winter NAO (β= 0.02, 95%CI [-0.019, 0.013], $\chi^2$1=0.17, p= 0.7) or summer NAO (β= 0.02, 95%CI [-0.002, 0.04], $\chi^2$1=2.73, p= 0.1) were found.

An increase in foraging during August also increased the number of colony visits during this time (β =12.889, se=4.826, z=2.671, p<0.01). A separate mixed effects model of August GLS data pooled from year 0 and year 1(n=63) using chick peak mass measurements available from Skomer island, validated that colony visits appear indicative of chick provisioning (β= 2.13, 95%CI [0.69, 3.60], $\chi^2$1= 8.82, p<0.01). There was no significant effect of the date peak mass was reached on the measurement, which indicates the effect of increased number of colony visits in August is not occurring as a product of later (β= -9.52, 95%CI [-26.04, 8.38], $\chi^2$1= 1.29, p=0.2). Therefore, increased colony visitation rates over August are correlated with higher chick peak mass. Neither foraging effort nor the number of colony visits in August had a significant effect on departure date from the colony (figure 1). Autumn southbound migration start date was, however, significantly related to the start date of the next spring's northbound migration (β=0.352, se=0.045, z=7.808, p<0.001), which defined return date to the colony in the following breeding season (β=0.712, se=0.035, z=20.491, p<0.001). Therefore, individuals departing later on southbound migration from the colony appeared to return later next year. Neither the SOI nor overwintering foraging effort had a significant effect on spring migration start date (figure 1). Phenology, therefore appeared separate to the effects of environmental variability via the SOI.

Discussion

Path analysis finds the most likely route by which chronologically linked variables might correlate, indicating the most likely causative cascade. Our results suggest an indirect pathway by which ENSO conditions may ultimately affect behavioural outcomes later in the migratory cycle for Manx shearwaters. While GLS position data are inherently noisy, they are ideally suited to questions on the global scale addressed here, where the signal to noise ratio is nonetheless excellent, and where our large sample size allows us to detect year-round behavioural correlations. Hence here we have been able to use these data to show how broad scale environmental conditions, breeding behaviour and wintering behaviour are related in chronological cascades in a trans-hemispheric migrant.

During El Niño years, birds over-wintered further north and foraged less. Furthermore, this went on to impact the subsequent breeding attempt, 10,000 km away, lower foraging effort correlated with a lower foraging effort and colony visitation during chick-rearing (figure 2). Chick peak mass data available for a subset of Skomer birds provided evidence to suggest that higher colony visit numbers are indicative of increased chick provisioning. Indeed, it is unlikely that a breeding bird would break from foraging to return to the colony without feeding the chick. We can therefore infer that reduced colony attendance following El Niño is associated with reduced chick provisioning.

An alternate explanation is that no carry over effect is present and birds are simply responding to local conditions at the breeding site. ENSO is also known to influence northern hemisphere weather, and potentially even other major drivers of climate such as the North Atlantic Oscillation (Mokhov and Smirnov, 2006). However, no direct effects of ENSO on breeding season behaviour were found in this path analysis and, furthermore, we found no evidence of the NAO, a major driver of European climate, having an effect on breeding season foraging. Whilst local conditions have known importance in determining breeding behaviour, this

analysis demonstrates the importance of over-wintering foraging and distribution. Additionally, the carry-over effects demonstrated here extend beyond the breeding season, with August foraging also being related to foraging effort in the subsequent January. Future foraging effort therefore seems to be influenced by an interaction between previous foraging activity and environmental conditions during the winter.

The SOI summarises pressure differences that can equate to a range of environmental conditions including changes in sea level, ocean acidification, storms, sea surface temperature and precipitation; all known to impact seabird behaviour (Quillfeldt and Masello, 2013; Risaro, Chidichimo and Piola, 2022). Such indexes are thought to allow ecologists to make inferences about how seabirds might respond to climate without multiple hypothesis testing, with potentially more predictive power than local variables (Szostek and Becker, 2015). However, a northward shift in chlorophyll distribution along the Patagonian shelf during El Niño years, thought to be partially driven by wind anomalies, was documented by (Machado, Barreiro and Calliari, 2013). We therefore conducted a secondary analysis (figure 2) using aqua modis derived chlorophyll a data that suggested birds are significantly shifting their latitude to that at which the maximum chlorophyll in the south west Atlantic is centred (NASA, 2023). Despite the limitations of using chlorophyll content as a proxy for prey distribution, this might suggest the observed shifts in latitude are food driven (Kane *et al.*, 2020). Understanding how birds vary their behaviour with shifting resource distribution is important in terms of understanding current and future climatic changes, with future ENSO events predicted to become more extreme under anthropogenic warming (Cai *et al.*, 2021). In this analysis, within-individual changes in distribution between years were found to be significant using the subject centring method of (van de Pol and Wright, 2009). This suggests that individuals plastically adjusted their position with environmental conditions and confirms this was not the result of individual turn-over in our sample compounded by some sampling bias propagating through the annual cycle. Additionally, many avian species are seeing changes in phenology so as to

align breeding with peak prey availability (Gordo, 2007). Interestingly, migratory dates were highly correlated with one another (figure 5). We found that birds that leave earlier on southbound autumn migration do not have longer over-wintering periods, but instead returned to the colony earlier next year. Therefore, correlations in migratory timings from one season to another allow birds to return earlier to breeding site and potentially to commence reproduction at an earlier date. Breeding earlier is linked to higher success in many avian taxa, including shearwaters, so shifts in phenology as a result of environmental change may have fitness consequences (Lambrechts *et al.*, 1997; Schaper *et al.*, 2012; Winkler *et al.*, 2020). However, we did not find any convincing effects of ENSO on migratory timings in Manx shearwaters (figure 2).

Understanding how migratory and breeding behaviour of seabirds vary in response to large scale climate oscillations is essential given current climatic changes. Carry-over effects for Manx shearwaters have been previously measured both in natural behaviour (Shoji et al. 2015) and experimentally demonstrated, where reduced over-winter foraging occurred as a result of costly breeding seasons (Fayet *et al.*, 2016). By exploiting a powerful, 13-year GLS dataset to measure carry-over effects, we have been able to provide unique insights into the interactions between ENSO-determined over-wintering conditions and cyclic animal behaviour, providing a link between a trans-hemispheric migrant's behaviour and climate. We suggest that future collaborations between biologists and climatologists may prove useful in identifying the driving environmental mechanisms behind seabird behaviour, especially in under-sampled regions such as the south-west Atlantic.

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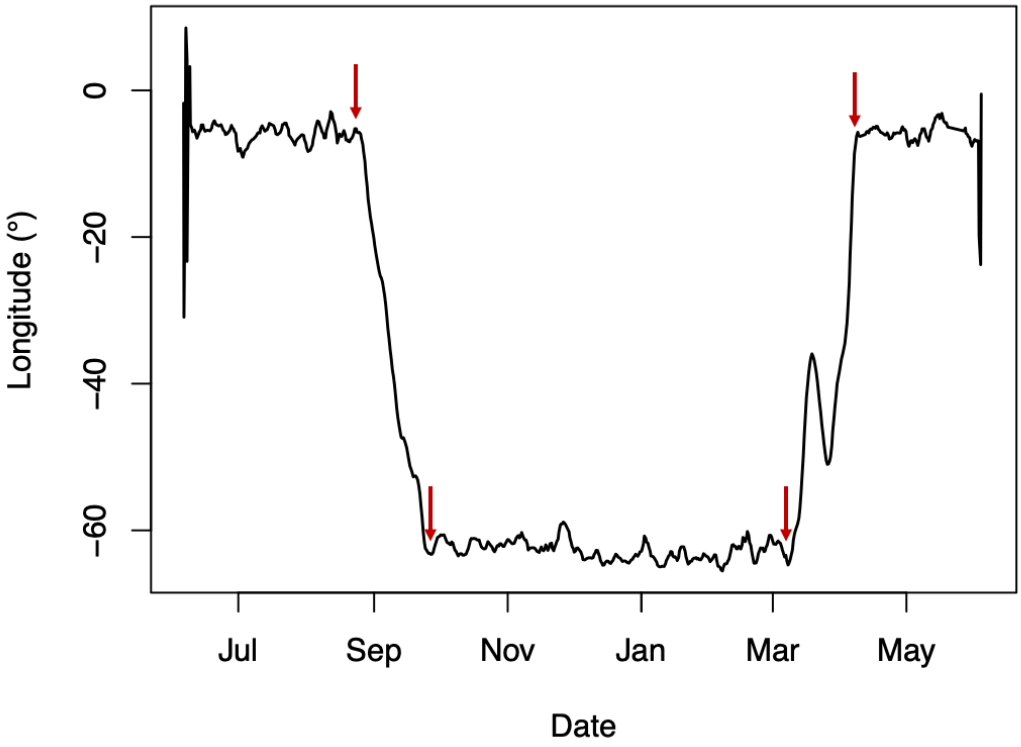
Supplementary Materials



Supplementary 1. An example of an individual Manx Shearwater trace showing GLS derived longitudinal variation over time. Red arrows represent migration start and end dates that were allocated by visual identification.

Night flight facilitates migratory catch-up in a long-distance migratory seabird

3

With contributions from Joe Wynn, Sarah Bond, Lewis Fisher-Reeves, Oliver Padget , Greg Morgan, Jóhannis Danielsen, Holly Kirk, Annette Fayet, Natasha Gillies, Martyna Syposz, Akiko Shoji, Lou Maurice, Tim Guilford

Abstract

Long-distance migrants must optimise their timing of breeding such that they capitalise on resources in one location and migrate in time to capitalise on resources at the wintering site. In species with protracted breeding seasons, such as the procellariform seabirds, departing on migration as early as possible might be advantageous but constrained by needing to finish the ongoing breeding attempt. Here we investigated how breeding timing affects migratory timing in the Manx shearwater (*Puffinus puffinus*), a trans-hemispheric migratory seabird with large temporal variation in the onset of breeding. Using a long-term geolocator tracking dataset, we found that that early-laying shearwaters departed earlier on autumn migration; had increased migratory duration; stopped with greater frequency; and foraged for a greater proportion of the day whilst stopped. In contrast, later departing birds flew more at night during migratory stints. We further found that night flight was increased with moon illumination, which could reflect moonlight providing the light conditions required for visually guided shear-soaring flight. Accordingly, birds that experienced higher levels of moon illumination whilst migrating had shorter migration durations. Interestingly, we found that birds appeared to time their departure from the breeding site with the lunar cycle; with later departing birds leaving at an earlier lunar day, possibly to coincide with brighter overall moonlight conditions during migration, partially mitigating for their late departure. We suggest that birds use an understanding of prevailing environmental conditions to execute the most efficient migration available, allowing them both to complete breeding and capitalise on resource availability at the wintering site.

Introduction

Post-breeding migration in high latitude animals is considered to be an adaptation to shifting but predictable seasonal resources (Thorup *et al.*, 2017; Winger *et al.*, 2019). When freed from the constraints of breeding, birds migrate to regions of higher seasonal productivity, sometimes travelling thousands of kilometres. Whilst some birds complete their migration in a single bout of flight, the majority break up their journey with a series of stopovers (Newton, 2008). Stopovers can have multiple functions, but are considered to be primarily for refuelling (Schmaljohann, Eikenaar and Sapir, 2022). For many species, stopovers are more prevalent in pre- rather than post- breeding migration since birds must make a timely return to commence reproduction (Gordo, 2007; Duijns *et al.*, 2019). However, mistiming post-breeding migration can be costly if birds arrive at over-wintering sites before foraging opportunities are plentiful, or alternatively remain at the breeding grounds after resources have ceased to be available.

Timing migration to the wintering grounds will therefore require optimising several trade-offs that exist within constraints. For example, life history trade-offs may exist such as whether the bird stays to finish the breeding attempt and has the best chance of fledging healthy offspring or instead leaves early to maximise its chance of coinciding with winter resources and thus surviving; or trade-offs based on the spatiotemporal distribution of resource such as the timing of the decline of local resource and the expected increase in non-breeding site resource availability; the speed of migratory flight; the potential for refuelling along the way or, conversely, travel over unsuitable habitat (Lameris *et al.*, 2018; Schmaljohann, Eikenaar and Sapir, 2022). Natural selection positions animals at the points along trade-off axes that maximise the net benefit from the two variables trading off, since this should be fitness maximising. However, in the case of timing the return migration after breeding, flexibility in phenology might be not be possible owing to the cost to the current reproductive effort of leaving early (presumably chick death and failure) and birds that breed late may continue to provision for their chicks whilst local conditions decline owing to the magnitude of this cost. Later-breeding birds might, however, have some flexibility in resorting to alternative migratory strategies to 'catch up' and reach areas of higher seasonal abundance, but mechanisms that reduce the cost of late breeding are not well understood. Optimal migration theory, first suggested by Alerstam (1991) has led to studies of migration strategy incorporating an optimisation perspective (Alerstam, 1991, 2011). Assisted by technological advances in biotelemetry, we have gained insight into some of the ways in which long-distance migrants optimise migration; timing departure with favourable environmental conditions and stopping at productive foraging sites (Franke *et al.*, 2011; Domer *et al.*, 2021; Schwemmer *et al.*, 2021).

However, despite taking some of the longest documented avian migrations, and having some of the most constraining and protracted breeding periods, studies into optimisation of migration phenology in seabirds are scarce.

Manx shearwaters are procellariform seabirds that take a long-distance, trans-equatorial migration (Guilford *et al.*, 2009). Despite evidence that earlier laying birds rear fledglings with greater survival rates, there is approximately one month of variation in lay dates in Manx shearwaters (Storey and Brooke, 1991). It follows therefore that there will be similar variation in the time at which adult birds will finish chick provisioning and depart for migration (Wynn *et al.*, 2022). A study of Cory's shearwaters found that birds departing earlier on migration took longer to reach the over-wintering grounds and had more stopovers than later birds (Dias, Granadeiro and Catry, 2012). This suggests that phenology might cause differences in migration behaviour between individuals; with earlier birds being able to take advantage of foraging opportunities *en route*, whilst later birds maximise migration speed. When migrating between stopovers, Cory's shearwaters were shown to fly both by day and night, flying more on nights of higher moon illumination (Dias, Granadeiro and Catry, 2012). In Manx shearwaters, moonlight has been shown to reduce breeding season colony attendance, with birds favouring darker, less risky nights to avoid predation while they are vulnerable on land at the colony (Riou and Hamer, 2008). However, during migration, predation risk to seabirds is presumably low and moonlight may instead provide an opportunity to make use of night flight during migration stints. In a study of 21 migrant seabird species, an increase in flight activity with moonlight was found in most species, but was not detected in Manx Shearwaters (Bonnet-Lebrun *et al.*, 2021). With eyes optimised for day light, Manx shearwaters are generally diurnal in their at-sea behaviour, with breeding season foraging behaviour restricted to daylight, along with most commuting flight (Guilford *et al.*, 2008; Darby *et al.*, 2022). Manx shearwaters utilise shear-soaring or flap-gliding flight, both of which rely on the ability to assess accurately the distance to the sea surface (Gibb *et al.*, 2017; Kempton *et al.*, 2022). Therefore, one expectation might therefore be that shearwaters are constrained in their ability to migrate at night by darkness, and therefore spend more time migrating on nights with greater moon illuminance.

As long-distance migrants with individual variation in breeding schedules and a high number of stopovers when compared to other seabirds (Freeman *et al.*, 2013; Bonnet-Lebrun *et al.*, 2021), Manx shearwaters are an excellent species in which to investigate optimisation of migratory phenology. Here, we aim to establish whether variation in migration departure date is caused by differences in lay date between individual birds and – given the behaviour of the

closely-related Cory's shearwater (Dias, Granadeiro and Catry, 2012) – whether early and late departing birds vary their migratory strategies to compensate for variation in breeding phenology. This we assessed using a large multi-year dataset of geolocator-derived Manx shearwater migratory movements, with which we aim to provide a detailed exploration of how migratory behaviour may vary within a species.

Methods

Fieldwork

From 2006 to 2020, 774 geolocator (GLS) devices were attached to Manx shearwaters during the breeding season to record their migratory behaviour in autumn (and subsequent behaviour). Devices were attached using cable ties to custom built plastic leg rings. Fieldwork was carried out on Rum (57.01°N, 6.33°W); Skomer (51.74°N, 5.29°W); Ramsey (51.74°N, 5.29°W); Copeland (54.68°N, 5.53°W), Lundy (51.18°N, 4.67°W) and the Faroe Islands (61.98°N, 6.65°W). Handling time was kept to a minimum (5-15 minutes).

Multiple models of combined immersion and light loggers were used as part of this study: British Antarctic Survey (BAS) mk15 (2.5g; 0.6% of average bird mass) and Migrate Technology intigeo C330 (3.3 g; 0.83% of average bird mass), C65 (1g; 0.25% of average bird mass), C250 (3.3G; 0.83% of average body mass) and C65-Super (1g; 0.25% of average bird mass). On Skomer island lay dates were obtained through daily egg checks, totalling 105 geolocator burrows across all years. Following the removal of birds who did not lay an egg, this left a total of 90 lay dates for analysis.

Data Processing

All data processing was carried out in R Studio Version 4.1.2 (R Core Team, 2021). Position was calculated using GLS-recorded light data through the R package geolight; where latitude is defined by day length, and longitude by time of midday (Lisovski and Hahn, 2012). We used a sun elevation angle of -4.5° to minimise the number of positions over land as in Wynn *et al* (2022). Migration start date and end was determined via visual inspection of longitudinal changes between August and December; as in supplementary 1. Longitude, smoothed using a 3-day rolling mean, was used since it is not subject to equinox error. Immersion was summed by the device every 10 minutes to create a summary score ranging from 0 (dry for the whole period) to 200 (wet for the whole period). To analyse patterns of activity, data were filtered to

remove tracks with incomplete migrations and only tracks where immersion was summed at consistent intervals were retained. This left 606 complete migrations for analysis, 343 of which had immersion data.

To assign stopovers, days and night were first separated using the devices' light logger. Only days were used to identify stopovers; as previous studies of Manx shearwaters suggest foraging occurs only during daylight hours (Shoji *et al.*, 2016; Darby *et al.*, 2022b). The number of dry ten-minute bins were summed per day to indicate the amount of time spent in flight. A mixture model was then implemented from the r package mixtools (Benaglia *et al.*, 2009) to identify two discrete distributions in the number of dry bins in a day. Each bird-day was then assigned to either distribution based on the probability of fitting into either curve (>0.5). Following the assignment of stopovers, the total number of stopover days was summed for each track. The proportion of time spent foraging at stopovers was calculated per day. Foraging was classified as ten-minute bins with intermediate immersion scores, a method which has previously been validated using co-deployed Time Depth Recorder (TDR) data during breeding (Guilford *et al.*, 2008; Fayet *et al.*, 2016; Shoji *et al.*, 2016)

To investigate flight behaviour whilst birds are migrating, stopover periods were excluded, so as to assess periods where birds are actively travelling. Moon illumination was obtained from the R package lunar (Lazaridis, 2022) and moon rise and set times were obtained from the R package suncalc (Thieurmel and Elmarhraoui, 2022) using the light curve calculated positions from the GLS data. Given that moon rise and set times do not show substantial variation on small spatial scales, light derived positions, despite their subjectivity to error, provided an adequate estimate of position for which to obtain daily moon timings.

Statistical analysis

To test the effects of autumn migration departure date and moon factors on migration duration, stopover activity and hours of flight/foraging we used mixed-effects models, fitted with maximum likelihood (Bates *et al.*, 2015). We accounted for non-independence between years, colonies and individuals by including them as random effects in all models. Significance was obtained using likelihood ratio tests between the full model and a null model with the parameter of interest dropped, implemented using the R package lme4 (Bates *et al.*, 2015). Confidence intervals and effect sizes were generated using bootstrapping methods through the arm package in R to resample model effects 1,000 times (Gelman and Hill, 2006).

We predicted that if shearwaters are constrained to fly under visual control (i.e. require light for migration), late departing birds might be able to mitigate for their late departure by timing their migration with the lunar cycle so as to have more moonlit nights, allowing for increased night flight and a faster migration. To understand whether late and early departing birds time their migration differently with the lunar cycle, we used a randomisation approach where we compared the lunar day of migratory departure of the latest and earliest birds with randomly chosen birds. As this analysis did not require immersion data, we were able to use a wider dataset of migration start times (n=606). Late birds were defined as those with leave dates above the 90% percentile of the population (>=30th September) and early birds were those whose departure date were below the lower 10% population percentile (<=29th August). This included 64 late birds and 60 early birds from all sampled years and colonies. The lunar day of each departure date was first transformed into radians (as lunar day moves in cycles). The departure dates of all birds were then resampled 10,000 times with replacement (with n being equivalent to the respective sample size of early/late birds). A Watson's two-sample test (with a significance level of 0.05) was conducted for each iteration, examining whether the observed mean directions (lunar days in radians) of early and late birds deviate significantly from those of the resampled lunar days. This analysis was performed using the circular package developed by Agostinelli and Lund (2023). We then evaluated the proportion of instances in which early and late birds exhibited departure on distinct lunar days compared to the resampled data.

Figures

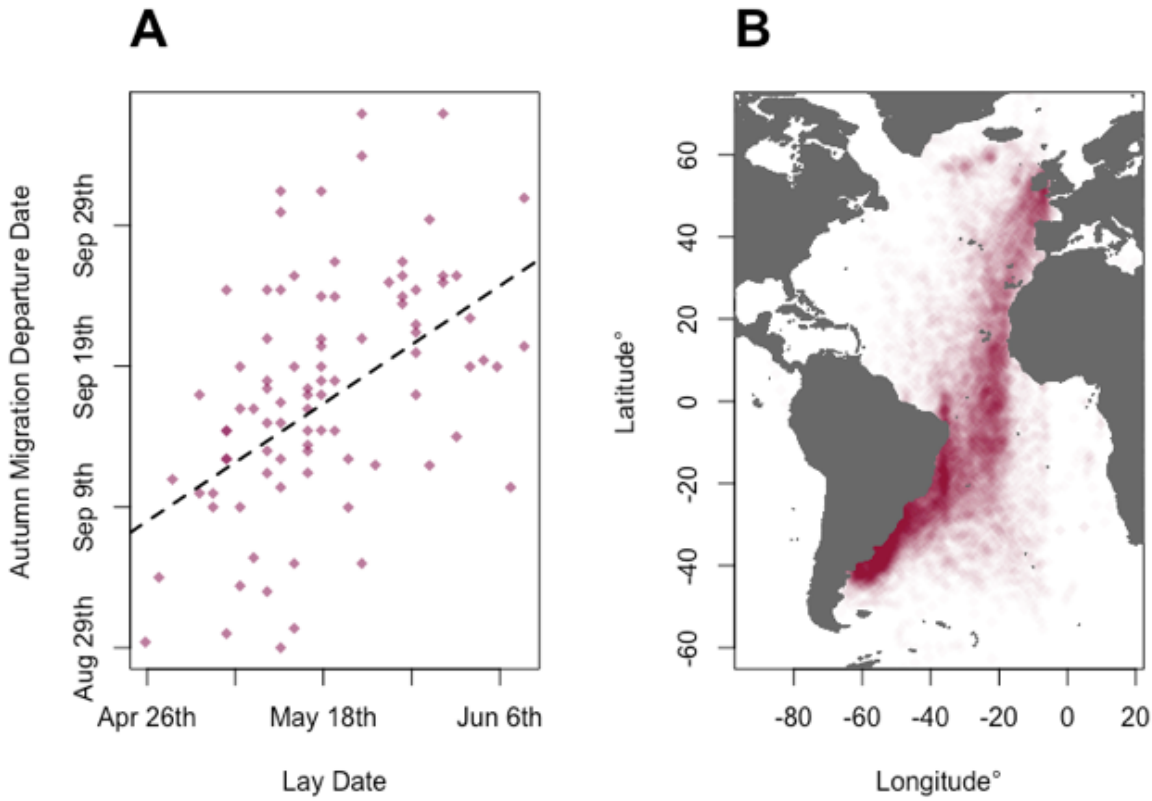


Figure 1. Visualising autumn migration and its relationship with breeding phenology. **A)** Lay date plotted against GLS determined autumn migration date (n=89; Skomer birds only). The regression line is derived from our linear mixed-effects model (see Table 2). **B)** The post-breeding migration of 343 shearwaters plotted with transparency from GLS derived position estimates.

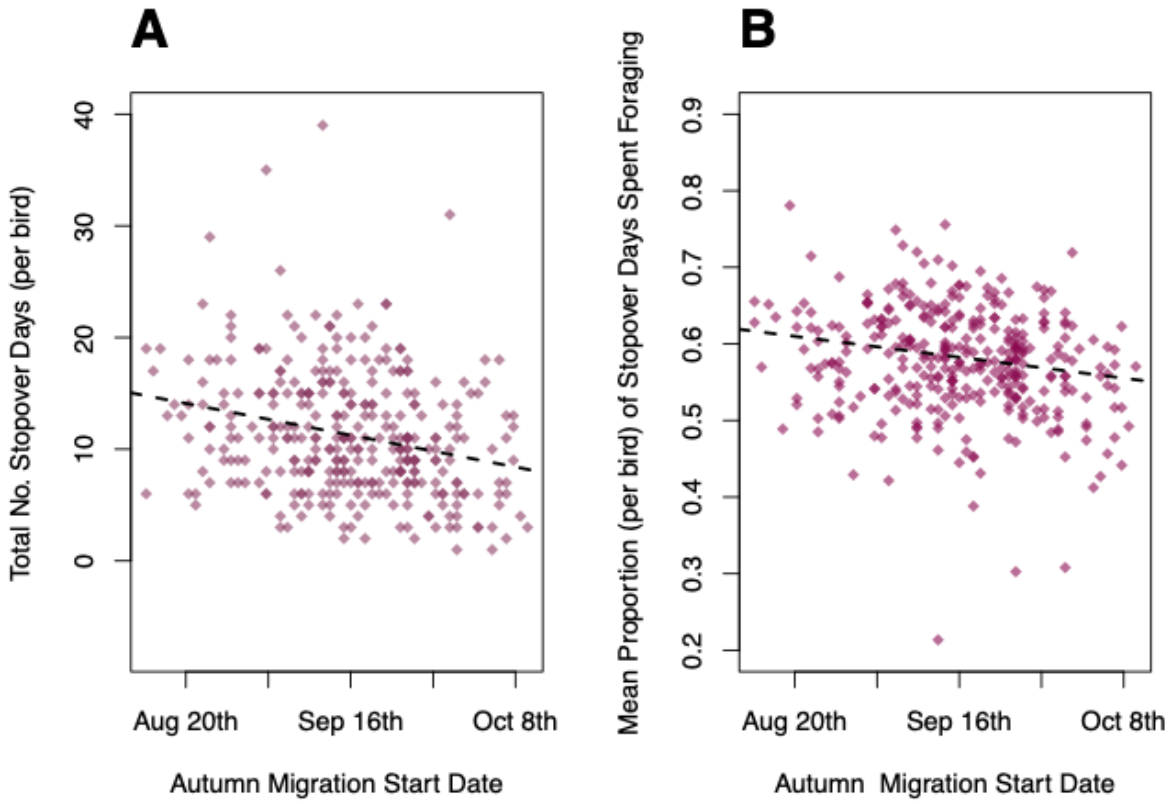


Figure 2. The effect of autumn migration date on stopover behaviour. **A)** The total number of stopover days plotted against autumn migration departure date. **B)** The mean proportion of the day foraging whilst at stopovers plotted against autumn migration date. In both plots the regression line is derived from our linear mixed-effects model (see Table 2), and each point represents the phenotype of a single bird.

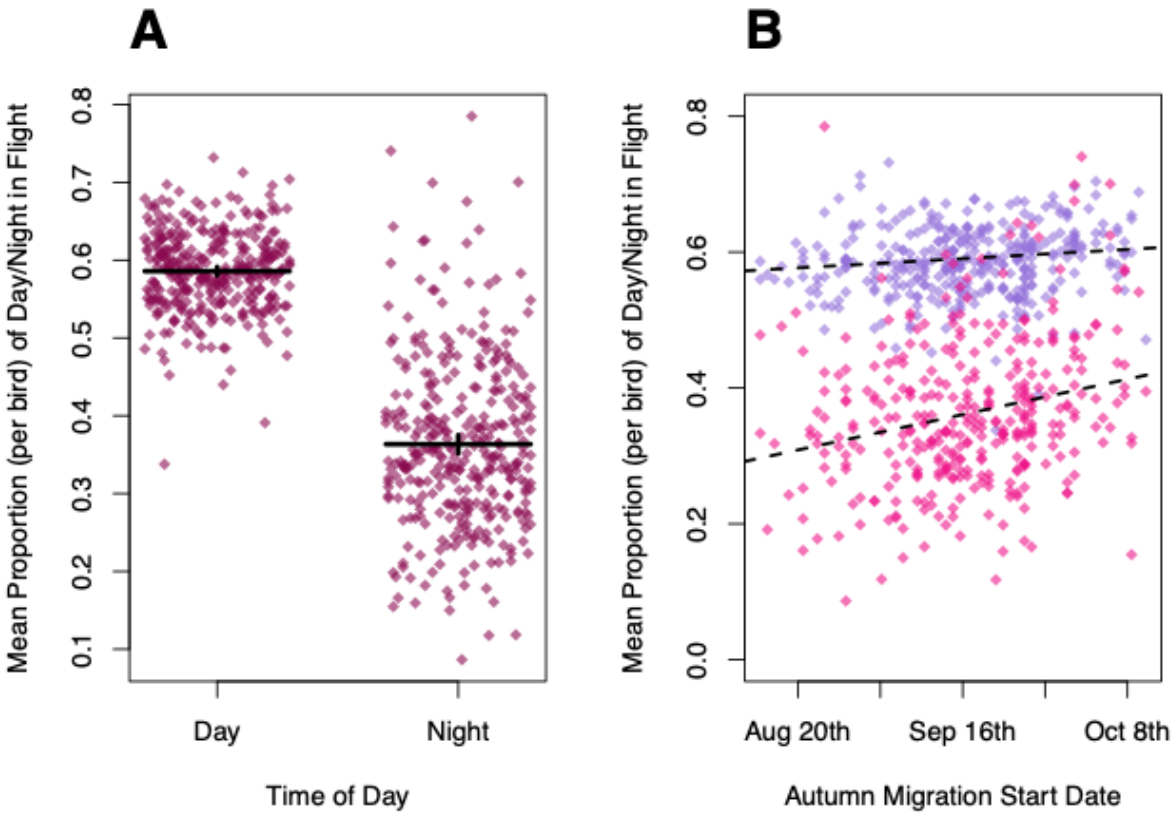


Figure 3. The number of hours spent in day and night flight during migration. **A)** Mean number of hours of flight per day and night plotted with horizontal 'jitter'. Solid black lines represent the population mean ± the 95% confidence interval. **B)** Mean hours of flight for day (purple) and night (pink) plotted against autumn migration start date. The regression lines are derived from our linear mixed-effects model (see Table 2). In both plots, each point represents the phenotype of a single bird.

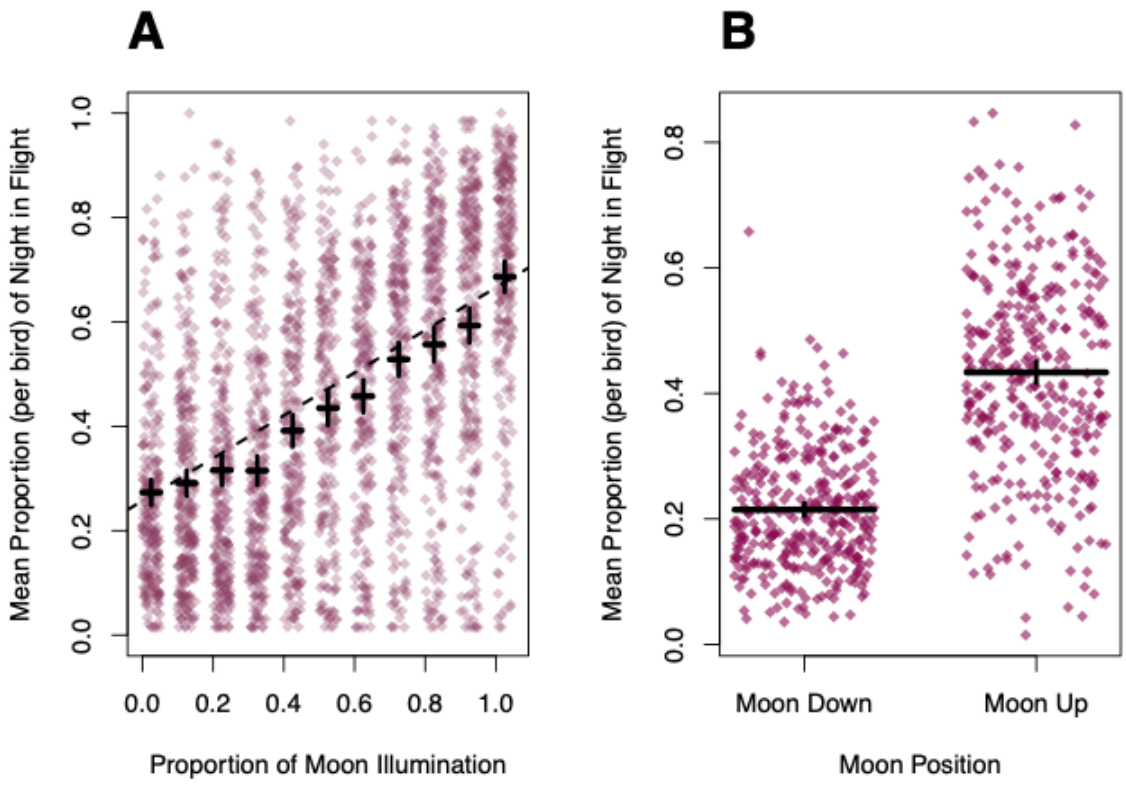


Figure 4. The effect of moonlight on the numbers of hours spent flying at night. **A)** The mean hours of night flight per proportion of moon illumination (0-1. The regression lines are derived from our linear mixed-effects model (see Table 2). **B)** The effect of moon position on the mean hours of night flight. Both plots are plotted with horizontal 'jitter' and black solid lines represent the overall mean for all birds ± the 95% confidence interval whilst each point represents the mean of a single bird

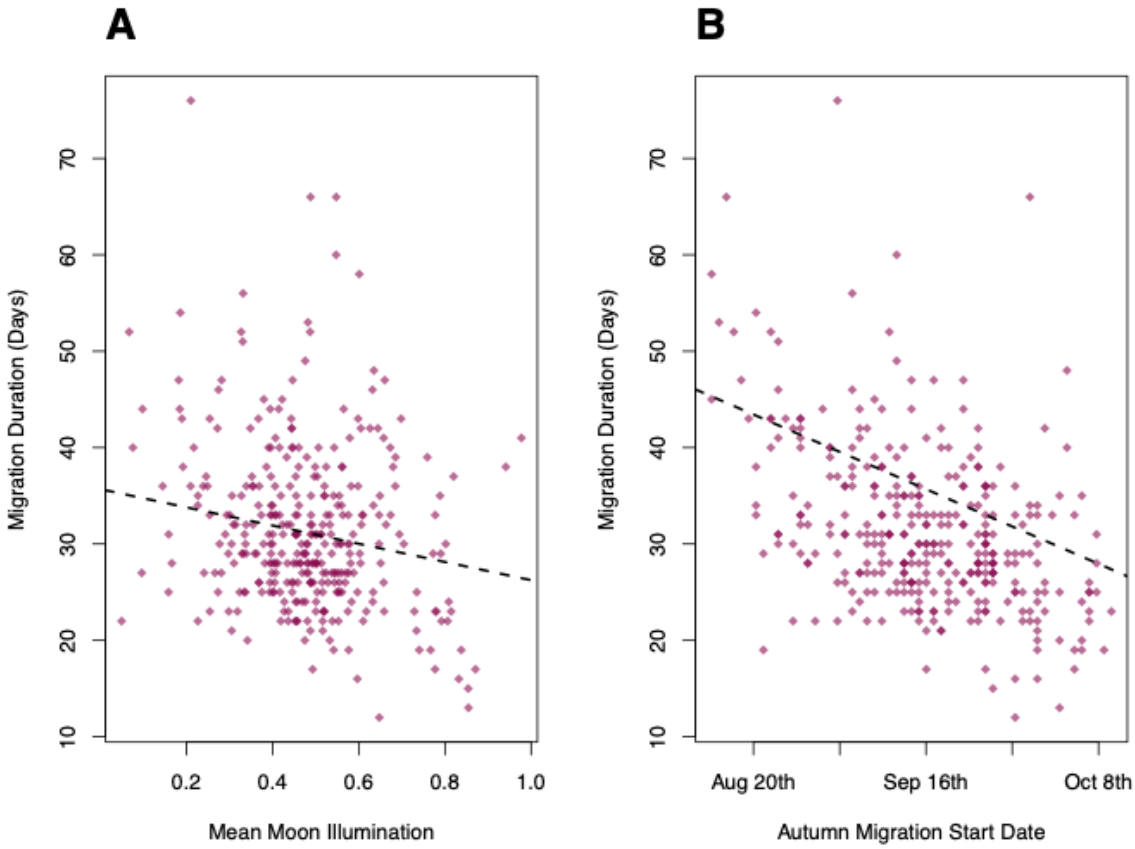


Figure 5. The effect of moon illumination on migratory phenology. **A)** Migratory duration plotted against mean moon illumination and **B)** Migration duration plotted against the migratory start date. In both plots the regression line is derived from our linear mixed-effects model (see Table 2), and each point represents the phenotype of a single bird.

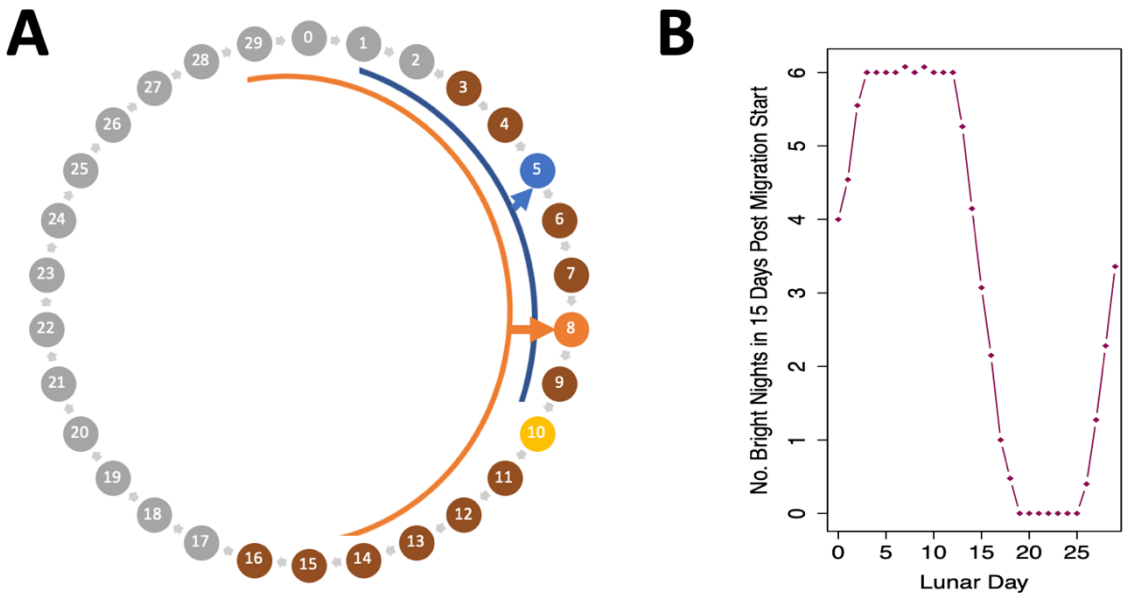


Figure 6. The effect of migration departure date on lunar timing. **A)** A graphical representation displaying variations in the circular mean lunar day of departure. The population mean lunar day of departure is highlighted in yellow, whilst the interquartile range is in brown (n=606). Early departing birds (n=60) are depicted in orange, with the circular mean shaded and a line representing the interquartile range. Late departing birds (n=64) are likewise illustrated in blue. **B)** A graph representing the number of nights where moon illumination is >=0.9 in the 15 days post each lunar day of the moon cycle. Lunar days starts at 0 with day 14 representing the full moon.

	Mean	Minimum	Maximum
Migration Start Date	September 14th ± 1.33 days	August 8th	November 11th
Migration End date	October 16th ± 1.23 days	September 11th	December 4th
Migration Duration	31.55 ± 0.93 days	12 days	76 days
Stopover number	4.62 ± 0.20	1	12
Total Stopover days	11.33± 0.60 days	1	39
Stopover length	2.59 ± 0.13 days	1 day	18 days
Time between stopovers	3.92 ± 0.20 days	1 day	24 days
Continuous flight	0.88 ± 0.02 hours	0.17 hours	20.33 hours
Lay date (n=89)	May 17th ±1.57 days	26th April	6th June

Table 1. Summary statistics of autumn migration parameters. For all parameters we present the mean (of individual means) ±95% confidence intervals and minimum and maximum values derived from 343 bird migrations (except in the case of lay date where n=89).

Response	No	Coefficient	Effect Size	Confidence Intervals	Chi-squared	p value
Proportion of Day/Night Spent Flying	1	*Intercept* **Night** **Departure date** **Interactive term**	0.590 -0.230 0.001 0.038	0.575, 0.606 -0.238, -0.222 0, 0.002 0.022, 0.054	- 2645.5 53.029 20.805	- < 0.0001*** < 0.0001*** < 0.0001***
Proportion of Night Spent Flying	2	*Intercept* **Moon** **Departure date** Interactive term	0.257 0.409 0.002 0.029	0.230, 0.283 0.387, 0.430 0, 0.005 -0.015, 0.072	- 1209.4 20.104 1.8512	- < 0.0001*** < 0.0001*** >0.05
Proportion of Night Spent Flying	3	*Intercept* **Moon up**	0.217 0.219	0.200, 0.233 0.206, 0.233	- 913.32	- < 0.0001***
Stopover Time (days)	4	*Intercept* **Departure date**	11.252 -0.234	10.353, 12.197 -0.333, -0.135	- 21.636	- < 0.0001***
Foraging at stopovers (proportion)	5	*Intercept* **Departure date**	0.583 -0.002	0.567, 0.598 -0.003, -0.001	- 14.4	- < 0.0001***
Migration duration (days)	6	*Intercept* **Mean moon** **Departure date** Interactive term	35.759 -9.408 -0.517 -3.177	32.164, 39.059 -14.681, -3.902 -0.936, -0.083 -12.907, 5.92	- 10.621 70.655 0.382	- 0.001 ** < 0.0001*** >0.05
Departure Date (days)	7	*Intercept* **Lay date**	5.566 0.566	0.900, 10.207 0.372, 0.749	- 27.354	- < 0.0001***

Table 2: A table representing all mixed-effects models present in this analysis (1-8). For each coefficient, confidence intervals and effect sizes were obtained through bootstrapping, whilst chi squared and p values were obtained through likelihood ratio tests. Significant predictors are highlighted in bold and significance levels indicated by the number of asterisks (< 0 '***', <0.001 '**', <0.01 '*'

Results

We identified 1,570 stopovers of varying lengths in 343 tracks, with stopovers being present in all tracks. The mean contiguous stopover length was 2.59 ± CI 0.13 days, with the longest stopover being 18 days. On average birds stopped for 11.33 ± 0.6 days over a migration. The mean migration start date was September 14th and the mean migration end date the 16th October. The mean migrating time between stopovers was 3.92 ± 0.2 days and the mean number of continuous hours of flight was 54 ± 1.2 minutes for all birds. However, birds were capable of flying much longer with the longest period of non-stop continuous flight recorded being 20.33 hours. Remarkably, one bird migrated from Wales to South America in just 12 days (table 1), implying a mean speed of 34.72 km h^{-1}.

We used Likelihood Ratio Tests and bootstrapped confidence intervals to evaluate the interactive, independent and random effects of models. For Skomer birds – where lay date data was available – a one-day increase in lay date increased migration departure significantly by 0.6 days (β= 0.57, 95%CI [0.37, 0.75], χ^2c =27.35, p< 0.0001; figure 1; model 7). The start date of autumn migration also reduced significantly the total number of stopover days observed on migration, with the number of stopover days decreasing by 0.23 for every 1 day increase in autumn migration date (β= -0.23, 95%CI [-0.333, -0.135], χ^2c =21.63, p< 0.0001; figure 2; model 4). As autumn migratory departure date got later, the daily proportion of time spent foraging at each stopover location decreased (β= -0.002, 95%CI [-0.003, -0.001], χ^2c =14.40, p< 0.0001; figure 2; model 5).

Birds flew for a significantly smaller proportion of the night than the day (β= -0.23, 95%CI [-0.24, -0.22], χ^2c =2645.5, p< 0.0001; figure 3). There was, additionally, a significant interaction between day/night and migration departure date on the proportion of flight per day/night (β= 0.04, 95%CI [0.02, 0.05], χ^2c =20.81, p< 0.0001; figure 3; model 1), meaning that birds leaving later on migration flew more at night. Both the proportion of moonlight (from 0-1 with 1 being a full moon) (β= 0.41, 95%CI [0.39, 0.43], χ^2c=1209.4, p< 0.0001; figure 4; model 2) and later migration departure (β= 0.002, 95%CI [0, 0.005], χ^2c =20.10, p< 0.0001; figure 4; model 2) significantly increased the proportion of hours of night flight during nights when birds were migrating. However, the interactive effect of moonlight and migration departure date was not statistically significant (β= 0.03, 95%CI [-0.02, 0.07], χ^2c =1.85, p>0.5; figure 4; model 2), suggesting that the effect of moonlight did not differ between early and late-migrating birds. Birds flew for a higher proportion of the night during the parts with moon illumination (β= 0.22, 95%CI [0.21, 0.23, χ^2c =913.32, p<0.0001; figure 4; model 3).

The time that migration to the Patagonian shelf took shortened as both mean moonlight illumination (β= -9.4,0 95%CI [-14.68, -3.9], χ^2c =10.62, p< 0.005; figure 5; model 6) and autumn migration departure date increased (β= -0.5, 95%CI [-0.9, -0.1], χ^2c =70.64, p< 0.0001; figure 5; model 6), with the interactive effect being non-significant (β= -3.18, 95% CI [-12.9, 5.92], χ^2c =0.38, p=0.5; figure 5; model 6). This means that moonlit nights and late departure date additively increased the amount of time spent flying at night, with the effect of moonlight not differing in birds migrating at different times.

In randomisations we tested whether later or earlier migrating birds departed on a different lunar day of the moon cycle. We used two-sample Watson tests to compare the circular mean lunar days between early/late departing birds against resampled data with equivalent sample sizes. For late departing birds, 96% of the 10,000 iterations resulted in significant differences between the mean circular direction of late birds and the resampled data (n=64 each time). In contrast, only 1.24% of iterations yielded significant differences between early birds and the resampled data (n=60 each time). This finding indicates that the circular mean lunar day of departure for late birds was consistently different to that of the general population whilst earlier birds did not show significant differences. The mean lunar day of departure for late birds was 5 days earlier than the general population (Figure 6). Consequently, it appears that birds departing later on migration tend to initiate their journey on an earlier day within the lunar cycle.

Discussion

Through the identification of breeding and migratory phenology, stopovers and at sea-behaviour from geolocator data, we investigated how Manx shearwaters finetune their southbound migration in the face of declining conditions in the northern hemisphere and improving conditions in the wintering grounds. Whilst migration in Manx shearwaters occurs close to the autumn equinox, which causes uninterpretable latitudinal estimates from geolocation, we were anyhow able to create interpretable migratory phenologies using longitude and immersion to classify behaviour (Lisovski and Hahn, 2012). We accounted for the structure of the data comprising repeated measures of individuals from different colonies across years by including them as random effects in all models. When visually assessed, trends remained both within individual years and colonies. Therefore, the results of this analysis appear to be primarily driven by individual differences in phenology.

In a seabird with substantial individual variation in lay dates (Storey and Brooke, 1991), we have found a phenological link between lay date and autumn departure date; with earlier layers departing earlier for migration (figure 1). While this is perhaps unsurprising, we found that lay-date predicted a sequence of knock-on phenological correlates with birds laying later going on to migrate at a later date, but with fewer, shorter stop-overs and a quicker migration suggesting that there are substantial parts of the shearwaters annual cycle in which there is little flexibility to make up lost time, but that migration duration may indeed respond flexibly to late breeding. This is consistent with the finding that late departing Cory's shearwaters took a faster migration (Dias, Granadeiro and Catry, 2012). By exploring at-sea behaviour using the immersion logging capacity of geolocators, we found that phenological variation among individuals was coupled with behaviour at stop-over sites, with earlier departing birds foraging for more of the day. One explanation for this could be that late birds increase their fuel loading prior to migration so as to fly longer migratory stints with minimal stopovers, whilst early birds refuel along the way (Alerstam, 1991; Klaassen, 1996). However, as foraging opportunities for later departing birds will be seasonally declining at the breeding site, this seems unlikely. Seasonal cycles in global productivity are largely affected by light, with productivity generally peaking in the spring and summer. (Yoda *et al.*, 1993; Mao *et al.*, 2019). As Manx shearwaters are trans-equatorial migrants, they are able to exploit summer conditions in both the northern and southern hemisphere. For later migrating birds, stopover sites in the northern hemisphere may be less profitable than the over-wintering grounds and they may therefore head across such sites more rapidly. Meanwhile, earlier departing birds, once released

from chick provisioning are able to exploit foraging opportunities along the way. With the maximum recorded stopover length reaching 18 days, we suggest that stopover sites for earlier migrating birds may not simply be for refuelling purposes, but may also represent the best seasonal foraging sites available at that time. Birds that lay later may therefore miss the opportunity to exploit stopover sites that provide good foraging during the intermediate seasons.

Possibly to facilitate migratory catch-up, later-laying birds spent more time in flight during migration stints and flew more at night (figure 3). To our knowledge, migratory night flight has not previously been documented in Manx shearwaters. Whilst a previous analysis of migratory movements did not find increased activity in Manx shearwaters via moon illumination, here we provide compelling evidence via a significantly larger dataset for the exploitation of moonlight (Bonnet-Lebrun *et al.*, 2021; figure 4). It appears that birds are using moonlight for migratory flight as opposed to foraging, with foraging activity being daylight restricted, and migration duration shortening when birds experience higher levels of moonlight during migratory stints (figure 5). Birds could be using the moon for navigation purposes, although its use as a compass is considered unlikely (Zolotareva and Chernetsov, 2021). It is more likely that birds are using the increased illumination to facilitate the use of visual cues related to flight control (Yamamoto *et al.*, 2008).

We were interested in understanding whether birds timed their migration to synchronise migratory stints with favourable moon conditions. Evidence for timing phenology with lunar cycles has been documented in many avian species (Lian-xian *et al.*, 2007; Kronfeld-Schor *et al.*, 2013; Norevik *et al.*, 2019). In seabirds arrival at the colony has been seen to correlate with lunar phase (Chapin and Wing, 1959; Pinet *et al.*, 2011). Here we found that later departing Manx shearwaters left at an earlier day in the lunar cycle (where moon illumination is low and the moon does not rise for a long period at night) than birds departing earlier. Departing earlier in the lunar cycle will provide a greater number of moonlit nights in the subsequent 15 days (figure 6). We suggest therefore that later departing birds may be timing their departure so as to gain more nights of higher moon illumination, allowing for increased night flight, and a potentially more rapid migration. Randomisation analysis revealed that early birds were not significantly more likely to depart at a different day in the lunar cycle than birds departing later (random birds). As earlier departing birds take longer, and fly less at night, they may be less likely than the general population to time their migration with favourable lunar conditions. Mixed-effects models revealed non-significant interactions between departure date and moonlight on the amount of night flight (table 2). Therefore, birds are seemingly unable to

increase their night flight per unit moonlight, yet later leaving birds nonetheless fly more at night. Our randomisation suggests that this is because migratory departure is timed differently in later migrating birds, and as such it appears that changes in timing of migration relative to the moon window facilitate migratory catch-up. Therefore, late departing birds can migrate more at night, and arrive more rapidly at the over-wintering grounds.

Here we demonstrate how long-distance migratory behaviour varies with the onset of breeding, confirming that variation in lay date affects the date of migration departure. Despite leaving later on migration, late-laying birds are able to catch up via flying more at night and stopping over less to forage. Previously undetected, we observe the exploitation of moonlight in Manx shearwaters, with birds flying more on moonlit nights. Supporting this, birds departing later on migration appear to time their migration with the lunar cycle to achieve more moonlit nights. To our knowledge, this has not previously been demonstrated in a seabird. Whilst our study shows the importance of autumn departure date in determining behaviour, it highlights the value of understanding determinants of phenology in long-distant migrants.

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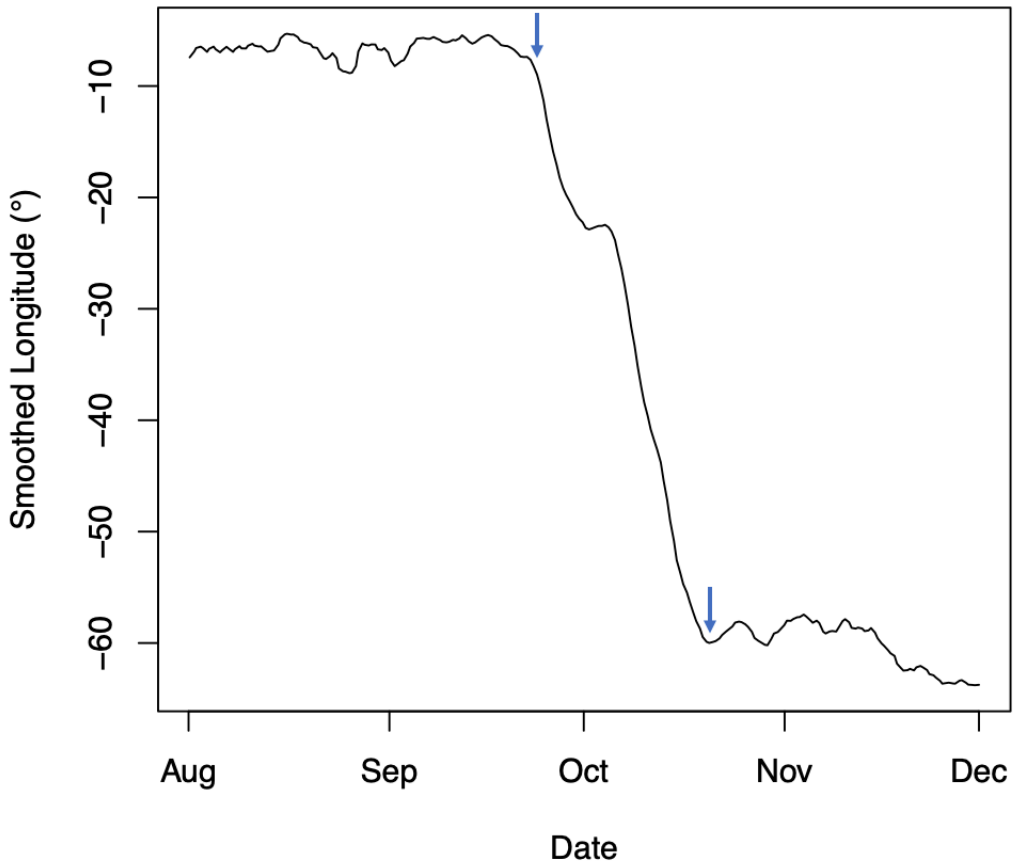
Supplementary Materials



Supplementary 1: Determination of migration start and end dates using smoothed longitude. Longitude was smoothed using a rolling 3 day mean due to associated geolocator error. Arrows indicate visually assigned migration start and end dates.

Photoperiod length imposes an ecological constraint on chick provisioning behaviour in a high latitude seabird

4

With contributions from Natasha Gillies, Joe Wynn, Oliver Padget, Greg Morgan, Jóhannis Danielsen, Annette Fayet, Sarah Bond, Martyna Syposz, Akiko Shoji, Lou Maurice, Tim Guilford

Abstract

Despite many animal behaviours being either diurnal or nocturnal, photoperiod is rarely considered as an ecological constraint. Animals that breed at high latitudes are subject to seasonal photoperiod variation that may limit light-dependent behaviours. The Manx Shearwater, *Puffinus puffinus*, is a visual hunter that forages only during daylight yet returns during darkness to the breeding colony to feed its chick when predation risk is lower. We investigated whether seasonal variation in photoperiod constrained chick provisioning and predator avoidance behaviour. Using a 4-year geolocator dataset of shearwaters at various breeding latitudes (51.7 – 62.0 degrees), we found that provisioning adults foraged for more hours and chicks gained more mass at longer daylengths, with this effect being strongest when chicks were young. At longer daylengths adults additionally returned more frequently to feed their chick, even when the chicks were older and visitation frequency generally decreased. We suggest that an increase in the number of daylight hours for foraging may allow provisioning adults to take shorter duration trips. Whilst these results indicate advantages to rearing chicks during longer daylengths, favouring birds that lay earlier or at higher latitudes, longer daylengths come at the cost of shorter nights. We found that colony visit length decreased during shorter nights and adults were also less able to time their colony visit with moonset. Therefore, although foraging opportunities appear to increase with daylength, there may be an increased risk of predation for adults provisioning during shorter nights.

Introduction

High latitude animals experience great variation in photoperiod. Shifts in photoperiod can be used as a cue to migrate, commence reproductive behaviour and align breeding efforts with seasonal abundance (Dawson *et al.*, 2001; Gordo, 2007). Whilst seasonality is understood to affect behaviour via shifts in food availability and temperature, little research has sought to investigate light itself as an ecological constraint (Hill *et al.*, 2004). Light, both its absence and presence, may be a limiting factor for diurnal or nocturnal behaviours, respectively. While anthropogenic light sources have been linked to changes in nocturnal behaviours such as courtship and predator avoidance (Botha, Jones and Hopkins, 2017; Czaczkes *et al.*, 2018) how animals respond to natural seasonal variations in photoperiod through planetary and lunar cycles is less frequently examined (Hill *et al.*, 2003).

In avian species that have substantial variation in the onset of breeding, it is generally found that earlier laying birds have a higher breeding success (Brooke, 1978; Lambrechts *et al.*, 1997; Schaper *et al.*, 2012; Winkler *et al.*, 2020). This is largely attributed to less favourable environments and lower resource availability (of both nesting sites and food) later in the season (Nussey *et al.*, 2005; Descamps *et al.*, 2011). However, seasonal variation in photoperiod length may also constrain a breeding birds' ability to provision for their offspring. Hunting in visual predators is limited to hours that have sufficient light in which to identify and pursue prey (Blachowiak-Samolyk *et al.*, 2006; Benoit *et al.*, 2010). Therefore, as days start to shorten in late summer, visual predators at high latitudes have reduced time in which to forage (Fort *et al.*, 2013; Boom *et al.*, 2023). Light may therefore especially constrain provisioning behaviour in birds with extended chick development periods such as procellariform seabirds (Bolton, 1995; Weimerskirch and Lys, 2000).

The Manx Shearwater is a procellariform seabird that breeds at high latitudes, where time from dawn to dusk can last up to 20 hours in mid-summer (Storey and Brooke, 1991). Chick provisioning prior to pre-fledgling abandonment for this species takes 60 days on average, covering the months that follow the summer solstice. They are therefore subject to great variation in day and night lengths, yet their breeding behaviours are light constrained. As visual hunters, foraging for chick provisioning is restricted entirely to hours that have sufficient

daylight (Shoji *et al.*, 2016; Darby *et al.*, 2022). Then, in order to return to the colony to feed their chick, the shearwaters must wait until darkness to avoid predation (Moegeuot and Bretagnolle, 2000). Shearwaters have been shown to avoid visiting the colony under moonlit conditions, returning when the moon is below the horizon (Riou and Hamer, 2008). However, night length may constrain such anti-predation behaviour by limiting the hours in which a bird can return to feed its chick without substantial risk.

Due to individual variation in phenology, chicks hatch during varying photoperiods. Therefore., earlier breeders have more daylight hours in which to forage, yet shorter nights in which to return to the colony to feed the chick. This represents a potential trade-off between the maximisation of foraging vs the minimisation of predation risk. Additionally, the frequency and size of food required for provisioning is thought to vary with chick age (Thompson, 1987; Storey and Brooke, 1991). As chicks develop, food requirements may increase (Bolton, 1995; Schekkerman *et al.*, 2003). Therefore, photoperiod variation may affect adult behaviour to varying extents dependent on the nutritional requirements of their chick. Here we investigated how light availability constrains the trade-off between investment and predation avoidance in Manx shearwaters. This study makes use of a 4-year geolocator dataset from shearwaters breeding at varying latitudes to assess how photoperiod and lunar variation affects chick provisioning behaviour in a high latitude animal.

Methods

Fieldwork

To determine chick provisioning behaviour, fieldwork was conducted from 2016 to 2021 at 5 colonies; Rum (57.01, -6.33); Skomer (51.74, -5.29); Ramsey (51.74, 5.29); Copeland (54.68, -5.53) and Nólsoy (Faroes) (61.98, -6.65). From 2017-2020, 212 geolocators were deployed to record immersion data and of these 163 were successfully retrieved. Device models included the C65 and C65 Super from migratetech, both weighing 1g, being ~0.25 % of the average shearwater body mass (~400 g for an adult shearwater). Devices were set to record immersion events every 6 seconds to create a summary score of immersion activity over 5 minutes that ranged from 0 (completely dry) to 50 (completely submerged). Geolocators were attached to a custom-built plastic ring, which was fitted on the tarsus. The devices were secured with 2 PanTy cable ties and a small amount of super glue. On Skomer island only, from 2017 to 2019, chicks were weighed to obtain the daily mass change. Data were not available for 2020 because of restrictions associated with the covid-19 virus. Whilst chick mass data were only available for one breeding colony (Skomer Island, Wales: 51.74, -5.29), photoperiod

substantially varied over the season from 12 to 18 hours. Handling time was between 5-10 minutes for the device deployment of adult birds and 1-2 minutes per day for each chick weighing.

Data processing

All data processing was carried out in RStudio version 4.0.2 (R Core Team, 2021). Chick hatch date was estimated by identifying known changes in breeding behaviour in the geolocator immersion data. Aside from a short brood guarding period, once the chicks are hatched the shearwaters typically spend most of their time at sea, returning to the colony at night. Therefore, the last day of incubation for each individual was identified visually (see supplementary 1 for an example) and used to provide an estimate of chick hatch date. Immersion data were then filtered to include data only from the estimated hatch date, leaving 71 tracks for analysis. In order to identify colony visitation during chick provisioning, nights were first separated using the suncalc package in R to identify dawn and dusk at each colony, defined as the start and end of nautical twilight (Thieurmel and Elmarhraoui, 2022). A normal probabilistic mixture model was then implemented using the mixtools package on the number of immersion bins per night in which immersion was present (Benaglia *et al.*, 2009). This identified two discrete distributions in the immersion data, with a peak at both low and high immersion values. Nights that had a greater probability of belonging to the dryer peak were assigned as those where a colony visit had occurred (figure 2B). The length of the longest continuous bout of dry data for each of these nights was used to estimate colony visit length. To assess whether visits coincided with moonlit conditions, the time of moon rise and set were obtained using the suncalc package and moon illumination levels from the lunar package (Lazaridis, 2022). Chick mass changes were taken every 3 days as opposed to daily measurements, so as to reduce the effect of daily mass fluctuations based on the time of weighing and measurement error. We filtered chick age to include data from 0 to 60 days (the average length of time in which adults are provisioning for their chicks prior to pre-fledging abandonment). Foraging was allocated to 5 minute bins that had an intermediate immersion score (between 0 and 50), a method which has been validated to successfully predict diving activity following co-deployment of geolocators with dive loggers (Dean *et al.*, 2013; Freeman *et al.*, 2013; Shoji *et al.*, 2016).

Statistical Analysis

We implemented mixed effects models using the lme4 package in R (Bates *et al.*, 2015). To examine how adult provisioning behaviour varied with chick age and day length, we fitted the interactive effect of both on (1) the daily mass gain of chicks (g), (2) the daily number of hours spent foraging using linear mixed effects models, and (3) the likelihood of colony visitation per night using a binomial generalised LMM. To examine whether colony visit duration was influenced by night length and chick age, we fitted an LMM to investigate changes in colony visit length. Given a bird had visited the colony, we were interested in understanding whether birds were more able to time their visit such that the moon was below the horizon on longer nights. We therefore fitted a binomial GLMM to assess whether visits were more likely to occur in moonlit conditions during colony visits as a function of increasing night length. Individual identity and colony (where multiple were used) were included as random effects in all models. Significance was assessed using Likelihood Ratio Tests, whilst the arm package was used to bootstrap 95% confidence intervals and effect sizes through 1000 simulations of model effects (Gelman and Hill, 2006).

Figures

Response	No	Coefficient	Effect Size	Confidence Intervals	χ^2	p value
Chick mass gain (g)	1	*Intercept* **Day Length** **Chick Age** **Interactive term**	-64.579 5.580 2.490 -0.143	-130.196, 3.636 1.737, 9.274 1.278, 3.687 -0.215, -0.073	- 7.999 15.183 14.768	- < 0.01** < 0.0001*** < 0.001***
Daily Time Spent Foraging (hours)	2	*Intercept* **Day Length** **Chick Age** **Interactive term**	-1.826 0.496 0.090 -0.006	-4.787, 1.027 0.343, 0.654 0.034, 0.145 -0.009, -0.002	- 40.227 9.508 10.512	- < 0.0001*** < 0.01** < 0.001***
Colony visitation (Visit Absent/ Present)	3	*Intercept* **Day Length** **Chick Age** **Interactive term**	-8.412 0.493 -0.081 0.005	-10.458, -6.324 0.380, 0.602 -0.123, -0.042 0.003, 0.007	- 67.416 4.248 14.898	- < 0.0001*** < 0.0001*** < 0.0001***
Colony Visit Length (days)	4	*Intercept* **Night Length** **Chick Age** **Interactive term**	-3.136 0.955 0.066 -0.010	-4.070, -2.246 0.808, 1.103 0.041, 0.093 -0.014, -0.007	- 109.12 13.208 31.569	- < 0.0001*** < 0.0001*** < 0.0001***
Visitation timing (during moon/not during moon)	5	*Intercept* **Night Length** Chick Age Interactive term	-1.480 0.386 -0.023 0.001	-3.183, 0.274 0.116, 0.659 -0.087, 0.039 -0.007, 0.010	- 11.515 4.5135 0.136	- <0.01 ** >0.05 >0.05

Table 1. Effect sizes and statistical values for all mixed effects models in the analysis (1-5). Coefficient estimates and 95% confidence intervals were obtained through bootstrapping, whilst χ^2 and p values were obtained through likelihood ratio tests. Significant predictors are highlighted in bold and significance levels are indicated by the number of asterisks (< 0 '***', <0.001 '**', <0.01 '*').

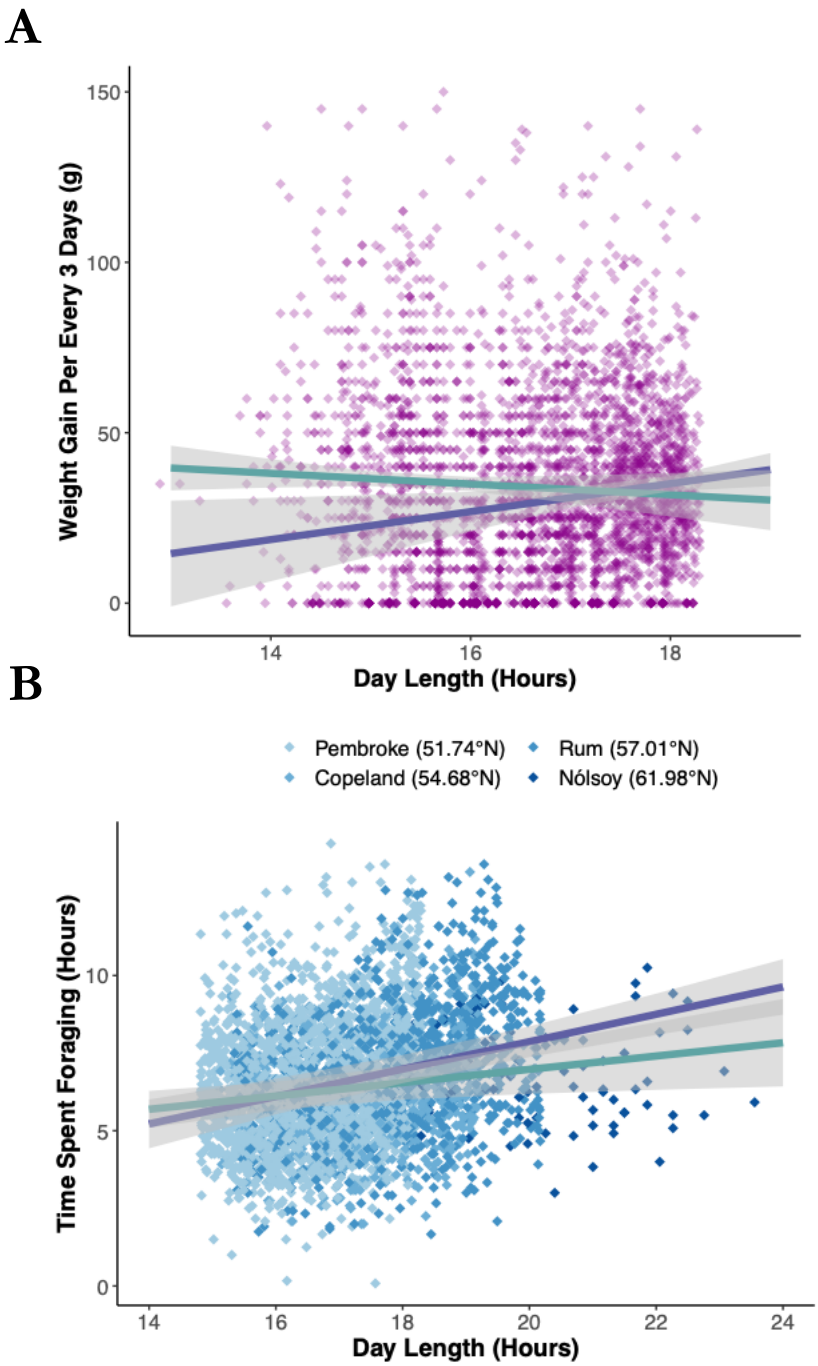


Figure 1. The effect of day length on chick provisioning behaviour. **A)** The daily weight gain per every 3 days of chicks (n=197) as a function of day length using measurements taken from Skomer island (51.74°N, -5.29°E). **B)** The number of hours spent foraging per day as a function of day length (n=70). Each point represents an individual birds' behaviour per each day length over the chick provisioning period. Points are coloured to display latitudinal variation in day length with the darkest shades of blue representing the highest breeding latitudes. Lines represent predicted trends for chicks aged 10 (purple) and chicks aged 50 (green) derived from linear mixed effects model.

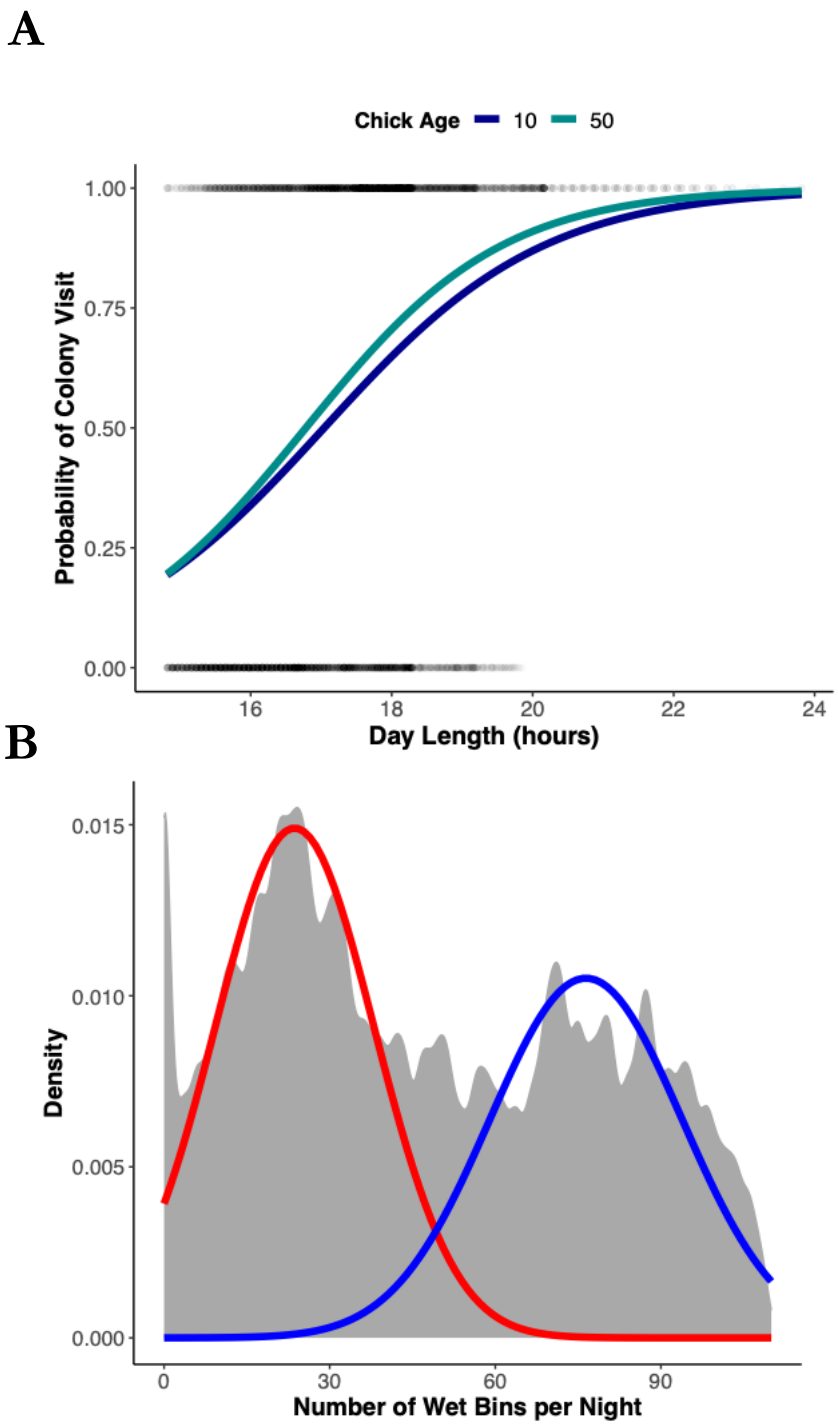


Figure 2. The effect of day length on adult colony visitation behaviour. **A)** The probability of a colony visit occurring as a function of day length. The lines represent predicted trends for chicks aged 10 (purple) and chicks aged 50 (green) defined from the binomial mixed effects model (model 3) and each point represents an individual bird night (n=71). **B)** A density plot representing the mixture model in which colony visits were defined for chick-rearing adults, where the red line represents the drier peak corresponding to a colony visit. The number of 5-minute bins where immersion was recorded are summed per individual bird night.

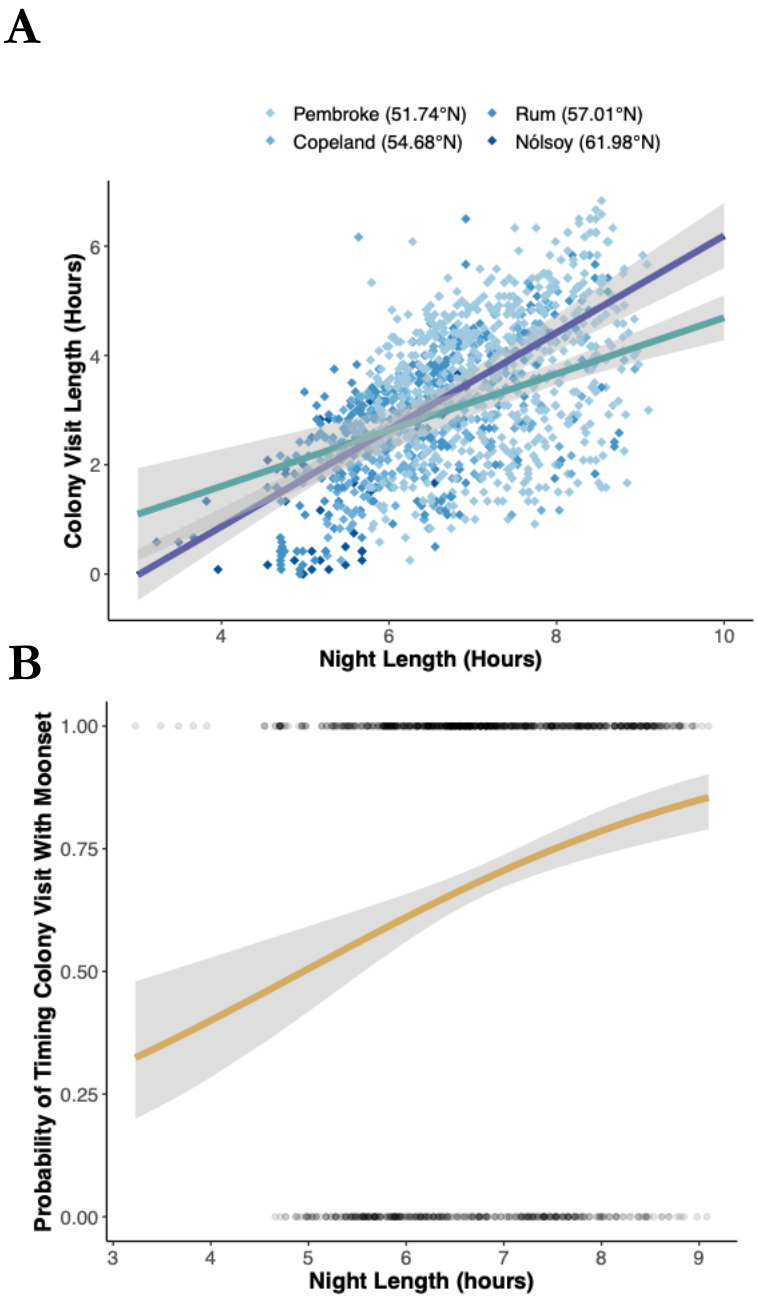


Figure 3. The effect of night length on colony visitation behaviour. **A)** Colony visit length (for visits <1 day) is plotted against night length (n=71). The lines represent predicted trends for chicks aged 10 (purple) and chicks aged 50 (green) derived from the linear mixed effects model. Each point represents an individual birds' behaviour per each night's length over the chick provisioning period. Points are coloured to display latitudinal variation in night length with the darkest shades of blue representing the highest breeding latitudes. **B)** The probability of a colony visit occurring during moonset as a function of night length. The line represents that of the binomial mixed effects model for chicks of all ages (model 5). All colony visits that occurred whilst the moon was up (n= 378) or that occurred once the moon had set (n= 820) are plotted with vertical against night length for 71 birds.

Results

We found that the interaction of chick age and daylight hours had a significant effect on both the mass gain of chicks (β= -0.14, 95%CI [-0.22, -0.07], χ^2c = 14.77, p<0.0001; figure 1) and the number of hours adults spent foraging (β= -0.006, 95%CI [-0.009, -0.002], χ^2c = 10.51, p< 0.0001; figure 1). As chicks got older they gained more mass (per every 3 days) (β= 2.49, 95%CI [1.28, 3.69]p< 0.0001, figure 1), and their provisioning parents foraged for more hours per day (β= 0.09, 95%CI [0.03, 0.14], p<0.01; figure 1). However, on longer days, chicks had a higher mass gain (β= 5.58, 95%CI [1.74, 9.27], p<0.01; figure 1) and adults foraged for more hours per day (β= 0.50, 95%CI [0.34, 0.65], p<0.0001; figure 1). The interaction of chick age and day length also had a significant effect on colony visitation (β= 0.005, 95%CI [0.003, 0.007], χ^2c = 14.90, p<0.0001; figure 2). Adults with older chicks visited the colony on less nights (β= -0.08, 95%CI [-0.12, -0.04], p<0.0001; figure 2). However, when day lengths were long, provisioning adults were more likely to visit the colony (β= 0.50, 95%CI [0.38, 0.62], p<0.0001; figure 2).

The interaction of night length and chick age had a significant effect on colony visit length (β= -0.01, 95%CI [-0.01, -0.007], χ^2c = 31.57, p< 0.0001; figure 3) with visits extending in length with chick age (β= 0.07, 95%CI [0.04, 0.09], p< 0.0001; figure 3). However, as night length increased these age effects were less apparent, and adults that were provisioning for younger chicks had colony visits of longer duration (β= 0.96, 95%CI [0.80, 1.10], p< 0.0001; figure 3). On long nights, adults were more likely to visit the colony when the moon was set versus on short nights (β= 0.39, 95%CI [0.12, 0.66], χ^2c = 11.52, p< 0.01; figure 3). Neither chick age (β= -0.02, 95%CI [-0.09, 0.04], χ^2c = 4.51, p>0.05; figure 3) nor the interactive effect of chick age and night length (β= 0.001, 95%CI[-0.07, 0.01], χ^2c = 0.14, p>0.05; figure 3) had a significant effect on the likelihood of visiting the colony when the moon was up or down. Therefore, it appears the likelihood of visitation during moonlit conditions is driven primarily by night length rather than provisioning requirements that are dependent on chick age.

Discussion

Here we show how seasonal photoperiod variation can restrict or promote light dependent breeding behaviours. We found that long days were associated with increases in adult foraging effort, colony visitation and chick mass gain (per every 3 days; figures 1-2). We propose that long days allow more time for adults to gather resources for their offspring, meaning they could return on more nights to feed their chick and in doing so provide their chicks with a higher quantity of food per colony visit. Chick provisioning behaviour therefore appears to be promoted by increased light availability. However, whilst foraging activity is restricted to daylight hours, food delivery must wait until darkness to avoid predation (Riou and Hamer, 2008). When days are long, nights are short. Variation in seasonal photoperiod therefore evoke trade-offs between foraging and feeding the chick without substantial predation risk.

When nights were shorter, adults were more likely to come in during moonlit conditions, suggesting that adults were unable to time their visit for when the moon is set (figure 3). This suggests that birds may be less able to avoid predation risk during shorter nights, forcing birds to choose to trade off this risk against the necessity to feed the chick. It follows that shearwaters breeding earlier in the season may have higher initial predation risk, given that nights will be shorter when chicks hatch. This effect will also be exacerbated at higher latitudes, where nights are both lighter, and considerably shorter. The known breeding range of Manx shearwaters does not extend past southern Iceland, north of which there is 24 hours of daylight during midsummer. Despite our finding that the longer day lengths associated with high latitudes can benefit chick provisioning adults by allowing more time for resource gathering, it is likely that shearwaters cannot breed further northwards without the risk of predation becoming too high (Storey and Brooke, 1991).

We additionally found colony visit length to be significantly affected by night length, with adults increasing their visit duration when nights were longer (figure 3). Birds visiting the colony on shorter nights have fewer hours of darkness to enter and exit the colony without substantial risk from predation. However, this does not explain why birds spend longer at the colony when there are more hours of darkness available. There is likely some fitness benefit to spending time at the breeding site, such as having increased time for nest defence and maintenance (Werner, Paiva and Ramos, 2014). Resting on land may be less energetically expensive than resting at sea due to better thermoregulation (Tremblay *et al.*, 2022). Additionally, as we found that colony visit length also increased with chick age, having more

time to feed the chick may allow, or be a consequence of, larger quantities of feed to be delivered (Storey and Brooke, 1991).

Chick age affected adult provisioning behaviour in numerous ways. As chicks grew older, chick mass increased at a greater rate and provisioning adults foraged for more hours per day, even where day lengths were shorter (figure 1). As the chicks aged they required an increased food quantity, a phenomenon which has been observed in multiple seabird species (Bolton, 1995; Weimerskirch and Lys, 2000). Despite this, adults visited the colony less frequently as their chick aged. However, adults provisioning for older chicks were more likely to return to the colony when day lengths were longer. We suggest that an increase in the light available for foraging may allow provisioning adults to take shorter duration trips at later chick stages (figure 1). The ageing of chicks is correlated with both the decline of seasonal food abundance, and shortening day lengths. It is therefore difficult to disentangle these correlated effects from one another. However, given there is substantial variation in phenology between shearwater individuals, in this analysis we were able to draw some separation between the effects of chick age and photoperiod.

Whilst it is difficult to separate the effects of early season abundance from the effect of light itself as a constraint, this analysis provides evidence to suggest that foraging time, colony visitation and chick weights increase with the number of available daylight hours. It is therefore likely that photoperiod length has an additive seasonal effect in determining the frequency and size of delivered food, potentially favouring earlier breeders and birds at higher latitudes that experience longer day lengths. This increase in foraging opportunities with longer days comes at the cost of shorter nights, leading to a reduction in anti-predation behaviour such as moonlight avoidance. We suggest that such trade-offs may determine phenology and breeding distributions in high latitude animals. Seabird populations are thought to lay later at higher latitudes, to time chick provisioning with peak seasonal abundance (Burr *et al.*, 2016). Whilst this study was unable to investigate latitudinal differences in phenology, we suggest that seasonal variation in photoperiod could also play a role in defining lay dates for nocturnally active animals such as shearwaters.

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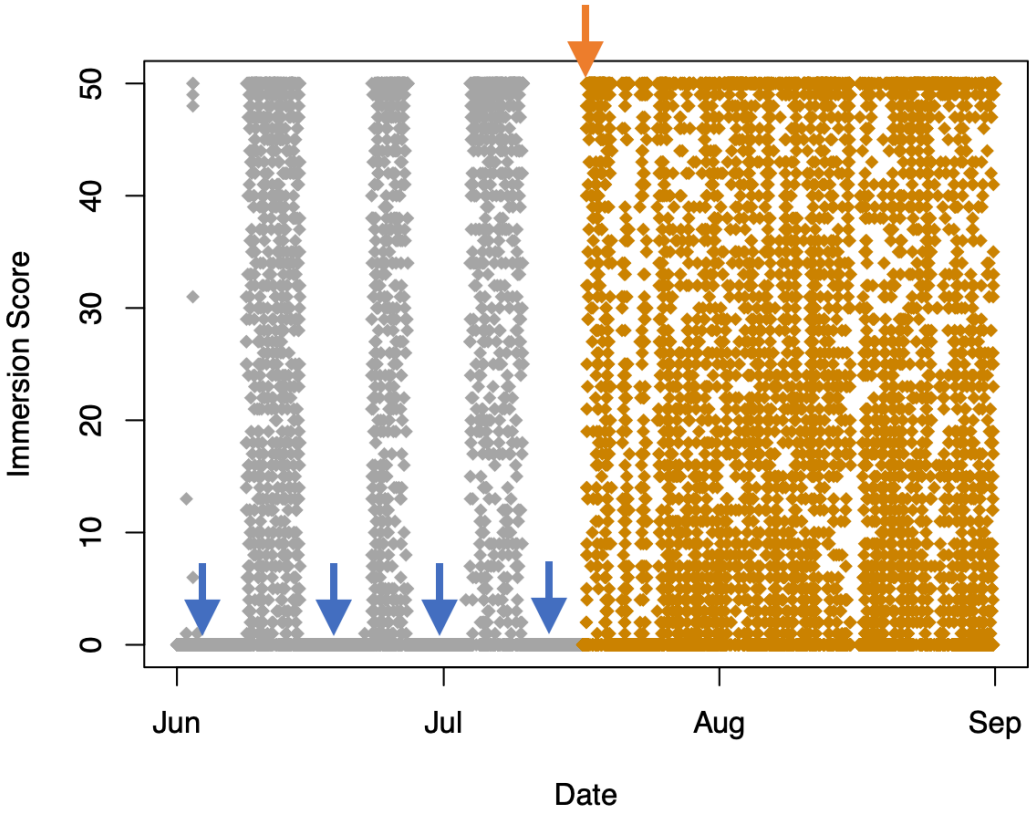
Supplementary Materials



Supplementary 1. A plot representing the visual identification of the start of chick provisioning using immersion scores from the GLS loggers. Immersion scores represent the total immersion over a 5-minute period and range from 0 (completely dry) to 50 (completely immersed). Grey points represent visually identified incubatory behaviour, with blue arrows pointing to likely incubatory stints on the egg, marked by long dry continuous periods of several days. Following the last incubatory stint, the points in orange represent those during chick rearing. These are characterised by a lack of distinctive dry periods, and the device remaining immersed as the bird forages at sea. The orange arrow marks the date allocated for the start of chick provisioning that was therefore used to estimate chick age.

Intra-seasonal sex differences in foraging behaviour and novel description of Manx Shearwater *Puffinus puffinus* diet using DNA metabarcoding

5

With contributions from Gemma Clucas, Lewis Fisher-Reeves, Joe Morford, Oliver Padget, Joe Wynn, Patrick Lewin, Sarah Bond, Paris Jaggers, Tim Guilford

Abstract

Sex differences in foraging behaviour can arise in monomorphic species when reproductive roles differ. In a procellariform seabird, *Puffinus puffinus* the Manx shearwater- we compare foraging between pre- and post-laying periods using a combination of biotelemetry and DNA metabarcoding for diet. Prior to laying, sex roles are thought to differ when breeding females must build the egg whilst males are engaged in nest defence. We found that pre-laying females took longer, more distant at-sea trips, whilst males visited the colony more frequently. These differences did not persist post-laying, where reproductive roles became more equivalent between sexes. Foraging behaviour differed between sexes, with both an increase in diving effort and shallower dive depths observed in males. We hypothesise that male colony visitation during pre-laying may constrain male foraging to sites closer to the colony and these may be of poorer quality to those reached by females that are not constrained by colony attendance. We additionally found increased male colony visitation restricted evening foraging opportunities, most likely due to birds commuting to the breeding site for nocturnal visits. We examined prey during the between pre- and post-laying periods. While we were unable to quantify differences between sexes in diet, the first DNA metabarcoding analysis of diet for this species nonetheless identified six species of fish, including both sandeel and rockling. Here we show how foraging can be constrained by differing behaviour between sexes at specific life history stages and suggest that understanding this variation is of fundamental biological relevance and conservation interest.

Introduction

Pronounced sex differences in foraging behaviour are thought to occur predominantly in dimorphic animal species (González-Solís, Croxall and Wood, 2000; Shaffer, Weimerskirch and Costa, 2001). In species where notable dimorphism is present, these differences can be attributed to contrasting physiological capabilities, energetic requirements and competitive abilities (Weimerskirch *et al.*, 1997; Bearhop *et al.*, 2006; Catry, Phillips and Croxall, 2006). In cases where dimorphism is minimal, the drivers of foraging differences are less clear. Seabirds provide a study system in which to better understand this phenomenon; as although they are largely monomorphic, sex differences in foraging behaviour have nonetheless been reported for a number of species (Lewis *et al.*, 2002; Pinet *et al.*, 2012; Bennison *et al.*, 2022). One hypothesised explanation is that during certain breeding stages, reproductive roles differ causing variation in foraging requirements and constraints between sexes. For example, male common guillemots undertake a continued role in post-fledgling feeding; constraining which areas they can exploit and increasing foraging effort (Burke, Montevecchi and Regular, 2015). Meanwhile, females have a more active role in chick provisioning leading to females diving more than males in this period (Thaxter *et al.*, 2009). Understanding differences that arise from sex-specific reproductive behaviour has conservation implications where differential impacts of pollution, fish stock depletions and wind farms may lead to different demographic outcomes and have implications for population viability (Rodríguez *et al.*, 2019; Jarrett *et al.*, 2020; Fayet *et al.*, 2021).

A breeding stage with a marked sex divide among seabirds is pre-laying, which in procellariform seabirds, these can be especially pronounced. Females take an extended egg building foraging trip, widely known as the 'pre-laying exodus', that ranges in length from approximately 3 to 50 days. (Pinet *et al.*, 2012; Hemmings and Birkhead, 2020). Meanwhile, males do not typically embark on a pre-laying exodus, but instead regularly visit the breeding colony for nest defence (Ramos *et al.*, 2014; Werner, Paiva and Ramos, 2014). Therefore, the foraging behaviour of males is constrained by central place foraging; whilst females face increased energetic demands via egg synthesis (Perrins, 1996). Following egg laying, sex differences in reproductive roles often reduce as breeding pairs alternate between near-equal incubation shifts (Guilford *et al.*, 2008; Hedd *et al.*, 2014). Whilst it is largely understood that sex differences in reproductive roles exist during pre-laying, only a small number of studies have identified how this might relate to foraging behaviour (Navarro, González-Solís and Viscor, 2007; Rigou and Guillemette, 2010). However, despite being a significant life history

stage that determines breeding, pre-laying periods are generally understudied relative to other stages of a seabirds breeding season (Merkel *et al.*, 2019).

One procellariform seabird with minimal sexual dimorphism, *Puffinus puffinus* the Manx shearwater is thought to have notable pre-laying sex differences in reproductive behaviour. (Storey and Brooke, 1991). Previous work that investigated foraging in sexed individuals during chick rearing did not identify any sex differences in dive behaviour (Shoji *et al.*, 2016). We hypothesise that in pre-laying, where there are known differences in reproductive role between males and females, sex variation in dive behaviour will be present. We first aim to quantify variation in reproductive behaviour via trip and colony parameters derived from the deployment of geolocator (GLS) loggers, comparing pre-laying to post-laying behaviour, where we expect roles to become more equivalent between sexes. Through dive parameters derived from Time Depth Recorder (TDRs) data we then investigate intra-seasonal sex variation in foraging. To provide a greater understanding of foraging behaviour, biotelemetry studies can be combined with an analysis of diet (Jarrett *et al.*, 2020; Fayet *et al.*, 2021). Despite being a well-studied bird, very little is known about the diet of the Manx shearwater. The last investigation was conducted in the 1980s, the results of which suggested pre-laying diet might be distinct to other breeding season stage (Thompson, 1987). However, as diet was investigated through stomach flushing, most fish could not be identified to a high taxonomic level. Here we employ a newer alternative approach for sampling seabird prey, using DNA metabarcoding of faecal samples. This method has potential to provide semi-quantitative information and can distinguish between morphologically similar prey types (Deagle *et al.*, 2007, 2019). Here, we aim to provide novel dietary information; establishing the prey species present in the diet of Manx shearwater and combining our results with biotelemetry to assess any sex and intra-seasonal differences present in foraging behaviour.

Methods

Device Deployment

Fieldwork was carried out on Skomer island (51.7358° N, 5.2964° W) from 2021 to 2023 under the relevant BTO licences. In 2021 51 migratetech C65 Super geolocator devices were deployed on Manx shearwaters to record the pre-laying and incubatory movements of the following breeding season. Devices weighed 1g and were therefore ~0.25% of the average shearwaters' body weight (400g). 36 devices were retrieved in 2022 to assess pre-laying behaviour; of these 13 complete incubation periods were available. GLS devices were mounted onto a custom made darvic leg ring, using cable ties and a small amount of super glue. GLS devices were set to record light and immersion, with immersion recorded every 6 seconds to generate an immersion score; with 50 representing total immersion and 0 being completely dry. In 2022, 20 CEFAS G5 Time Depth Recorder (TDR) devices were co-deployed with a GLS on both members of 10 breeding pairs from April to May. TDR devices were set to record in 'burst mode', where devices were activated when the device descended below 1.5 metres, recording at 1hz until the bird resurfaced. Prior to handling the bird, the TDR was prefixed onto a darvic plastic leg ring using a thin piece of duct tape. To deploy the device, the leg ring was fitted around the leg using a small amount of super glue, and an extra piece of duct tape to secure attachment. Burrows were monitored daily to obtain lay dates, the first day an egg was found. For breeding pairs that laid an egg (n=8) devices were retrieved and redeployed for incubation. During incubation, 10 additional birds had a GPS device deployed to obtain higher resolution spatial data. GPS were not deployed during pre-laying due to concerns over sensitivity to deployment prior to laying (Gillies *et al.*, 2020). Two models of GPS device were used; the Snapper and the Technosmart 'gipsy'; both set to record at 1hz. They were attached with tesa tape on to feathers on the back of the bird using methods stated in Dean *et al* (2013). Handling time for all deployments was typically between 5 to 10 minutes per deployment. Device weight was within the 1-2% body size limits. Sex was assigned through morphometric differences using cloacal inspection on the lay date. This method was validated for a sub sample of birds (n=57) using DNA sexing from 5 plucked feathers (Fayet *et al.*, 2021).

Diet Sample Collection

From the 29th April to the 17th June, 153 dietary samples were collected from Skomer island in Wales (51.74, -5.29) during pre-laying and incubation; 94 of which were from males, 57 from females and 2 of which were from birds of unknown sex. In order to obtain a pre-laying sample, burrows were checked every day prior to laying for present adults. For incubation samples, birds were sampled 1-2 weeks after laying. We placed each bird individually in a closed cardboard box for up to one hour. The boxes were lined with non-absorbent materials; either parchment paper or tin foil. The box was checked every 10 minutes. If the bird defecated, it was removed from the box and placed back in its burrow. Out of 199 attempts, 116 were successful. 25 samples were additionally obtained opportunistically from clothing, or from vegetation. Faecal material was collected using sterile sticks and placed in a 2ml screw-cap tube containing 1ml Zymo Research DNA/RNA Shield. Samples were stored at room temperature until DNA extractions could occur. Each sampling material was also swabbed using a collection stick to create a blank to monitor for background contamination. As we found it difficult to obtain pre-laying samples from females, 11 samples were additionally collected through swabbing the egg on the lay date, to remove any faecal material present. 78 % of birds were still incubating their eggs when checked 2-3 weeks after sampling. This is consistent with the natural egg failure rates observed on Skomer island (Storey and Brooke, 1991).

DNA Extraction of Diet Samples

DNA extractions and PCR set-up were performed in a clean lab dedicated to the handling of low DNA-content faecal samples. Prior to DNA extractions, we homogenised samples (including the field blanks, which were treated the same as samples throughout) via bead beating on a BioSpec Mini-BeadBeater-16. We used a combination of 0.5 mm and 1 mm diameter zirconia/silica beads which were added to the samples, followed by bead beating for 2 minutes. We then centrifuged the samples at 10,000g for 1 min and transferred 200 ul of the supernatant to two 96-well plates for DNA extraction following a modified version of the Zymo Research Quick-DNA Faecal/Soil 96 Magbead Kit, run on an Opentrons OT-2 liquid handling robot (protocol is available from: https://github.com/GemmaClucas/Opentrons_OT2_protocols/blob/main/Zymo_fecal_bead_extractions_12columns.py). The OT-2 was fitted with a HEPA-filter to provide a sterile environment and positive pressure to reduce the chance of cross-contamination among

samples. On each plate, we included six negative controls that were treated the same as samples throughout all subsequent steps, allowing us to monitor for contamination during the extraction process. We also mixed samples by sex and breeding stage across the two plates, to reduce batch effects.

We used a hierarchical approach to amplify prey DNA from the faecal samples. We used the universal eukaryotic primers developed by McInnes et al. (2017) to amplify the v7 region of the small subunit rDNA (hereafter 18S), allowing us to theoretically identify all prey to the family- or order-level. Then we used the MiFish primers developed by (Miya *et al.*, 2015) to amplify the 12S rRNA gene from any fish DNA found in the faecal samples, since these primers have been shown to allow species-level identifications in a diverse array of fish. For both PCRs, we used a two-step approach, whereby the target amplicon is amplified in the stage-one PCR, and then a second PCR is used to add sequencing adapters and indexes, prior to pooling samples.

In the first stage PCR for the 18S amplicons, we added Nextera tails to the primer sequences from (McInnes *et al.*, 2017) such that our forward and reverse primers were: 18S_Nx_F 5'-TCGTCGGCAGCGTCAGATGTGTATAAGAGACAGGGTCTGTGATGCCCTTAGATG-3' and 18S_Nx_R 5'-GTCTCGTGGGCTCGGAGATGTGTATAAGAGACAGGGTGTGTACAAAGGGCAGGG-3', respectively. We included two no-template controls on each plate to monitor for contamination during PCR set-up, and a positive control (mock community) containing DNA extracted directly from five known fish. The 12 µL PCR reaction included 6 µL of Amplitaq Gold 360 Master Mix, 0.84 µL of each of the forward and reverse primers at a 5 µM concentration, 0.5 µL of BSA at 20 mg/ml concentration, 2.82 µL of molecular grade water, and 1 µL of template DNA. Thermocycling conditions were: 95 ^{0}C for 10 min, 35 cycles of 95 ^{0}C for 30 seconds, 67.5 ^{0}C for 30 seconds, and 72 ^{0}C for 30 seconds, followed by a final extension at 72 ^{0}C for 7 minutes. Each PCR was performed in duplicate for each sample, and PCR products were visualised via gel electrophoresis to confirm amplification and check that negative controls were clear, before products from each duplicate were combined and diluted before the second stage PCR.

The first stage PCR for the MiFish amplicons followed the same methods, with each plate of samples run in duplicate and the inclusion of positive and negative controls. We added TruSeq tails to the original primer sequences developed by (Miya *et al.*, 2015)) such that our primers were: MiFish-U-F-TruSeq 5' ACACTCTTTCCCTACACGACGCTCTTCCGATCTGTCGGTAAAACTCGTGCCAGC-3 and MiFish-U-R-TruSeq 5' GTGACTGGAGT

TCAGACGTGTGCTCTTCCGATCTCATAGTGGGGTATCTAATCCCAGTTTG-3'. The 12 µL PCR reaction included 6 µL of KAPA HiFi HotStart ReadyMix 2x, 0.7 µL of each of the forward and reverse primers at 5 µM concentration, and 4.6 µL of template DNA (or molecular grade water for the no-template controls). For the mock community, we added 1 µL of template DNA and 3.6 µL of molecular grade water.

For both MiFish and 18S amplicons, the second stage PCR was performed by the Hubbard Centre for Genome Studies at the University of New Hampshire and used the diluted product from the first stage PCR as template. The second stage PCR added the flow cell binding sites and sequencing primer binding sites, in addition to i7 and i5 indexes used to identify samples. We used unique dual indexes, such that any reads affected by tag-jumping would be removed during demultiplexing. Sequencing was performed using a small percentage of a lane on a NovaSeq 6000 system, using 250bp paired-end chemistry.

Bioinformatics of Diet Samples

Bioinformatics were performed using Qiime2 v2021.4 (Bolyen et al. 2018). For both 18S and MiFish amplicons, forward and reverse primers were trimmed using the cutadapt plugin (Martin 2011). For the MiFish amplicons, we denoised and merged paired-end reads using the DADA2 plugin (Callahan et al. 2016), truncating the forward and reverse reads to 133 and 138 bp, respectively, and specified a minimum overlap of 50 bp between them. After denoising, data from both sequencing plates were merged, and taxonomy assignments were made using an iterative BLAST method against a custom reference database. To create the reference database, we used the RESCRIPt plugin (Robeson et al. 2021) to download any 12S or mitochondrial genomes from GenBank that originated from fish or birds that were studied in our lab. Downloaded database sequences were cleaned and dereplicated using RESCRIPt default parameters and finally, a human mitochondrial genome was added to the database, as this is a common source of contamination. The iterative BLAST method then took each representative sequence from our samples and blasted it 80 times against the reference database, increasing the percent identity incrementally from 70 – 100 %, thus circumventing the limitation of the BLAST method, which keeps only the first hit that meets the search criteria, rather than the best hit. The script for the iterative BLAST method is available from https://bitbucket.org/dwthomas/qiime2_tools/src/master/mktaxa.py. We chose this method to assign taxonomy rather than training a Naïve Bayes classifier as this method correctly identified all species in our mock community correctly, while a trained classifier mis-identified one species. Next, we filtered out unassigned reads, reads originating from human

contamination or reads originating from the birds themselves. We then created rarefaction curves using the diversity plugin to determine the sequencing depth needed to adequately capture the fish diversity in each sample. We found that 400 reads were sufficient, so we rarefied all samples to a sequencing depth of 400, discarding samples that had fewer than 400 reads. We then manually checked all species assignments in the remaining samples by blasting the representative sequences against the full GenBank database and checked that the fishes' ranges overlapped with the foraging areas used by Manx shearwaters.

For the 18S amplicons, we followed a similar pipeline with a few modifications. We truncated the forward and reverse reads to 150 bp during denoising. T4hen, to assign taxonomy to the sequences, we trained a Naïve Bayes classifier using the feature classifier plugin (Bokulich et al. 2018, Pedregosa et al. 2011). We downloaded a Qiime compatible version of the SILVA database (v132, released 10-Apr-2018) downloaded from https://www.arb-silva.de/download/archive/qiime and, using the 99% clustered version of the database, we extracted the region bounded by our sequencing primers and trained the classifier on this region. We then filtered out non-metazoan, avian, and mammalian DNA.

Geolocator Data Processing

All processing and statistical analysis was carried out in RStudio version 4.0.2. Light data were processed using the geolight package to calculate position from twilight events defined by a light intensity threshold of 10 (Livoski, Hahn, 2012). Day length was used to estimate latitude, whilst the timing of midday/midnight was used for longitude. The sun elevation angle used to define twilight was -4.5, the angle at which the greatest number of points were not over land. A rolling 3-day mean was applied to both longitude and latitude to smooth out error. The pre-laying period was defined as the period between migration's end and the lay date obtained from colony monitoring. Migration end was determined from the GLS twilight defined longitude, as it is not subject to equinox error. Homewards migration could clearly be visualised by a steep increase in longitude towards the colony, and migration end was defined as the first date past a threshold of 6° W.

Colony visits during incubation period were determined via visual identification of extended periods of dark and dry, where the bird is incubating the egg. However, during the pre-laying period Manx shearwaters often arrive and depart from the colony in one night. Using the suncalc package, days and nights were separated from one another based on local sunrise and sunset times (Teets, 2003). For each night, the number of 5-minute bins where immersion was recorded was summed to calculate the number of wet events per night. To identify nights with colony visits, a probabilistic normal Expectation Maximisation (EM) mixture model was

applied using the R package mixtools (Benaglia *et al.*, 2009). Nights with colony visits were assigned to those which they had a greater probability of belonging to the drier peak.

TDR Data Processing

As TDR devices were activated based on a pressure threshold (>1.5 metres) the device recorded some false dives. Given that TDR devices were co-deployed with GLS devices, dives that occurred when the bird was identified as being at the colony from GLS immersion data were excluded. Dives shorter than 4 seconds and longer than 100 seconds were excluded. Additionally, dives where there was little depth change, most likely triggered by birds sitting on the sea surface were identified by calculating for each dive L. The equation essentially compares the time spent at a stable depth (t) to the product of the time spent at maximum dive depth (d) and the total dive length (l). If the numerator is relatively large compared to the denominator, it suggests that a significant portion of the dive involved little depth change, indicating a behaviour consistent with birds sitting on the sea surface.

$$L = \frac{t}{d*l}$$

t= the length of time where the depth did not change (where depth change per second is <0.1 metres), d= the time spent at maximum dive depth and l= the total dive length.

By calculating a summary metric that identifies false dives owing to little change in depth we were then able to separate real dives from when the device was triggered by the bird being sat on the water through applying a probabilistic normal Expectation Maximisation (EM) mixture model on L using the mixtools package in r (Benaglia *et al.*, 2009). This identified two groups, and dives were assigned to each one based on a threshold of >0.5 probability. Following the visual inspection of a random subset of 200 dives in each group, one group consistently identified false dives (see supplementary 1 for exemplar dives). Excluding these removed 4643 dives leaving 54419 dives for analysis.

Statistical Analysis

To quantify sex differences in reproductive roles in both incubation and pre-laying; we used parameters to describe time allocated to at-sea trips and colony visitation derived from

geolocator data. T-tests were implemented on each parameter in pre-laying (n= 36) and incubation (n=13). Assumptions of normality and variance for T tests were met. We then applied Mixed effects models from the R package lme4 to assess intra-seasonal sex differences in dive number and dive depth; using a two-way interaction between stage (incubation/pre-laying) and sex (male/female) (Bates *et al.*, 2015). When assessing variation in the number of dives per time of day, exploratory analysis indicated a pattern where males appeared to dive less in the evenings during pre-laying than females. This pattern did not exist during incubation, where both males and females dived in the evening. We predicted that evening patterns of dive frequency during pre-laying may occur as a result of increased male colony restraints. Therefore, evening dives (6-10pm) were subset and we fitted 2 mixed effects models; one including a two-way interaction between sex and stage; the other a two-way interaction between colony visitation (whether a colony visit occurred later that same evening) and stage on the number of evening dives. An AIC comparison of these 2 models was used to determine whether sex or colony visitation was as better predictor of evening dive frequency. P-values were computed using chi-squared Likelihood Ratio Tests and bootstrapping methods via the arm package were used to generate 95% confidence intervals and effect sizes through 1000 simulations of model effects (Gelman and Hill, 2006). Individual and date were included as random effects in all models. To assess variation in the number of prey species between individuals sampled during pre and post-laying, a Krustal Wallis test was implemented.

Kernel density estimation plots were used to visually assess sex differences in pre-laying and incubation positions in the R package adehabitatHR (Calenge, 2006). For pre-laying, GLS derived positions were used. Given the associated error with geolocation; only 50% kernels were applied to represent core area (h=0.1; grid=2000). For incubation movements, kernels were generated using GPS data. As GPS data is satellite derived and at a higher resolution (1 hz) there is increased confidence in position. Therefore, 90% kernels were used to assess incubatory movements (h=0.1; grid=200). Whilst GPS and GLS devices provide data of different resolution, a comparison of 50% kernels from GLS data and 90 % kernels of GPS data over the same period in incubation presented little difference in the identified areas of habitat use (supplementary 2). For visual assessment of the oceanographic areas birds were associated with, bathymetric data was accessed through the marmap package in r (Pante and Simon-Bouhet, 2013).

Figures

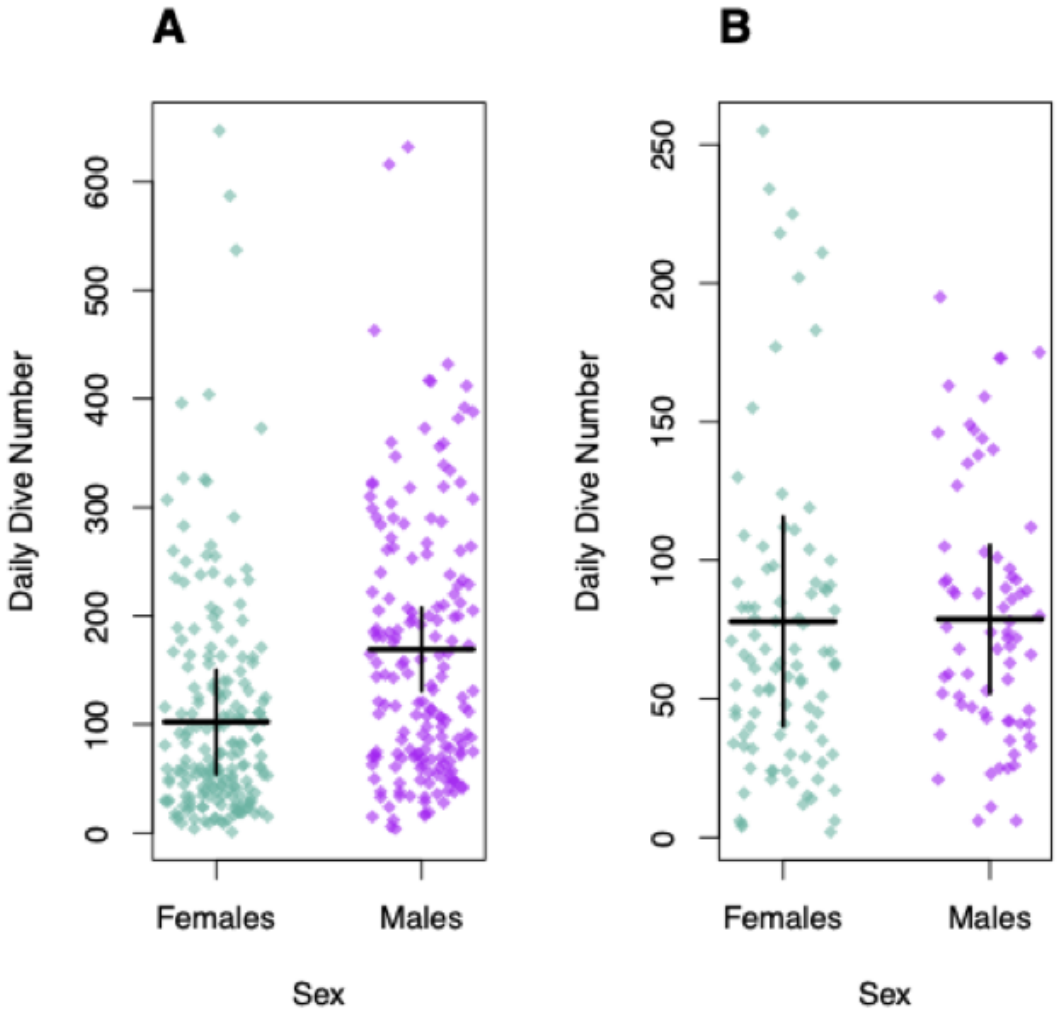


Figure 1. Comparing patterns in dive frequency between pre-laying and incubating females (green) and males (purple). **A)** Pre-laying sex differences in daily dive number (n=10 for both sexes). **B)** Post-laying sex differences in daily dive number (n=8 for both sexes). Each point represents the daily dive number for a day at sea for one bird and are plotted with 'jitter' to visualise the data. Black solid lines indicate the mean daily dive number (of individual means) and associated standard error.

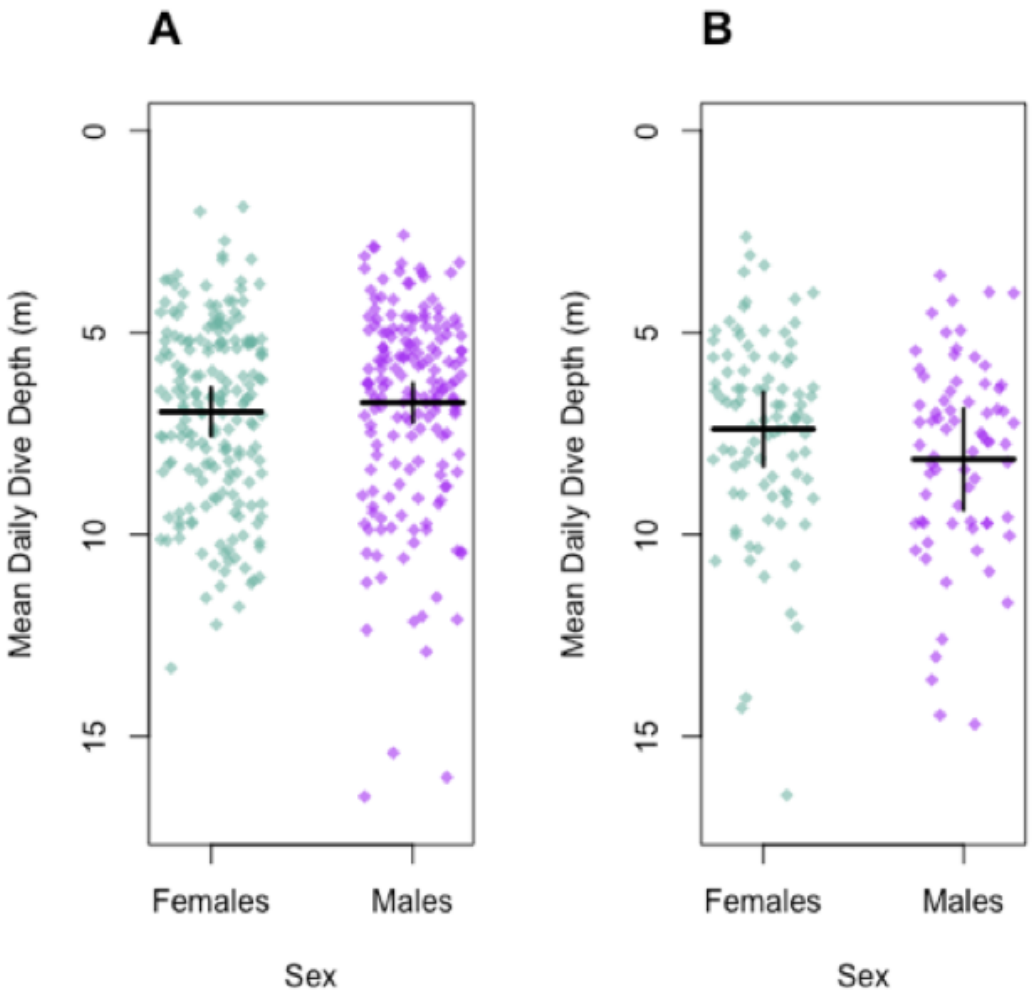


Figure 2. Comparing patterns in maximum dive depth (per dive) between pre-laying and incubating females (green) and males (purple). **A)** Pre-laying sex differences in dive depth (n=10 for both sexes). **B)** Post-laying sex differences in dive depth (n=8 for both sexes). Each point represents the mean daily dive depth for a day at sea for one bird and are plotted with 'jitter' to visualise the data. Black solid lines indicate the mean daily dive depth (of individual means) and associated standard error.

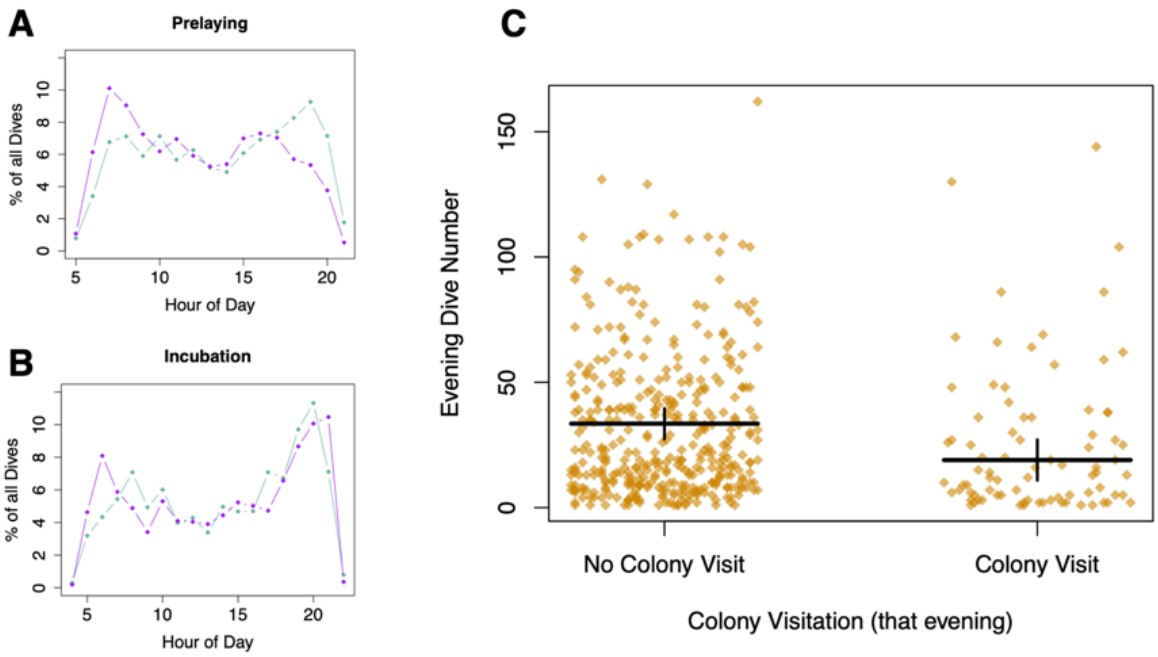


Figure 3. Comparing diurnal patterns in evening dive number as a result of colony visitation. **A)** Pre-laying sex differences in the % of all totalled dives per hour of the day for males (purple) and females (green). **B)** Incubation sex differences in the % of all totalled dives per hour of the day for males (purple) and females (green). **C)** Evening dive number (dives between 6-10 pm) plotted with 'jitter' for birds that did or did not visit the colony later that evening. Points represent the number of evening dives for one bird day at sea. Black solid lines indicate the mean evening dive number (of individual means) and associated standard error around the mean.

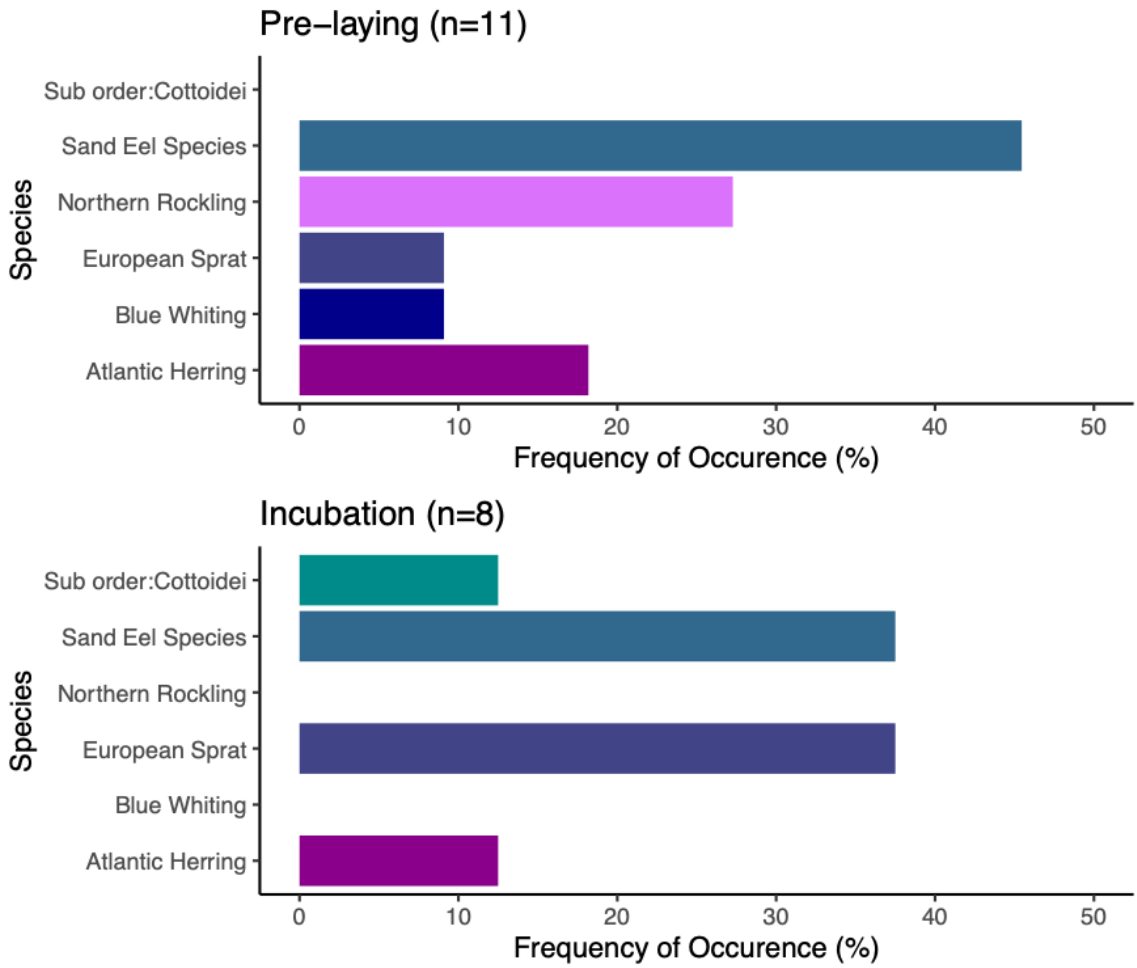


Figure 4. Results from the DNA metabarcoding of faecal samples to assess the diet of pre-laying (n=11) and incubating birds (n=8). The frequency of occurrence represents the number of individuals that had each prey species present in their diet. Both sexes were pooled given the small sample sizes (n=3) available for females.

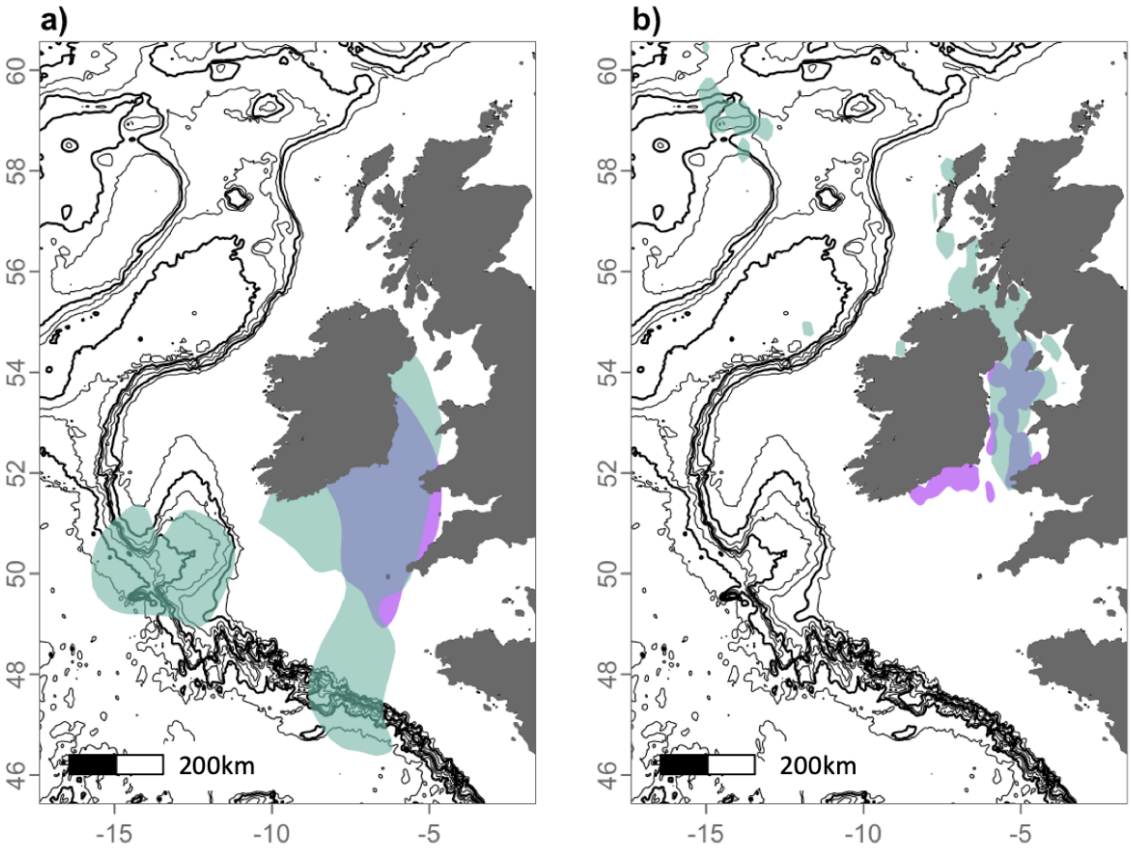


Figure 5. Kernel density estimation plots representing sex differences in pre-laying and incubatory movements**. A)** Pre-laying movements (50% kernels) from GLS derived position (females; n=19 and males; n=17). **B)** Post-laying movements (90% kernels) from GPS (females; n=4 and males; n=6). Females are plotted in green, whilst males are in purple. Bathymetry was plotted through the marmap package in r (Pante and Simon-Bouhet, 2013).

	Pre-laying		
	Females (n=19)	**Males** (n=17)	**T Test Results**
Mean Trip Length (days)	8.97 ± 2.91	3.78 ± 1.82	**$T_{(30)}$=3.18 95%[1.86, 8.52] ****
Longest Trip (days)	18.59 ± 3.27	10.92 ± 3.89	**$T_{(32)}$=3.19 95%[2.77, 12.57] ****
Mean Colony Visit Length (days)	1.11 ± 0.31	0.63 ± 0.17	**$T_{(27)}$=2.77 95%[0.12, 0.82] ****
Longest Colony Visit (days)	4.27 ±1.36	6.74 ± 2.02	$T_{(31)}$=0.36 95%[-0.6, 0.87]
Colony Visit Number	4.68 ± 1.64	12.41 ± 4.15	**$T_{(21)}$=-3.66 95%[-12.11, -3.34] ****
Proportion of Time Spent at Sea (over pre-laying period)	0.78 ± 0.09	0.71 ± 0.07	$T_{(34)}$=1.19 95%[-0.04, 0.4]
	Post-laying		
	Females (n=6)	**Males** (n=7)	**T Test Results**
Mean Trip Length (days)	7.88 ± 1.07	7.00 ± 1.02	$T_{(12)}$=1.45 95%[-0.44, 2.2]
Longest Trip (days)	8.96 ± 0.68	8.18 ± 1.24	$T_{(9)}$=1.35 95%[-0.52, 2.08]
Mean Colony Visit Length (days)	6.88 ± 1.62	7.35 ± 0.76	$T_{(9)}$= -0.90 95%[-2.33, 1.01]
Longest Colony Visit (days)	8.14 ± 1.74	9.21 ± 1.13	$T_{(10)}$= -1.25 95%[-2.94, 0.82]
Colony Visit Number	3 ± 0	3.71 ± 0.45	**$T_{(6)}$=-3.87 95%[-1.17, -0.26] ****
Proportion of Time Spent at Sea (over post-laying period)	0.31 ± 0.05	0.37 ± 0.06	$T_{(10)}$= -1.93 95%[-0.13, 0.01]

Table 1. A table presenting trip and colony visitation parameters for pre-laying (n=36) and incubating (n=13) birds. The mean plus standard error is included for males and females for each parameter; as is the results of each t test (t value, degrees of freedom and 95% confidence intervals). Significant t tests are indicated in bold and levels of significance are indicated by asterix number where * is $p<0.05$ and ** is $p<0.01$.

Response	No	Coefficient	Effect Size	Confidence Intervals	χ^2	p value
Number of Daily Dives	1	*Intercept* Stage (pre-laying) Sex (male) **Interactive term**	85.818 16.714 -12.676 75.205	54.636, 114.839 -8.336, 41.919 -57.238, 34.189 42.522, 107.969	- 3.296 18.425 16.35	- >0.05 >0.05 < 0.0001***
Maximum Dive Depth	2	*Intercept* **Stage (pre-laying)** Sex (male) **Interactive term**	7.539 -1.018 1.074 -1.901	6.916, 8.171 -1.323, -0.728 0.276, 1.865 -2.129, -1.664	- 141.45 0.744 244.65	- < 0.0001*** >0.05 < 0.0001***
Number of Evening Dives	3	*Intercept* Breeding Stage (pre-laying) **Colony Visit (Present)** Interactive term	32.913 -0.406 -22.695 14.964	26.842, 38.829 -6.743, 5.616 -36.279, -9.299 0.033, 30.195	- 4.084 14.214 3.694	- >0.05 <0.0001*** >0.05

Table 2. A table representing all mixed effects models present in this analysis (1-3). For each coefficient, confidence intervals and effect sizes were obtained through bootstrapping, whilst χ^2 and p values were obtained through likelihood ratio tests. Significant predictors are highlighted in bold and significance levels indicated by the number of asterisks (< 0 '***', <0.001 '**', <0.01 '*'

Results

Movement behaviour

During pre-laying females took longer trips than males ($T_{(30)}$=3.18 95%[1.86, 8.52];p <0.01; table 1), with the average trip length of females being 5.19 days longer. The mean longest trip that females took during pre-laying was 18.59 days; most likely corresponding to the pre-laying exodus; which was significantly longer than the longest mean trip for males which was 10.92 days during pre-laying ($T_{(32)}$=3.19 95%[2.77, 12.57]; p<0.01; table 1). However, despite females taking trips that were longer there were no significant differences between the proportion of time spent at sea between sexes during both pre-laying and post-laying. Meanwhile, males visited the colony significantly more during pre-laying than females, with males averaging 7.73 more visits. ($T_{(21)}$=-3.66, 95%CI [-12.11, -3.34]; p<0.01; table 1). However, although males visited the colony more frequently; when females did visit the colony, they spent a longer time at the colony than males; with their visits being a mean 0.48 days longer ($T_{(27)}$=2.77 95%[0.12, 0.82]; p<0.01; table 1). In incubation, there were no detected significant differences between male and female trip lengths (table 1). However, males took a higher number of incubation stints ($T_{(6)}$=-3.87 95%[-1.17, -0.26];p<0.01; table 1). No statistical differences were detected in incubation stint length. From GLS derived 50% kernels; pre-laying males occupied a smaller range than that of the females, which extended towards the continental shelf edge of the Bay of Biscay. During post-laying movements, 90% GPS derived kernels indicate that birds foraged in a small area more local to the colony; with males and females occupying similar areas in the Irish Sea.

Diving behaviour

The number of dives per day was significantly predicted by the interaction between sex and stage, where males took 63 more dives a day during pre-laying than females (β= 75.20, 95%CI [42.52, 107.97], χ^2c =16.35, p< 0.0001; figure 1; model 1). Meanwhile, post-laying, males and females took a comparable number of dives per day (β= -12.68, 95%CI [-57.24, 34.19], χ^2c =18.43, p> 0.05; figure 1; model 1). Additionally, there was a significant interaction between sex and stage in relation to dive depth, with males taking dives that were 1.9 metres shallower in pre-laying than in post-laying (β= -1.90, 95%CI -2.14, -1.66], χ^2c =244.65, p< 0.0001; figure 2). Exploratory analysis revealed diurnal patterns in dive activity during pre-laying, with males diving less in the evening. We explored post hoc whether this occurred as a result of increased colony visitation (figure 3) by comparing with AIC the fit of two non-nested linear models, predicting evening dive number either with sex or colony visitation (whether there was a

colony visit later that night). The two models had an ΔAIC 14, providing stronger support for the model including colony visitation as a predictor of evening dive numbers. Colony visitation was the only significant variable in the model (β= -23.00, 95%CI [-36.86, -9.53], χ^2c =14.21, p< 0.0001; figure 3; model 3). There was no significant effect of breeding stage (β= -0.65, 95%CI [-6.90, 5.37], χ^2c =4.08, p>0.5; model 3) nor interactive effect between breeding stage and colony visitation (β= 15.46, 95%CI [-0.35, 31.29], χ^2c =3.69, p>0.5; model 3) on the number of evening dives. Therefore, birds visiting the colony that night were less likely to dive during the evening and this effect occurred independently of breeding stage.

Diet

For the MiFish primers, of the 153 dietary samples, 19 samples retained prey information in the diet and 7600 sequences were retained. The other samples did not contain prey material, containing only DNA of the bird itself. The 18S primers for broader invertebrate identification contained some information on secondary predation (copepods), but mostly contained bird DNA or parasites. Therefore, here we present only the results of the fish diet (figure 4). Manx shearwaters consumed 6 different types of identifiable prey. Northern rockling and whiting were found only in the pre-laying diet, whilst fish of the suborder Cotttoidei were found only in incubation. Sandeel, sprat and herring were found in both seasons; with a greater proportion of sprat present in the post-laying diet. A Kruskal–Wallis test found no significant difference in the number of prey species identified per individual that was sampled during pre and post laying (χ^2c $_1$=0.25, p=0.6). However, given the small sample size these results are not conclusive. We were unable to make sex comparisons, as of the total successful samples only 3 were female.

Discussion

In a species with minimal sexual dimorphism, here we demonstrate how reproductive role can cause variation in foraging behaviour between sexes and provide the first description of diet for Manx shearwaters using DNA metabarcoding. Through the quantification of trip and colony parameters using geolocators, we first demonstrate how reproductive roles differ in pre-laying; where females visited the colony less frequently than males and took foraging trips that were of a greater duration and distance (table 1; figure 5). This fits with the generally accepted hypothesis that males attend the colony to defend the burrow, whilst females forage away to build the egg (Hedd *et al.*, 2014; Ramos *et al.*, 2014; Werner, Paiva and Ramos, 2014). Despite having a smaller sample size for incubating birds, this analysis suggests that following egg laying, sex differences in reproductive roles largely reduce.

During pre-laying, males unexpectedly took more dives a day than females. This difference did not persist following laying, which indicates the drivers of increased male diving are likely to be pre-laying specific. However, given the energetic demands of egg synthesis for females pre-laying, we had expected that females might dive more. Whilst unexpected, we suggest that increased male diving may have several functions, the first being that males may have greater energetic demands during this time than previously considered. During pre-laying , males have a more active role in colony defence, and usually take the first incubation stint (Ramos *et al.*, 2014; Werner, Paiva and Ramos, 2014). Additionally, we found that males spend more time incubating the egg than females do (table 1). They therefore must build up sufficient body reserves through foraging (Elliott *et al.*, 2021). Alternatively, increased male diving may be representative of a lower quality area that requires more effort to successfully locate and catch prey. Males are operating as central place foragers during this period, returning frequently to the colony between foraging trips. Meanwhile, females can locate a high-quality feeding patch at greater distance from the colony, and remain there without commuting. Kernel density plots of geolocator derived positions indicate that females forage in a much wider area than males during pre-laying (figure 5). If foraging conditions were equivalent, it seems unlikely that females would incur the energetic costs of travelling further (Shoji *et al.*, 2014). Seabirds often forage in further, more productive areas when colony constraints are released (Charrassin *et al.*, 1998; Afán *et al.*, 2014; Phillips *et al.*, 2021). This analysis revealed that males took shallower dives during pre-laying than in incubation when they take longer trips, which could suggest a reduction in prey quality closer to the colony (Shoji *et al.*, 2014). Colony constraints were additionally revealed to impact diurnal patterns of dive activity, with birds diving less in the evening if they were visiting the colony later that night (figure 3). As males

visited the colony more during pre-laying (table 1), this meant evening foraging opportunities were restricted during this period. We suggest that birds visiting the colony may be less likely to forage during the evening as they are more likely to be commuting back or rafting in adjacent waters.

While we were unable to explore whether differences in at-sea behaviour (diving) and shearwaters foraging locations at sea translated into diets that differed between the sexes, this study nonetheless provided the first description of diet for Manx shearwaters using DNA metabarcoding, identifying six fish species consumed during pre-laying and incubation (figure 4). Although there was a limited number of samples (n=19) with dietary material suitable for analysis, it appears that birds adapt their diet to seasonal fluctuations in prey species. We found a high presence of sandeel across dietary samples. Sandeel is a critical prey item for many breeding seabirds that is largely declining due to oceanic warming (Fayet *et al.*, 2021). A small number of samples additionally had rockling species present in the diet. It was previously unconsidered that Manx shearwaters might feed on benthic species (Thompson, 1987). Alternatively, the presence of rockling in the diet could indicate feeding from fisheries discards (Furness, Edwards and Oro, 2007), but unlike other closely related shearwaters, Manx shearwaters are not known to follow fishing vessels. These results, although from a small sample, demonstrate the necessity of further work to investigate diet in pelagic far-ranging species (Grémillet and Boulinier, 2009). Owing to the small number of successful samples, especially for females, in this study, we were unable to compare sexes to understand whether specific prey is needed for egg synthesis. We think our small sample size for females might be a consequence of pre-laying behaviour itself, with females taking long trips out to sea and potentially excreting dietary material before returning to the colony where they can be sampled. For future dietary studies, we suggest sampling opportunistically during periods of high colony visitation such as in chick rearing, where birds return frequently to feed their chicks. Egg swabbing, as trialled in this study, may be more successful than faecal sampling for obtaining the pre-laying diet of females.

To conclude, here we show sex differences in reproductive role exist during pre-laying, an understudied reproductive period, where females take long trips out to sea and males attend the colony. Unexpectedly, we found that males took more dives per day than females in pre-laying and dived to shallow depths. Colony restraints impose on evening foraging opportunities; especially for pre-laying males who return to the colony frequently to defend the nest. Here we also provide the first description of fish species using DNA metabarcoding and find that the diet of pre-laying and incubating birds does not appear to vary-although we

suggest further dietary sampling is necessary to gain an understanding of sex differences. If organisms are constrained at certain life history stages by differing energetic demands or reproductive role, this may limit their ability to adapt their foraging behaviour to changing environmental conditions. This study emphasises the importance of obtaining sex specific foraging information in future studies of foraging behaviour.

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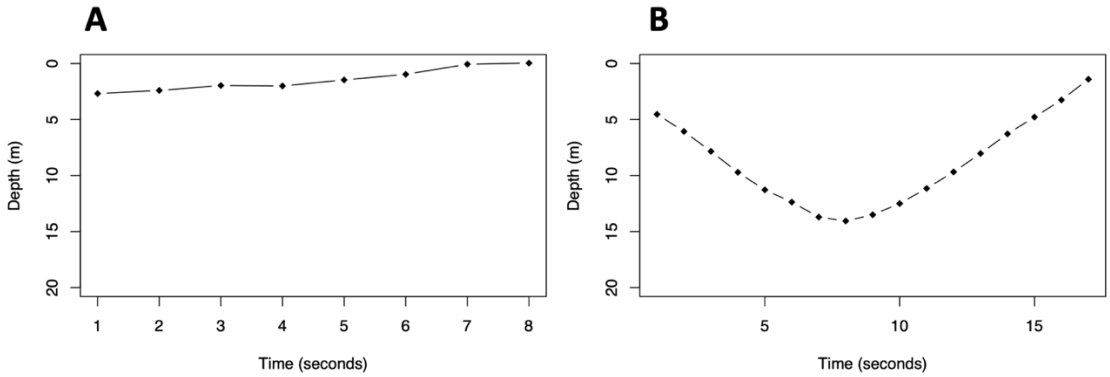
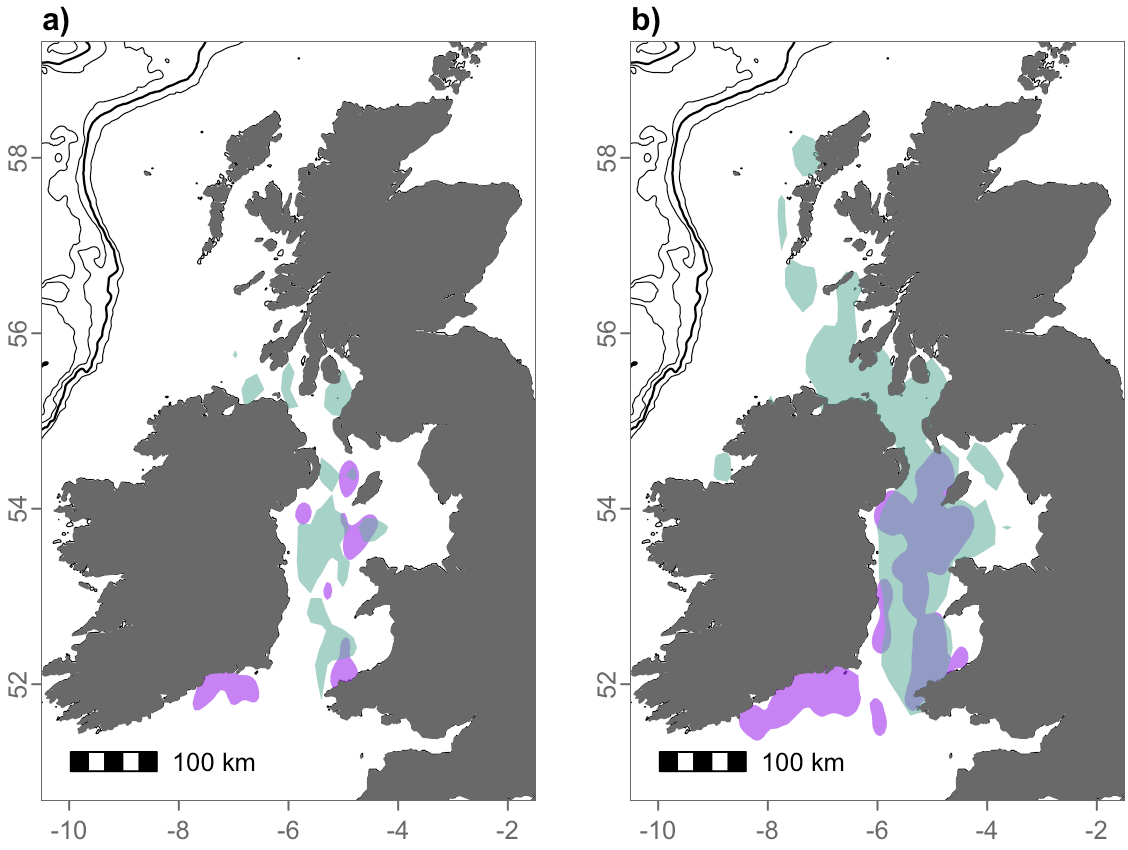
Supplementary Materials



Supplementary 1. Examples of real and false dives recorded by the Time Depth Recorder (TDR) logger where the device was activated based on a pressure threshold (>1.5 metres). **A)** Depth plotted against time for a dive which was identified as false where the bird is most likely sat on the water. In **B)** depth is plotted against time for a dive that was identified as real.



Supplementary 2. Kernel density estimation plots comparing post-laying movements recorded by GLS and GPS devices**. A)** Post-laying movements (50% kernels) from GLS derived position (females; n=6 and males; n=7). **B)** Post-laying movements (90% kernels) from GPS (females; n=4 and males; n=6). Females are plotted in green, whilst males are in purple. Bathymetry was plotted through the marmap package in r (Pante and Simon-Bouhet, 2013).

Discussion

6

Introduction

How animals survive despite shifting environmental conditions has long fascinated and motivated the research of behavioural ecologists (Tinbergen, 1963; Barrett *et al.*, 2013). Given the current rate of anthropogenic environmental change, the necessity for such studies has increased (Newton, 2008; Rodríguez *et al.*, 2019). Shifts in behaviour are often studied via large-scale population change (Crawford *et al.*, 2014; Rotics *et al.*, 2018). However, it is individuals, not populations, that can make decisions and adjust their behaviour (McFarland, 1977; Descamps *et al.*, 2011). As large datasets accumulate multiple years of individual data, we can start to investigate individual responses in natural systems (Liechti *et al.*, 2018; Conklin, Lisovski and Battley, 2021). Through the novel extraction of behavioural information from a long-term, multi-colony biotelemetry dataset, in this thesis I aimed to gain a greater understanding of how individuals respond to shifting conditions and constraints. I specifically investigated the responses of a trans-hemispheric migrant, the Manx shearwater, a highly mobile seabird with an extreme life history strategy (Harris, 1966; Storey and Brooke, 1991; Guilford *et al.*, 2009). In this thesis, I explored how shearwaters might respond to different environmental constraints and how those responses might differ between individuals based on previous behaviour or inherited factors.

In chapter 2, 3 and 4 I explored how individuals respond to variation in environmental conditions. In **chapter 2** I investigated how large-scale environmental oscillations influence the behaviour of over-wintering shearwaters and carry over into later breeding. I found evidence that individuals are able to adjust their position between years with the El Niño Southern Oscillation to match resource distribution, a phenomenon that was previously unknown. However, despite individual plasticity I detected carry over effects into later breeding with El Niño conditions. In **chapter 3** I explored how individuals adjust their south-bound migratory behaviour with variation in lay date and found novel evidence for the timing of migration with lunar conditions. I found that birds that lay earlier, and so departed earlier on migration, had more stop-over foraging sites and longer migration durations. Meanwhile, birds that departed later to their over-wintering grounds flew more during the night, probably using moonlight for visual guidance. In **chapter 4** I found that seasonal variation in photoperiod length during chick provisioning affects light restricted behaviours such as nocturnal colony visitation and diurnal foraging. I found evidence that birds are less able to time their provisioning visits to avoid moonlit conditions during shorter night lengths, potentially increasing predation risk. In **chapter 5** I investigated how reproductive role constrains males and females differently during pre-laying. I detected sex variation in dive

depth, frequency and in diurnal patterns of foraging, with males taking fewer evening dives than females as a result of increased male colony visitation. In this closing chapter I will integrate my findings in this thesis, and discuss their wider implications within the field of behavioural ecology. I will discuss how the previous chapters provide evidence for individual response and plasticity to changing environmental conditions. I will also discuss where this work was limited and provide suggestions for future work.

How do Individuals Respond to Shifting Environmental Conditions?

The yearly rotation of the earth around the sun induces the predictable phases of photoperiod, temperature, food availability and weather patterns that are used to describe seasons. Migratory animals can respond to inter-seasonal shifts in environmental conditions through positioning themselves in areas where peak food resources are available (Egevang *et al.*, 2010; Winger *et al.*, 2019). From an evolutionary perspective, it may be useful for individuals to visit regular sites of seasonal abundance (Alerstam, 1991; Domer *et al.*, 2021). Therefore, although migratory birds are capable of over-wintering and breeding in a range of locations, the sites used are often near consistent between years (Fayet *et al.*, 2016; Camprasse *et al.*, 2017). Whilst in their non-migratory periods, birds must therefore find ways to respond to any additional environmental variation that occurs. In chapters 2 and 4 I aimed to understand how shearwaters respond when environmental conditions change at these established seasonal sites. Given the great distances shearwaters traverse each year, you might expect individuals to move elsewhere if conditions become unfavourable (Freeman *et al.*, 2013). However, even highly mobile animals are subject to constraints on their movement. Although seabirds can be far-ranging, whilst breeding their movement is restricted by parental care (Wakefield *et al.*, 2011; Shoji *et al.*, 2014; Sánchez *et al.*, 2018). They often operate as central place foragers, foraging in a smaller area during this period. During the non-breeding period we might expect migratory animals to be less restricted in their behaviour (Desprez *et al.*, 2018; Carneiro *et al.*, 2020).

The results of chapter 2 provided evidence that individual shearwaters can adjust their over-wintering latitude with variation in El Niño Southern Oscillation conditions. Few studies have been able to investigate in detail how individual birds move foraging sites with environmental variation, as they require large datasets of over-winter positions. Previous studies have found shifts in distribution to occur in one direction, for example many avian species in the Northern hemisphere have shifted northward with temperature increases in their previous habitat (Van Buskirk, Mulvihill and Leberman, 2010; Meier *et al.*, 2017). On the Patagonian shelf, it appears that the El Niño Southern Oscillation shifts food resources both northwards and southwards

dependent on what phase is present (Machado, Barreiro and Calliari, 2013). Chapter 2 shows us that birds are capable of shifting their over-wintering position in multiple directions dependent on where resources are distributed. Individuals therefore appear plastic in their movement behaviour, and responsive to environmental change. However, although birds were able to adjust their position to match resources, in this chapter I additionally demonstrated novel carry over effects through the use of a non-experimental dataset.

In chapter 2, birds not only adjusted their position with environmental oscillations, they also adjusted their behaviour, foraging less during El Niño years. Interpreting foraging effort variation can be difficult, as it could plausibly be indicative of both better or worse conditions. For example, birds might forage less as they are efficiently exploiting resources or, alternatively, foraging effort might be proportional to the resources available (Daunt *et al.*, 2006; Bost *et al.*, 2009). The method I chose for interpreting changes in foraging effort was to look for any associated fitness consequences. I therefore extracted behavioural information on chick provisioning rates during the following breeding season. Even though shearwaters over-winter and breed in different hemispheres, they appear unable to provision to the same extent following El Niño phase over-wintering conditions. With this effect occurring independently of local environmental conditions at the breeding site, this study increases our understanding of the impact that over-wintering conditions can have on adult condition (Barbraud, Lormée and LeNevé, 2000; Pelletier *et al.*, 2020). Manx shearwaters are a species that invest large amounts of parental effort into rearing their chick over a protracted period of 60-70 days (Storey and Brooke, 1991; Akiko Shoji *et al.*, 2015). Through reducing chick provisioning effort after a costly over-wintering period, breeding adults appear to trade-off rearing heavier chicks with promoting their own survival. A previous study on shearwaters by Shoji *et al.*, 2015 found that birds that skipped breeding in one year bred more successfully in the next. Therefore, adults may be better able to breed more successfully in future years if they reduce provisioning effort when their condition is reduced by costly over-wintering periods.

Are Individuals Constrained by their Environment?

The results of chapter 2 provide insight into the complexities of individual response to environmental conditions. Individuals were able to shift their over-wintering distribution to match resources, but were unable to control completely for reduced foraging opportunities in El Niño years. Therefore, environmental variation affected behaviour not only at the site where adverse conditions were experienced, but carried over into later breeding when

provisioning was reduced. This study highlights the necessity to understand how events in one season impact another, and this approach should be considered when understanding individual responses to climate change (McNamara and Houston, 2008; Franke *et al.*, 2011). In chapter 4 I explore individual response to changing environments through a variant that is often unconsidered, the photoperiod. Unlike in chapter 2 where birds experience different environments between years, birds must contend with the same seasonal shifts in photoperiod each year. If breeding is to be successful, birds are constrained to return to the colony for chick provisioning and are therefore less able to switch their distribution when better conditions are present elsewhere (Guilford *et al.*, 2008; Tyson *et al.*, 2017). Photoperiod is a seasonal source of variation that is not commonly considered, yet has the potential to play a significant role in determining light specific breeding behaviours (Dawson *et al.*, 2001; Hill *et al.*, 2004).

Feeding a chick could be seen as a job split into two main tasks, one is foraging to gather the food, and the other is food delivery to the chick. For shearwaters, foraging occurs exclusively during daylight when it is light enough to visually pursue prey (Darby *et al.*, 2022). Meanwhile, food delivery to the chick at the colony occurs during the night, when it is dark enough to avoid predation (Perrins, Harris and Britton, 1973; Riou and Hamer, 2008). As the number of hours of daylight and darkness vary significantly over a season at high latitudes, this creates potential trade-offs between foraging and food delivery. I found that longer day lengths promoted chick feeding, allowing more hours of foraging, increased food delivery and ultimately increased chick weight gain. However, adults provisioning for chicks during long days had shorter nights to return to the colony. Whilst shearwaters typically avoid moonlit conditions when returning to the colony, I found that during shorter nights birds were less able to time their visit with moon-set (Riou and Hamer, 2008). Therefore, despite the benefits of increased foraging during longer days, birds during this time may be less able to avoid predation during certain moon phases. Photoperiod may therefore be another factor to consider when timing reproduction.

Can Individuals 'Catch Up' Timings on Parts of their Annual Cycle?

As in many avian species, Manx shearwaters have a large variation in breeding phenology, with earlier laying birds generally having higher breeding success (Brooke, 1978; Winkler *et al.*, 2020). The success of earlier laying birds may be attributed to better alignment with peak seasonal food abundance, and as indicated by the results of chapter 4, increased day light length in which to forage and gather these food resources (Burant *et al.*, 2022). As previously mentioned in chapter 1, although there are advantages to early egg laying for birds, they might not be capable of doing so if they are in suboptimal physical condition (Chastel, Weimerskirch and Jouventin, 1995; Barbraud, Lormée and LeNevé, 2000). We might therefore assume that earlier laying birds are in fairly good condition. Throughout this thesis I have considered a bird's choice of lay date to be a trade-off between individual condition and synchronising reproductive timings with peak food resources. Where individuals lay later, I sought to investigate whether they are able to catch up on their timings to arrive at the over-winter grounds during peak seasonal abundance (Dias, Granadeiro and Catry, 2012).

In chapter 2 I found that migratory timings were highly correlated with one another. That is, birds that left later on south-bound migration departed later on their north-bound migration. It therefore appears that phenology carries over from one season to the next. This suggests that individuals may have limited capacity to adjust their migratory timings from year to year. However, in chapter 3 I found that later laying birds took shorter duration migrations to catch up on their timings. These birds took fewer foraging stopovers and flew more at night, with night flight increasing during moonlit nights. Moon guided night flight is a phenomenon observed in multiple seabird species, yet had not been previously detected in Manx shearwaters (Bonnet-Lebrun *et al.*, 2021). Later laying birds additionally appeared to time their migratory departure with earlier phases of the lunar cycle. We hypothesised that this occurs so individuals can increase the number of moonlit nights during migration, therefore allowing birds to exploit more hours of flight over a 24 period. Therefore, through the exploitation of moonlit nights and reduced foraging stopovers, it appears that later-laying individuals are partially able to catch up on their migratory timings. This provides insight into how individuals are able to adjust for previous behaviour in order to maximise their fitness.

Are Individuals Constrained by Heritable Factors?

Whilst I have discussed the constraints that may arise as a result of environmental conditions, in chapter 5 I investigated how individuals are constrained by heritable factors. I specifically investigated sex-based differences in reproductive role, finding that males and females were subject to different constraints during pre-laying. Unlike in the other lifecycle stages considered in chapters 2 to 4, during the pre-laying period reproductive roles differ between sexes (Jouanin *et al.*, 2001; Pinet *et al.*, 2012). During egg synthesis, females take long duration foraging trips, whilst males visit the colony frequently and remain in a foraging area nearby. The deployment of dive loggers (TDRs) revealed that males took a higher number of dives per day than females and males took shallower dives during the pre-laying period. In other studies, such differences in dive behaviour are usually explained by physical dimorphism. For example, the larger member often dives deeper as a result of increased oxygen storage capacity allowing for consumption of higher tropic level prey (Halsey, Butler and Blackburn, 2006; Weimerskirch *et al.*, 2006; Quillfeldt *et al.*, 2011). Additionally, differences in wing loading have been argued to affect flight performance causing differing foraging distributions between sexes (Shaffer, Weimerskirch and Costa, 2001; De Pascalis *et al.*, 2020). There is also the potential for competitive exclusion of the smaller sex from foraging areas (Catry, Phillips and Croxall, 2006). However, although slight size differences between sexes can be present in Manx shearwaters, they are unlikely to be sufficient to drive this (Storey and Brooke, 1991).

Pre-laying differences in dive behaviour between sexes are more likely attributed to the different foraging areas exploited and potential prey present in these. Males are constrained to areas local to the colony, whilst females can exploit and locate the highest quality foraging areas. Additionally, whilst females took the majority of their pre-laying dives in the evening, males appeared less able to exploit evening foraging opportunities. This was due to increased male colony visitation meaning evenings were spent commuting or rafting close to the colony instead of foraging. When reproductive roles became near equal post-laying, males and females both took the majority of their dives in the evening. This suggests the evening may be a more profitable time for foraging, and that increased male colony attendance during pre-laying may constrain male diving behaviour. This is the first study to specifically investigate how varying colony constraints between sexes may impact dive behaviour. Although females appear unconstrained during pre-laying, they may require specific food resources for egg synthesis, a phenomenon observed in other species (Mallory and Forbes, 2008; Hemmings and Birkhead, 2020). Chapter 5 demonstrates that sex differences in foraging behaviour may be present in monomorphic species, and highlights the necessity for detailed investigations of foraging when behavioural constraints may vary between sexes. This is especially true during

understudied periods such as pre-laying, when behaviour may determine reproductive success (Wojczulanis-Jakubas, Jakubas and Chastel, 2014).

Future Directions

This thesis draws primarily on a long-term geolocator dataset of light and immersion. Whilst changes in light have long been used to estimate position, in this thesis I implement novel approaches for analysing geolocator data. Through utilising an understanding of the underlying biology of the species in question, I have demonstrated it is possible to use patterns in the light and immersion data to extract behavioural data. Specifically, I applied mixture models on patterns in the immersion data to assign nocturnal colony visitation in chapters 2, 4 and 5, and to assign stopover behaviour in chapter 3. Additionally, I used the immersion data to allocate when foraging occurred, gaining insight into an individual's at-sea behaviour. In chapter 2, I validated that colony visitation rates accurately reflect chick provisioning trips by aligning these rates with chick measurements obtained at the colony. Additionally, in chapter 4 I was able to provide an estimate of chick age through identifying a switch from incubatory to provisioning behaviour in the immersion data. In this thesis, only chick measurements and information on phenology from one of the study colonies was available. On Skomer Island shearwaters breed in burrows that are often reachable by hand, or can be accessed through a purpose-built hatch. Regular colony measurements would not be possible at many of the study colonies in this thesis. Some study sites such as Rum or Nólsoy Island are relatively remote and would be challenging to monitor over long periods. Additionally, the shearwaters often breed in deep, inaccessible burrows. Through extracting breeding metrics from geolocator data, in this thesis I was able to remotely obtain breeding information from study sites with low accessibility.

One of the major limitations of this thesis is that geolocator-derived positions are subject to substantial error (Lisovski and Hahn, 2012; Bridge *et al.*, 2013). I have partially tackled this limitation through utilising large sample sizes to improve the signal to noise ratio. Additionally, where possible I used longitudinal position which is known to be less subject to error than latitude. However, it would be useful in future work to gain a greater understanding of an individual's spatial behaviour throughout its annual cycle. For example, in chapter 3 we could gain a greater understanding of individual migratory strategies by obtaining data on the location of stopovers and routes taken by individuals. However southbound migration in shearwaters occurs almost directly during the autumn equinox, where latitude estimates are

difficult to interpret. Whilst new methods of geolocator position estimation are being developed, these methods may not be time efficient for large datasets such as that used in this thesis (Rakhimberdiev *et al.*, 2017; Roy *et al.*, 2020). Previous work using geolocator deployments have identified the main over-wintering and breeding foraging areas for numerous seabirds, increasing our knowledge of seabird hotspots and species-specific area use (Guilford *et al.*, 2012; Fort *et al.*, 2013; Carneiro *et al.*, 2020). However, it is difficult to provide detailed spatial information using geolocators. As biotelemetry technology continues to develop, GPS devices that record position to a high spatial resolution are becoming increasingly miniaturised, and therefore have potential for long term deployments on relatively small avian species such as shearwaters (Whitford and Klimley, 2019; Bolton, 2021; Isaksson *et al.*, 2021). Future studies may therefore be able to answer many of the questions that lead on from this thesis, some of which I will discuss throughout this next section.

How Far can Individuals Respond to Environmental Change?

The results of chapter 2 suggest that individuals have some plasticity in their over-wintering site selection, the mechanisms of which are still largely unknown among avian species. It is unclear how far an individual can adjust their over-wintering site from year to year. There is evidence for multiple mechanisms by which migratory information is inherited (Newton, 2008). Some migratory routes may be culturally inherited by following conspecifics or through individual exploration during a bird's first few years (Harrison *et al.*, 2010; Mueller *et al.*, 2013). For example, Atlantic puffins appear to learn individual over-wintering grounds following an exploration phase (Guilford *et al.*, 2011). In many cases, migratory routes appear genetically inherited (Yoda *et al.*, 2017; Merlin and Liedvogel, 2019). Previous geolocator deployment on Manx shearwaters suggests that fledglings reach the over-wintering grounds via a genetically inherited migratory vector (Wynn, Guilford, *et al.*, 2022). However, this was based on only 3 individuals, of 55 that were originally tagged as fledglings. To understand the development of migratory routes in shearwaters and other avian species, increased tracking of juvenile birds is required (Corbeau *et al.*, 2020). Given that it is difficult to relocate fledgling shearwaters for device retrieval, future work should involve using remote download tags to track first migrations. Additionally, as large scale oscillations are predicted to intensify due to anthropogenic warming, I suggest that continued adult tracking is needed (Grémillet *et al.*, 2008; Quillfeldt and Masello, 2013). Although the shearwaters in chapter 2 were able to vary their over-wintering latitude with changing ENSO conditions, they all over-wintered around the Patagonian shelf. If individuals are constrained by inherited migratory destinations, they may be less able to individually respond to extreme climatic changes. This thesis therefore

provides support for the increased monitoring and the collection of long-term datasets of animal movement.

Similarly, if environmental conditions were to become unfavourable at the breeding grounds, it is unclear whether shearwaters would be able to relocate. Although highly mobile species such as shearwaters are able to take long range foraging trips, in chapter 5 we see how central place foraging can constrain the exploitation of higher quality foraging grounds further afield (Guilford *et al.*, 2008). Shearwaters, like many seabird species are often philopatric and rarely exploit new breeding sites (Wynn, Padget, *et al.*, 2022). Food availability is not the only factor that defines where seabirds breed. They also require a breeding site that minimises predation risk and provides suitable conditions for nesting (Wakefield *et al.*, 2011; Werner, Paiva and Ramos, 2014; Rubolini *et al.*, 2015). Philopatry therefore allows birds to return each year to established breeding sites. However, this potentially constrains birds to breed within certain areas where environmental conditions may become unfavourable as anthropogenic climatic changes accelerate. At many seabird colonies, food availability at local foraging sites has already declined and breeding success has largely reduced (Carroll *et al.*, 2015; Fayet *et al.*, 2021). Specialised and long-lived seabird species such as albatrosses and petrels are considered most at risk of extinction (Richards, Cooke and Bates, 2021). In order to assess whether any plasticity in breeding locations may exist, it is important to understand how breeding sites are established. One way to understand how prospective breeders choose their sites would be to conduct future work tracking immature birds (Péron and Grémillet, 2013). In doing so we might gain a better understanding of dispersal behaviour under different environmental conditions.

Future work should additionally aim to further understand plasticity in diet. In chapter 5, I conducted a novel DNA metabarcoding analysis of Manx shearwater diet, the results of which suggested that shearwaters may be generalist in their prey choice. These results are however based on only 19 individuals as the majority of samples did not retain prey material. We were unable to look for sex differences in pre-laying diet, one of the primary objectives for the dietary analysis. Therefore, we still have little understanding of whether female shearwaters may require specific prey for egg formation (Mallory *et al.*, 2008; Hemmings and Birkhead, 2020). Understanding where dietary specificities may arise is fundamental within the context of climate change induced changes to prey community structure, especially during pre-laying where diet may influence egg formation (Jouanin *et al.*, 2001; Fayet *et al.*, 2021). Whilst DNA metabarcoding has proven to be a successful method of identifying prey in multiple pelagic species, we suggest that sampling procellariform seabirds may present a new set of challenges

(McInnes *et al.*, 2017; Deagle *et al.*, 2019). Procellariforms take long trips out to sea and may have excreted dietary material prior to returning to the colony to be sampled. Female foraging trips during pre-laying can be especially long as females undertake a 'pre-laying exodus'. Indeed, I obtained a lower number of faecal samples from females than males, with 45% of female sampling attempts resulting in sample collection whilst 63% of male sampling attempts were successful. Additionally, of the 19 samples that retained prey material, only 3 of these were from females. Given the pelagic pre-laying behaviour of females, it appears especially challenging to sample female pre-laying diet. One method we trialled as part of this thesis was to swab faecal material from 11 recently laid eggs, which could prove to be a more successful method for sampling female pre-laying diet. Alternatively, cloacal swabs could be taken, which might retain a higher amount of residual faecal material. I suggest that trialling new methods of dietary sample collection may improve the quantities of prey retained for future DNA metabarcoding studies investigating the pre-laying diet of shearwaters and other procellariform seabirds.

What Factors Determine Breeding Phenology?

In this thesis, I have repeatedly highlighted the importance of breeding phenology. In chapter 4 I explored how lay date influences how much light is available for chick provisioning behaviours. Meanwhile, in chapter 3 I found that lay date influences post-breeding migratory strategies, with later laying birds taking faster migrations. In chapter 2, I identified how migratory phenology appears to carry over from one season to the next, with birds leaving earlier on southbound migration returning earlier to breed the next season. Breeding phenology therefore appears to play a role in defining behaviour throughout the entire annual cycle. It is therefore important in future work to understand what factors might influence breeding phenology, especially as earlier lay dates are repeatedly linked to higher breeding success in avian species (Shipley *et al.*, 2020; Winkler *et al.*, 2020). In Manx shearwaters, lay dates have previously been found to be fairly individually consistent between years (Storey and Brooke, 1991). However, as female shearwaters age, there appears to be a general trend towards laying earlier (Brooke, 1978). An individual's lay date may therefore be defined by a combination of physical condition, age and previous behaviour.

In this thesis I used chick provisioning metrics as an indicator of adult breeding condition. To further understand how adult condition influences lay date, we must first theoretically determine what we are referring to when we discuss condition. Are we simply referring to an individual's body fat index, or is condition more physiological and therefore difficult to determine from morphology alone? Investigating such questions will likely require future

collaborations between physiologists and behavioural ecologists. Additionally, although I found no relationship between global scale oscillations and phenology, phenology may still be correlated with more specific environmental factors, unconsidered in this analysis. If shearwaters have lay dates that are near individually consistent, it is unclear whether they can adjust their phenology with environmental variation. Future work should provide a detailed exploration of relationships between phenology and sources of environmental variation such as wind, temperature and prey availability. As sampling increases across colonies of shearwaters, future work should also be able to better understand phenological variation between latitudinally distinct colonies. As it is difficult to age adult Manx shearwaters, this thesis was unable to investigate any age effects on phenology. However, through a combination of tagging both juveniles and known age birds ringed as fledglings, we might start to better understand the role of age in breeding phenology.

Concluding Remarks

This thesis draws on multi-year biotelemetry data to gain a greater understanding of seabird annual behaviour. Through the novel extraction of behavioural information from biotelemetry data I have been able to assess over-wintering, migratory and breeding behaviour and simultaneously investigate how individuals respond to constraints within each of these annual stages. Throughout this thesis I have described how individuals contend with the resultant trade-offs on which survival traits to maximise. For example, in chapter 3 I saw how individuals that depart later on their southbound migration maximise their behaviour so as to arrive quicker at the over-wintering grounds. However, in doing so, these individuals' trade-off the exploitation of stop-over foraging sites along the way. In chapter 4, I found that individuals who laid earlier or lived at higher latitudes trade off extended daylight hours for foraging with reduced night lengths for provisioning and predation avoidance. In chapter 5, I saw how pre-laying males trade off exploiting productive further afield foraging grounds with attending the breeding site for nest defence, and respond by taking an increased number of dives per day to maximise foraging opportunities.

Individuals appear responsive to environmental change, at the scale of both annual seasonal variation and longer phase climatic oscillations. However, in chapter 2 I saw that despite individuals adjusting both their distribution and foraging behaviour with shifting El Niño Southern Oscillation conditions, there were still carry over effects into subsequent breeding. Whilst this thesis highlights the behavioural plasticity of Manx shearwaters, the current rate of anthropogenic climate change may be beyond what individuals can adjust to. Therefore, the collection of long-term datasets of animal movements is essential for understanding how individuals continue to respond to environmental change. Additionally, I suggest that analysis of long-term data should link life cycle stages together to better understand the complex behaviour of individual animals.

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