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Environmental and phylogenetic drivers of European Storm Petrel (*Hydrobates pelagicus*) foraging behaviour from two colonies in Ireland

Thesis presented by

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for the degree of

Master of Science

University College Cork

School of Biological, Earth & Environmental Sciences

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Declaration: This is to certify that the work I am submitting is my own and has not been submitted for another degree, either at University College Cork or elsewhere. All external references and sources are clearly acknowledged and identified within the contents. I have read and understood the regulations of University College Cork concerning plagiarism.

Acknowledgements

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Abstract

Seabird populations are globally in decline. In order to successfully devise and implement conservation protocols, an understanding of their at-sea distribution is required. Miniature GPS devices were used to investigate the foraging movements of European storm petrels (*Hydrobates pelagicus*) breeding on two islands along the west coast of Ireland. In this study storm petrels appeared to perform a combination of long and short foraging trips. The mean foraging trip duration, total distance travelled and foraging range of the tagged storm petrels that performed long foraging trips were 53 hours, 749 km, and 226 km, respectively. On short trips the mean values were 23 hours, 287 km, and 114 km while the mean trip metrics for all foraging trips combined were 38 hours, 518 km, and 170 km, respectively. A model was developed to investigate the energetics associated with performing foraging trips of long and short durations. The results suggest that storm petrels may be operating at an energy deficit when performing short foraging trips and consequently may use long-distance trips to replenish their energy reserves. On long foraging trips, storm petrels were recorded foraging at the continental shelf edge, but foraging by the coast was also evident. As a predictor of marine productivity, chlorophyll-*a* concentration was modelled with the GPS tracking data, and the transition to foraging behaviour was positively correlated with high chlorophyll-*a* for one of the colonies. Comparative analyses showed that phylogenetic relatedness is a key component influencing the foraging duration, distance, and range of procellariiform seabirds. These analyses also indicated that the storm petrel's foraging trips conform to the general patterns observed for a procellariiform species of its size during the chick-rearing phase of the breeding season, but that the storm petrel performs foraging trips that are shorter in duration, distance and range than would be expected during incubation. This study adds to the limited knowledge of the European storm petrel's foraging movements during the breeding season and provides insight into the factors influencing its foraging distribution.

1. Introduction

Seabirds are one of the most threatened avian groups (Croxall *et al*., 2012). Between 1950 and 2010, monitored populations (representing approximately 19% of the global seabird population) declined by 70% (Paleczny *et al*., 2015). Seabirds have been identified as good indicators of the condition of marine ecosystems (Parsons *et al*., 2008), which makes the dramatic decline a major concern. In a global assessment of the threats to seabird species, Dias *et al*. (2019) determined that invasive alien species, fisheries bycatch, and climate change/severe weather were the three main threats, impacting 165, 100, and 96 species, respectively. The majority of threatened seabird species are subject to multiple pressures (Dias *et al.*, 2019), affecting them at their terrestrial breeding colonies (e.g. invasive alien species, disturbance) and at sea (e.g. bycatch, pollution, offshore infrastructure, prey depletion due to competition with fisheries and/or climate change). Seabirds with a pelagic foraging habit have suffered the largest population decline over the past few decades (Paleczny *et al*., 2015) with albatrosses and petrels, which contain many far-ranging pelagic species, being two of the most threatened seabird groups (Dias *et al*., 2019).

Bio-logging

Understanding the distribution of biodiversity is crucial for effective management and conservation. This is especially challenging in the marine environment, where species are difficult to monitor. Overcoming this challenge has been aided by animal-borne monitoring technology. The opening decades of the 21st century have seen great developments in the field of biologging (the practice of attaching data-collecting devices to animals) and in the technology behind these devices. It is now possible to attach miniature, light-weight sensors to wild animals, which are capable of remotely monitoring species and their environment. These technological advances are revolutionising how wild animals can be studied, and are enabling researchers to answer questions on species behaviour, physiology, population demographics, foraging and migratory movements, and habitat selection (Wilmers *et al*., 2015).

One of the key areas of development has been global positioning system (GPS) telemetry technology. Modern animal-borne GPS devices allow researchers to examine the movements of animals with greater precision than ever before, including species on which it was previously impossible to conduct movement studies, such as

some marine and long-distance migratory species (Hebblewhite & Haydon, 2010). The use of GPS technology for tracking animal movements has been the subject of several detailed reviews (e.g. Cagnacci *et al.*, 2010; Tomkiewicz *et al.*, 2010) and these have highlighted numerous advantages of this technology compared to other tracking devices such as VHF (very-high frequency) and Argos satellite systems. Key advantages are the ability of GPS devices to very accurately determine the position of tagged animals (errors of 30 metres or less), to be operational 24 hours a day if required, and to rapidly update the position of the tagged individual (Cagnacci *et al.*, 2010; Tomkiewicz *et al.*, 2010). Thus, many researchers have successfully used GPS tags to address ecological questions, including the study of animal movements and habitat use for the purposes of management and conservation (e.g. Avgar *et al.*, 2013; Schofield *et al.*, 2007), the study of foraging movements and behaviour (e.g. Weimerskirch *et al.*, 2007), and the identification of non-breeding territories and population boundaries (e.g. Hallworth & Marra, 2015).

GPS technology has proven to be especially useful in avian research, and GPS devices have been used extensively in the study of colonially nesting, large seabird species (e.g. Grémillet *et al.*, 2016; Hamer *et al.*, 2009; Waggitt *et al.*, 2014; Votier *et al.*, 2010). Prior to the invention of GPS and other tracking technologies, research on the behaviour and ecology of seabirds was largely restricted to observational studies from vessels or at breeding colonies (Burger & Shaffer, 2008). Several limitations have prevented the widespread use of GPS devices for avian tracking studies, device size being the most important (Wikelski *et al.*, 2007). This has resulted in major gaps in the knowledge of the foraging ecology of small seabird species. It is universally accepted that the impact of tracking devices on tagged animals should be as minimal as possible, both for the welfare of the animal, and to provide confidence that the data gathered is representative of natural behaviours (Casper, 2009). Guidelines have been devised in an attempt to reduce negative impacts to animals, with the '5% rule' being widely cited. This guideline states that the entire load of the device and attachment apparatus should be less than 5% of the animal's body mass. However, when applying the '5% rule', Wikelski *et al.* (2007) noted that the smallest satellite tracking device on the market in 2006 was too heavy for approximately 81% of birds with known body mass measurements. Phillips *et al.* (2003), after reviewing the impact of devices on albatrosses and petrels, stated that transmitter loads should be kept below 3% of body

mass. Employing the device weight standard devised by Phillips *et al*. (2003) further reduces the range of avian species eligible for telemetry research. However, due to recent technological advancements, GPS tags weighing <1g are now available, allowing these devices to be deployed on bird species as small as 25-30g. The deployment of animal-borne tracking devices is enabling researchers to investigate seabird migratory and foraging behaviour (Croxall *et al*., 2005; Soanes *et al*., 2015) in detail and in species previously unattainable.

Seabird Ecology

There are a number of factors affecting the foraging distribution of central place foraging, pelagic seabirds during the breeding season. A major constraint is the requirement for breeding adults to return to the nesting site at regular intervals in order to care for their offspring (Quillfeldt *et al*., 2010). Breeding seabirds need to sustain the energetic demands of their chick, while maintaining their own body condition (Burke & Montevecchi, 2009). This conflict is expected to be especially evident in species that must travel long distances in order to access patchily distributed prey, as the energetic costs associated with commuting between the colony and feeding grounds can be a major limitation in the ability of each member of a breeding pair to fulfil both their own and their chick's requirements (Burke & Montevecchi, 2009). To overcome this conflict, many procellariiform seabird species have adopted a dual foraging strategy where breeding adults alternate between short and long foraging trips (Shoji *et al*., 2015). Repeated short foraging trips are conducted to maximise the chick provisioning rate, while long trips are performed for the adult's self-maintenance. Seabirds may profit from visiting distant foraging areas as they are highly productive (Magalhães *et al*., 2008), there is reduced resource competition (Wakefield *et al*., 2013), or they contain prey nutritionally more beneficial for adults than chicks (Alonso *et al*., 2012). However, the chicks are at a disadvantage as the feeding rate is decreased due to the long duration of the foraging trips. Dual foraging strategies have been identified in numerous procellariiform species including Blue petrels (*Halobaena caerulea*; Chaurand & Weimerskirch, 1994), Cory's shearwaters (*Calonectris borealis*; Magalhães *et al*., 2008), Manx shearwaters (*Puffinus puffinus*; Wischnewski *et al*., 2019), Short-tailed shearwaters (*Ardenna tenuirostris*; Weimerskirch & Cherel, 1998), Sooty shearwaters (*Ardenna grisea*; Weimerskirch, 1998), Streaked shearwaters (*Calonectris leucomelas*; Ochi *et al*., 2010), and Yellow-nosed

albatrosses (*Thalassarche chlororhynchos*; Pinaud *et al*., 2005). In some species which employ this dual foraging strategy, the adult's decision to perform a long or short foraging trip is controlled by the chick condition (e.g. Wischnewski *et al*., 2019; Ochi *et al*., 2010), whereas the breeding adults of other species prioritise their body condition, electing to embark on a large foraging trip when required, irrespective of the condition of the chick (e.g. Weimerskirch, 1998; Weimerskirch & Cherel, 1998).

In some species, such as the wandering albatross (*Diomedea exulans*; Weimerskirch *et al*., 1993), the foraging distribution of adults fluctuates during the breeding season due to the energetic requirements of the chick changing over time. Like all central place foragers, the adult is constrained by the requirement to return to its nest to provision its offspring (Antolos *et al*., 2017). During egg incubation, the non-incubating member of the breeding pair is able to perform long, far-ranging trips (approximately 2-3 weeks) while its partner fasts at the nest, however, trip duration has been shown to decrease to approximately 3 days when the chick hatches as the offspring requires regular meals, and then to increase again when the chick gets larger (Antolos *et al*., 2017).

The abundance and distribution of prey is another factor that influences the foraging distribution of seabirds. When the quality, quantity, and distribution of prey is favourable, a reduction in foraging trip duration and distance is expected (Quillfeldt *et al*., 2010). However, during periods of poor prey availability, some seabird species can temporarily increase their foraging effort by extending the duration of foraging trips and/or travelling further from the breeding colony (e.g. Kitaysky *et al*., 2000). Nevertheless, during the breeding season many seabird species are operating at tight energy constraints and as a result, for many species, breeding success is dependent on the predictability of resources (Weimerskirch, 2007). Prey resources in the marine environment have generally been assumed to be patchily distributed and unpredictable; however, it is now apparent that they may be more predictable than previously thought (Weimerskirch, 2007). Bathymetric features such as shelf edges have been found to support high levels of primary and secondary productivity (Cox *et al*., 2018) and so provide a predictable food source for marine mammals and seabirds (Weimerskirch, 2007). Therefore, the exploitation of profitable and predictable

foraging areas would be advantageous for breeding seabirds as it would reduce the time and energy spent searching for prey over large areas.

It is believed that procellariiform seabirds use their excellent sense of smell to locate profitable foraging zones within the vast, seemingly featureless marine environment (Nevitt, 2008). Dimethyl sulphide (DMS) is a scented compound produced as a by-product of the metabolic decomposition of dimethyl sulphoniopropionate in marine organisms, especially phytoplankton (Dacey & Wakeham, 1986). The rate at which DMS is released is increased when zooplankton graze on phytoplankton (Dacey & Wakeham, 1986). Experimental research has shown that some marine organisms such as procellariiform species (e.g. white-chinned petrels, *Procellaria aequinoctialis*; Nevitt *et al*., 1995) can detect and are attracted to DMS concentrations (Nevitt, 2008). DMS concentrations have been found to be associated with bathymetric features such as seamounts and upwelling zones; and DMS odours are not ephemeral but can persist for several weeks (Nevitt, 2000). The ability to detect DMS would be advantageous for seabirds as it would allow them to locate and exploit the highly productive waters surrounding the associated bathymetric feature (Nevitt *et al*., 1995) and Nevitt (2000) proposed that, at large spatial scales (thousands of square kilometres), procellariiforms use the olfactory landscape produced by DMS concentrations for navigation and to locate suitable foraging grounds. This therefore allows them to optimise energy acquisition. Nevitt (2000) also suggested that procellariiforms may use olfactory cues to pinpoint the location of prey on a finer scale.

Another factor influencing the foraging distribution of seabirds is body mass and wing morphology. A large body mass limits the flying ability of seabirds which employ a flapping flight technique (Paredes *et al*., 2015; Wilson *et al*., 2006). However, Pennycuick (1982) identified that heavier procellariiforms tend to have a larger wing span and wing area and that species with large wings typically used an energetically low cost gliding flight method. In contrast, smaller procellariiforms utilised flapping or flap-gliding (regular alteration between flapping and gliding) flight (Pennycuick, 1982). In general, procellariiforms with a large body mass are capable of performing foraging trips of longer durations and distances compared to their smaller relatives. There are numerous examples of large procellariiforms performing far-ranging foraging trips. Kappes *et al*. (2010), for example, used telemetry devices to record the

foraging trips of the Laysan albatross (*Phoebastria irrorata*), with a body mass of approximately 2.8 kg, during the incubation period and found this species to have a mean trip duration of 17.6 days, a mean distance travelled of 9564 km, and a mean foraging range from the colony of 2356 km. In contrast, during incubation the 45g Leach's storm petrel (*Hydrobates leucorhous*) was recorded to have a mean foraging trip duration of 4.6 days, a mean distance travelled of 1371 km, and a mean foraging range of 587 km (Pollet *et al*., 2014). However, there have been some recorded cases of small procellariiform species with extreme foraging distributions. One such example is the Barau's petrel (*Pterodroma baraui*) which is a small, burrow-nesting petrel weighing approximately 400g. Pinet *et al*. (2012) recorded this species' foraging movements during the incubation phase of the breeding season and, despite its small size, the Barau's petrel embarked on foraging trips lasting on average 17 days, covering a mean distance of 7796 km and ranging on average 3216 km from the colony. Despite exceptions like this, flight energetic calculations indicate that in procellariiforms, larger species can perform foraging trips of longer durations and distances, and range further from the colony, than smaller species (Pennycuick, 1982).

The European Storm Petrel

The European storm petrel (*Hydrobates pelagicus*) (hereafter "storm petrel") belongs to the northern storm petrel family Hydrobatidae, a family within the order Procellariiformes. The storm petrel is one of the smallest procellariiform species with a body mass of approximately 26g (Cadiou *et al*., 2010). The small size of the storm petrel has, until recently, prevented the use of satellite telemetry to study its movements, resulting in researchers relying on observations from vessels or the coastline, as well as diet analysis to examine foraging behaviour during the breeding season (Flood *et al*., 2009; Poot, 2008; D'Elbée & Hémery, 1998) and the use of sound lures and capture-mark-recapture methods when studying non-breeding individuals (Okill & Bolton, 2005). The storm petrel has a breeding distribution spanning the northeastern Atlantic Ocean and western Mediterranean (Cramp & Simmons, 1977) with large breeding populations being found on the Faroe Islands, Iceland, British Isles, and Ireland (Mitchell *et al*., 2004). As a result of genetic studies conducted by Cagnon *et al*. (2004) and observed morphological differences, it was determined that the Atlantic and Mediterranean populations are separate subspecies: namely *Hydrobates pelagicus pelagicus* for birds breeding in the northeast Atlantic, and *H. p.*

melitensis for birds breeding in the Mediterranean Sea. While *H. p. melitensis* typically stays within the Mediterranean Sea during the winter (Lago *et al*., 2019), *H. p. pelagicus* is a long-distant migrant which spends the winter off western and southern Africa (Cramp & Simmons, 1977) before migrating back to their north Atlantic breeding colonies in March or April (Cadiou, 2001). The storm petrel is considered to be mainly a pelagic species, only coming to land for breeding (Cramp & Simmons, 1977) and all behaviour at the breeding site is performed at night or in the nesting cavity to avoid detection from predators (e.g. Oro *et al*., 2005). This species has a range of nesting habitats, including natural cavities, under rocks and boulders, in dry stone walls, in self-excavated burrows, and in burrows previously excavated by other species such as Manx shearwaters (*Puffinus puffinus*) and rabbits (*Oryctolagus cuniculus*) (Cramp & Simmons, 1977). Due to the nocturnal habits and underground breeding behaviour of this species, censusing populations is challenging. Population censusing conducted between 1998 and 2002 estimated the population across Great Britain and Ireland to be approximately 125,000 pairs (Mitchell *et al*., 2004), representing 20-25% or the global population. Irish colonies accounted for around 80% of the combined Great Britain and Ireland total (Mitchell *et al*., 2004). Due to the difficulties associated with studying this species, it is not known if its global population is increasing, decreasing or stable (IUCN, 2021).

During the breeding season, storm petrels are central place foragers and a breeding pair lays a single egg which both the male and female incubate (Cramp & Simmons, 1977). After hatching, the chick is brooded for approximately 7 days before being left alone in the nest during the day, with the parents returning at night to provision (Davis, 1957). A study of the provisioning rate of storm petrels conducted by Bolton (1995) on the island of Mousa, Shetland, showed that chicks are fed in one day intervals almost 80% of the time, and the interval between feeds rarely exceeds two days. Both members of a breeding pair feed their chick but they operate independently of each other (Bolton, 1995). As a result, a chick can be fed by both, one, or neither parent on a given night.

Diet analysis has enabled researchers to examine the composition of the diet and has provided an indication of where this species forages for its food. The Atlantic and Mediterranean subspecies of the storm petrel appear to have varying foraging

behaviours and diets (Albores-Barajas *et al*. 2011; D'Elbée & Hémery, 1998), possibly due to the availability of different food resources, although further research in this area is required. The storm petrels belonging to the Atlantic subspecies studied by D'Elbée & Hémery (1998) were found to have a diet largely composed of zooplankton found over the continental shelf and likely caught from the ocean surface using a foraging technique known as pattering (Cramp & Simmons, 1977). In contrast, Albores-Barajas *et al*., (2011) discovered that the studied sample of the Mediterranean subspecies had a diet consisting mainly of pelagic fish species caught by diving below the surface. It was previously thought that the storm petrel was exclusively a pelagic species but both the D'Elbée & Hémery (1998) and Albores-Barajas *et al*. (2011) studies found evidence of foraging occurring in the intertidal zone. The use of olfactory cues to aid foraging over large and small spatial scales has not been examined in the European storm petrel, however, the closely related Leach's storm petrel (*Hydrobates leucorhous*) was found to be attracted to DMS (Nevitt & Haberman, 2003), and so it is possible the same is true for the European storm petrel.

While diet studies allow researchers to identify where seabirds are capturing prey, they do not provide information on all the movements of a foraging trip. Only two studies examining the foraging movements of storm petrels with GPS devices during the breeding season have been published to date. One study was conducted on the island of Mousa, Shetland Isles, UK (Bolton, 2020) and the second was conducted on the Mediterranean subspecies breeding on the island of Benidorm which is located in the southwest Mediterranean Sea (Rotger *et al*., 2020). Both studies revealed the capability of storm petrels to travel long distances on foraging trips. GPS analysis of foraging movements has not yet been conducted on storm petrels breeding in Ireland. Therefore, this study is the first to provide detailed insight into the foraging movements of Irish breeding storm petrels.

Aims

Through the deployment of GPS tags on breeding storm petrels from two colonies off the west coast of Ireland, this study will: (1) provide detailed information on foraging trip characteristics; (2) investigate the energetic demands of performing long and short foraging trips during the breeding season; (3) examine if this species' foraging distribution is influenced by the distribution and abundance of prey resources, for

which chlorophyll-*a* concentration will be used as a proxy; (4) examine if this species' foraging distribution is associated with bathymetric features, particularly the continental shelf edge. Additionally, this study (5) also includes a meta-analysis examining the interaction between body size and colony location with different foraging trip metrics (trip duration, trip distance, and foraging range) among species of the order Procellariiformes, and will assess how the European storm petrel's foraging abilities compare to its larger relatives.

2. Methodology

2.1 Study site

Fieldwork was carried out in mid-August 2020 on the island of Illauntannig (52º19'30.65"N, 10º01'18.79"W), the largest of the Magharee Islands, located off the coast of County Kerry, Ireland (Figure 1). Illauntannig is a low-lying island that is largely covered in grass and has an extensive stone wall field system. The Magharee Islands are found within a Special Area of Conservation and are considered to be of international importance for their colonies of breeding seabirds (BirdLife International, 2020). BirdLife International has classified this island group, along with the nearby islands of Mucklaghmore and Illaunnabarna, as an Important Bird Area (BirdLife International, 2020).

2.2 Tag deployment

The fieldwork was approved by University College Cork's Animal Experimentation Ethics Committee, and was licensed by the National Parks and Wildlife Service and the British Trust of Ornithology. During the chick-rearing phase of the breeding season, adult storm petrels nesting within stone field walls were caught at night using a combination of purse and mist nets. Purse nets were placed over suspected nest entrances and mist nets were draped over sections of stone wall. The nets were checked every ten minutes to ensure any caught storm petrel was not trapped for an extended period of time. Caught storm petrels were weighed to 0.1g and ringed by a licensed ringer. A Pathtrack nanoFix GEO-Mini tag was attached to the central tail feathers using three 2mm wide strips of Tesa® tape. Each tag weighed <1g (mean tag weight = 0.89g). Device deployment (tag plus tape) represented 3-4% of storm petrel

body mass. The manufacturer specifications of these tags state that they have a battery capacity of approximately 160 GPS attempts. The tags were therefore programmed to record GPS locations at 30-minute intervals to enable the recording of entire foraging trips lasting 1-3 days. Tag deployment was conducted on two consecutive nights, and this was followed by two consecutive nights of tag retrieval. Fieldwork was forced to end prematurely due to incoming bad weather and as a result it was not possible to retrieve tags deployed on storm petrels that performed foraging trips in excess of 3 days.

Mist nets, draped over the nest entrances of the tagged individuals, were used to recapture the birds and the nets were monitored at ten-minute intervals to ensure timely extraction. When a bird was recaptured the tag was removed and the bird was weighed. Recaptured birds were then released and the mist net was removed from their nest entrances. Caught untagged birds were removed from the net, and either manually placed under the net so it could access its nest, or released outside the net, depending on whether it had been leaving or entering its nest.

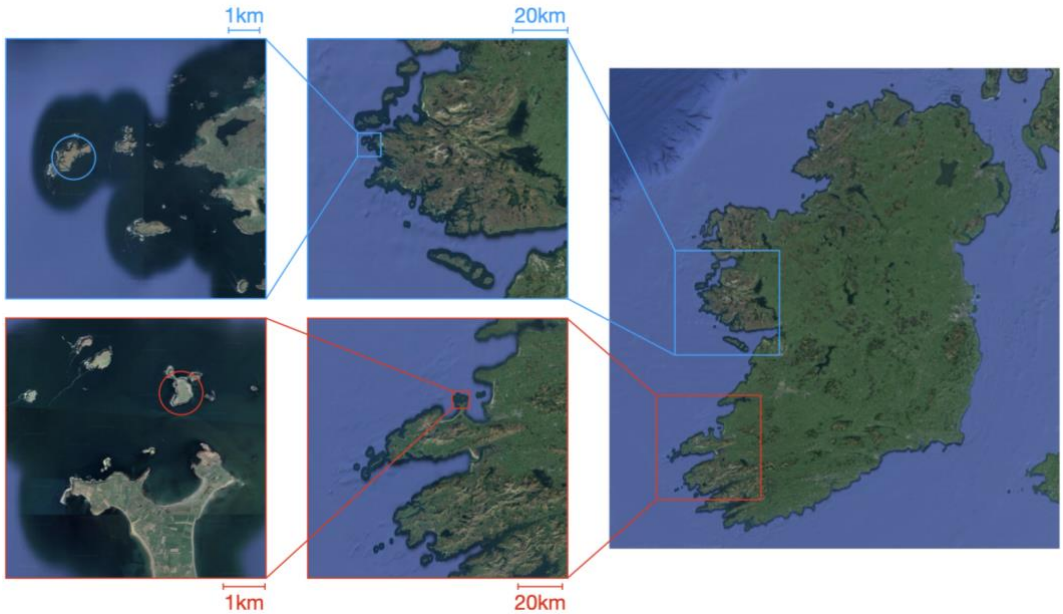


Figure 1. European storm petrel colonies from which data was collected for this study. Red: Illauntannig, Magharee Islands, Co. Kerry (2020). Blue: High Island, Co. Galway (2016). The circles indicate the exact location of each island. Source: Google Maps.

2.3 Potential impacts of tag deployment on foraging ability

The body mass of storm petrels before and after tag deployment was compared in order to investigate if the deployment of GPS tags on storm petrels had a negative impact on their foraging ability. No significant change in body mass would indicate that no negative impact was experienced.

2.4 Processing of tracking data

In addition to the data collected on storm petrels breeding on Illauntannig, further storm petrel GPS tracking data was provided for this project (Kane, pers. comm). This additional data was collected on High Island, County Galway (53º32'47.9"N, 10º15'26.3"W) in 2016 as part of ongoing seabird research at University College Cork (Figure 1).

Any journeys recorded that were less than 12 hours in duration were removed from the analysis as these were not considered to be foraging trips. In addition, any foraging trips that failed to return to within 0.5km of the breeding colony were considered as incomplete. When a tag recorded more than one foraging trip, the 0.5km buffer was used to determine when one trip ended and the other began. Any GPS locations recorded within the buffer were removed for the calculation of foraging trip metrics.

All analyses were conducted in R version 3.6.3 (R Core Team, 2020). The following metrics were calculated from the recorded complete foraging trips using the adehabitatLT (Calenge, 2006) and trajr (McLean & Skowron Volponi, 2018) R packages: (1) foraging trip duration (hours), defined as the length of time between the departure of a storm petrel from the colony (i.e. when the petrel was more than 0.5km from the colony) and its return to within 0.5km of the colony; (2) total trip distance (kilometres), defined as the sum of the distances between each successive GPS location recorded on a foraging trip, including the colony location at the start and end of the trip; (3) foraging range (kilometres), defined as the straight-line distance from the colony to the furthest location recorded during a foraging trip; (4) mean speed (kilometres per hour), defined as the average speed travelled by a storm petrel on a foraging trip; and (5) max speed (kilometres per hour), defined as the maximum speed travelled by a storm petrel between two successive GPS locations.

All but one of the foraging trips contained prolonged periods of time where the GPS tag failed to record locations. These periods of missing data were removed for the calculation of mean speed by splitting the foraging trips where there was a time lag of more than 61 minutes between two consecutive GPS locations (twice the sampling interval plus one minute to account for the slight variance in the programmed 30-minute sampling interval which occurred), resulting in the foraging trips being divided into multiple smaller sections of continuous location data. This was achieved using the cutltraj function in the adehabitatLT R package (Calenge, 2006). Speed was then determined by dividing the distance between each consecutive GPS location within the remaining foraging trip sections by the time taken to travel that distance. The mean speed of a foraging trip was then determined by finding the average of all the speed values calculated for that trip.

As the tags deployed on storm petrels from the High Island colony were programmed to start recording at 5am, by which time the petrels would already have been out at sea, the calculations of the duration of each trip from this colony were underestimates of the actual duration. Similarly, the total distance travelled values were also underestimates as the calculations assumed that the storm petrels travelled in a straight line from the colony to the point at which it was recorded at 5am, which is unlikely to have been the reality.

The correlation between different trip metrics (trip duration, total trip distance, and foraging range) was calculated employing Pearson's correlation coefficient on the complete trip data with the prediction that a significant correlation would exist between each of the variables. A 5% level of significance was used for this test.

2.5 Foraging energetics

Brandl and Gorke (1988) developed a model that examined the maximum foraging range breeding Black-headed gulls (*Larus ridibundus*) were capable of reaching without suffering a net energy deficit. Brandl and Gorke's (1988) model was adapted to separately examine the energy budget of long and short storm petrel foraging trips. In this study, it was assumed that the European storm petrel employed a dual foraging strategy where short trips were undertaken to maximise the chick provisioning rate, while long trips were performed for the adult's self-maintenance. The model is:

$$R = \frac{VLq_f}{2(1-q_f)E_r + q_f E_f + E_j}$$

where V is the flying speed (metres per second); L is the energy density the bird can carry (Joules), calculated by multiplying the capacity of food the bird can hold by the energy density of the food; q_f is the proportion of time spent flying; E_f is the energetic cost of flight (Watts); E_r is the energetic cost of other activities (Watts; i.e. any activity other than flight); E_j is the energy expenditure of the chick which has to be covered by one foraging adult (Watts); and R is the foraging range (metres but subsequently converted to kilometres), defined as the maximum straight-line distance from the colony a bird can reach with a balanced energy budget (i.e. no energy surplus or deficit).

As there is a lack of data on the energetics of European storm petrels, the Wilson's storm petrel (*Oceanites oceanicus*) was used as a proxy as this species has a similar ecology to the European storm petrel. However, the Wilson's storm petrel is larger (body mass ~40g; Obst *et al.*, 1987) and so the lower end of the range for their energetic estimates were used for the European storm petrel. Therefore, the energetic values used for E_f, E_r and E_j in this model were 1.04 Watts, 0.68 Watts, and 0.95 Watts, respectively (Obst *et al.*, 1987). The value used for flying speed was the mean flight speed recorded from the tracking data collected in this study. The proportion of time European storm petrels spend flying is high and an estimate of 95% was used. This model assumes that a storm petrel begins and ends a foraging trip with a balanced energy budget. A petrel could extend its foraging range by self-provisioning during the trip and for this it is assumed that for each 'feeding event' the storm petrel consumes its maximum capacity of food. European storm petrels are known to have the capacity to hold approximately 5g of food (D'Elbée & Hémery, 1998) and the food consumed by Wilson's storm petrels has an energy density of 4330 Joules per gram (Pennycuick *et al.*, 1984). Therefore, the energy density European storm petrels can carry was calculated to be 21650 Joules.

Two versions of this model were conducted, one to examine the energy budget of short foraging trips, and one for long trips. The model examining short foraging trips

included the energetic cost associated with chick provisioning (E_j = 0.95 Watts), whereas the model for long trips excluded the energetic impact of provisioning a chick (E_j = 0 Watts) as long trips were assumed to be primarily for adult self-maintenance. Each version of the model was conducted to determine the amount of feeding events required to achieve a foraging range with a balanced energy budget that is comparable to the results of the ranges of long (>36 hours) and short (<36 hours) foraging trips recorded from the GPS devices in this study.

2.6 Influence of prey distribution and abundance on storm petrel foraging distribution

Chlorophyll-*a* concentration is commonly used as an indication of ocean productivity with areas of high chlorophyll-*a* concentration being highly productive, and therefore suitable foraging grounds for higher trophic predators. Analyses were conducted to examine whether the storm petrel's foraging distribution was influenced by the presence and abundance of its zooplankton prey. Chlorophyll-*a* concentration was used as an indication of phytoplankton, inferring the abundance of zooplankton. If the foraging distribution of storm petrels is influenced by prey abundance, it is expected that foraging behaviour, as opposed to other behaviours such as transiting, would be associated with areas of high chlorophyll-*a* concentration.

In order to examine whether areas of high chlorophyll-*a* concentration were associated with the performance of foraging behaviour, behaviour transitions along the foraging trips first had to be defined. This was achieved by applying a two-state Hidden Markov Model (HMM) to the complete and incomplete foraging trip tracking data using the MomentuHMM package in R (McClintock & Michelot, 2018) as the use of HMMs has been shown to be an effective way of inferring behaviour states. Bennison *et al.* (2018) found that foraging behaviour states deduced from HMMs corresponded well with actual feeding events. The tracking data was interpolated to regularise the time intervals to 30 minutes by applying a Cathmull-Rom spline using the PathInterpolatR package (Long, 2020). Behaviours were annotated to the interpolated track points by considering step length and turning angle. A gamma distribution was used for the step length distribution (units in metres) and a von Mises distribution was selected for the turning angle distributions (units in radians). From the resulting HMM, the MomentuHMM function which applies the Viterbi algorithm was used to assign a behaviour state to each track point.

While it is common to use a three-state HMM for studies of this nature (e.g. Kane *et al*., 2020), which examine transiting, resting and Area-Restricted Search (ARS, reflecting putative foraging) behaviours, this study applied a two-state model as the European storm petrel is not considered to spend protracted periods of time resting on the water, and any resting behaviour that may have occurred would be challenging to identify with a time interval of 30 minutes. Therefore, the two states used in this HMM were assumed to be transiting and ARS/foraging. Transiting was characterised by small turning angles and large step lengths, while ARS had small to medium step lengths and large turning angles. Models were run for each colony that included and excluded the impact of chlorophyll-*a* concentration (monthly, 4km resolution) on the transition probabilities among behaviour states to examine if chlorophyll-*a* concentration triggered foraging. The resulting models were then compared using the Akaike information criterion (AIC). Chlorophyll-*a* concentration (monthly, 4km resolution) values were obtained from the National Aeronautics and Space Administration's Ocean Colour Forum using MODIS sensor data and these values were interpolated using an inverse-distance-weighted interpolation and annotated using the Env-DATA system on Movebank (Dodge *et al*., 2013).

2.7 Influence of oceanographic features on storm petrel foraging distribution

Several oceanographic features in proximity to the two storm petrel breeding colonies could potentially influence the distribution of foraging petrels. These include bathymetric features, such as the shelf edge of the Porcupine Bank and the slope and deep waters of the Porcupine Seabight (Figure 2a). There are also frontal zones within the storm petrel's potential range, namely the Shelf-Slope Front which runs along the edge of the Porcupine Bank, and the Mid-Shelf Front located between the continental shelf edge and coastline (Figure 2b). Using the behaviour states defined by the preferred two-state HMM model for each colony, the proximity of foraging behaviour to the shelf edges of the Porcupine Bank and Porcupine Seabight were examined. The distance of each behaviour point to the shelf edge was calculated using the dist2isobath function within the marmap package (Pante & Simon-Bouhet, 2013). For this calculation the shelf edge was represented by the -500m isobath. In order to conduct a chi-square test, each behaviour point was placed within a distance interval, depending on its proximity to shelf edge: 0-39.9km, 40-79.9km, 80-119.9km, 120-

159.9km, and 160+km. The chi-square test was conducted to examine if there was a significant difference in the number of foraging behaviour points in each of the distance intervals, or if the storm petrels foraged equally in each interval.

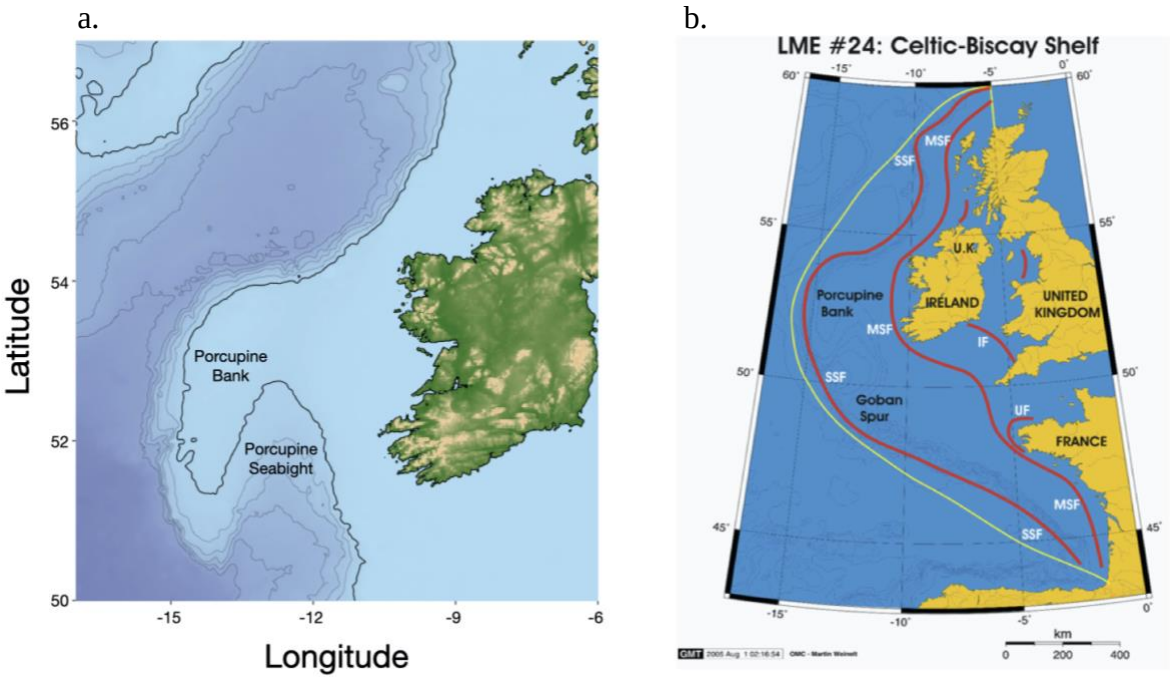


Figure 2. (a) Location of the Porcupine Bank and Porcupine Seabight. (b) Location of shelf fronts. SSF = Shelf-Slope Front, MSF = Mid-Shelf Front (Belkin *et al*., 2009).

2.8 Comparative analysis of foraging trip characteristics

A comparative analysis of procellariiform foraging trip characteristics was completed to examine how body mass influences foraging trip duration, distance and foraging range, and to test whether the storm petrel conforms to the general patterns observed. Breeding colony location was also included in this analysis, as well as a procellariiform phylogeny to account for non-independence as a result of common ancestry.

A literature search for studies in which telemetry devices were used to examine foraging behaviour of procellariiforms was conducted by searching through online databases such as Google Scholar and the University College Cork Library database. Additionally, the bibliographies of the studies found were searched for further references. Studies were included in the analyses if they met all of the following

criteria: (1) the study reported findings of a species from the order Procellariiformes; (2) the study reported at least one of the response variables of interest (foraging trip duration, foraging trip distance, foraging range) which the researchers determined through the use of telemetry devices; (3) the study was conducted during the species' breeding season and specified whether data collection was conducted during the egg incubation or chick-rearing period (studies that published findings which combined data from both of these phases were not included); and (4) the study stated the breeding colony location. The data extracted from the studies that met the selection criteria are outlined in Appendix 1. The body mass of each species (before deployment of the telemetry device) was obtained from the studies or, if missing, a further literature search was conducted to find published body mass values. If the body mass was reported separately for males and females, the mean mass was recorded as the difference between sexes was not being examined in this study.

As many procellariiform species behave differently during the egg incubation and chick-rearing breeding phases, a series of models were prepared separately for these two periods. For all models, body mass and the response variable were log-transformed. In addition, latitude was squared and 180 was added to the longitude data (as longitude ranges from -180 to 180 degrees) to make all values positive.

General Linear Models (GLMs) were prepared separately for each breeding phase (incubation and chick-rearing) and for each of the foraging trip characteristics (trip duration, trip distance and foraging range). For each GLM, the foraging trip characteristic was the response variable with body mass, breeding colony latitude, and breeding colony longitude included as fixed effects (Appendix 2 – GLM models). To account for non-independence as a result of common ancestry, Markov chain Monte Carlo (MCMC) models were prepared for each foraging characteristic during the two breeding phases, with a procellariiform phylogeny included as a random effect (Appendix 2 – MCMC models). Like the GLMs, the trip characteristic was the response variable with body mass, colony latitude, and colony longitude entered as fixed effects. Using the MCMCglmm function from the MCMCglmm package (Hadfield, 2010), a two-chain MCMC model was constructed. The model was run for 2,400,000 iterations with a burnin of 400,000 and a thinning of 1000. Non-informative priors were used for both the fixed and random effects in these models (variance = 1;

belief parameter = 0.002). Lynch's phylogenetic heritability index (H^2; Lynch, 1991) was used to assess the strength of the phylogenetic component. H^2 varies from 0 to 1, with a score of 0 indicating that the trait is evolving independently of phylogenetic lineage, and a score of 1 revealing that the trait is evolving in accordance to Brownian motion and therefore driven entirely by phylogeny. The Gelman-Rubin statistic (Gelman & Rubin, 1992) was used to test if the model chains converged. The scale reduced factors resulting from this test were all below 1.1, indicating that the chains of each model converged. The level of autocorrelation in each model was also checked with the autocorrelation of posterior probabilities all being less than 0.1. The effective sample sizes of the models were all greater than 1500.

The Jetz *et al*. (2012) Maximum Clade Credibility tree for procellariiform species was used in the MCMC models (Figure 3). Before this phylogenetic tree was included in the models, a few adjustments were made to it using the ape (Paradis, 2019) and Phytools (Revell, 2012) packages. Some species names were updated to their current names according to BirdLife International. In addition, since the publication of this phylogenetic tree, new species have been recognised. In order for these species, as well as some subspecies, to be included, additional nodes were added to the phylogenetic tree.

This study examined the relationship between body mass and each of the three foraging trip characteristics, and assessed if the storm petrel can spend longer, travel longer distances, or range further from the breeding colony on foraging trips than would be expected for a procellariiform of its size. Median trip duration, trip distance and foraging range values from Bolton (2020) were used to examine the storm petrel's foraging traits in the incubation phase, while mean trait values from this study were used for the analysis during the chick-rearing period.

The correlation between each of the procellariiform foraging traits (trip duration, total trip distance, and foraging range) was determined using Pearson's correlation coefficient (5% level of significance) for each of the breeding stages. The data used for this analysis can be found in Appendix 1. Some of the variables were transformed before conducting the correlation analysis.

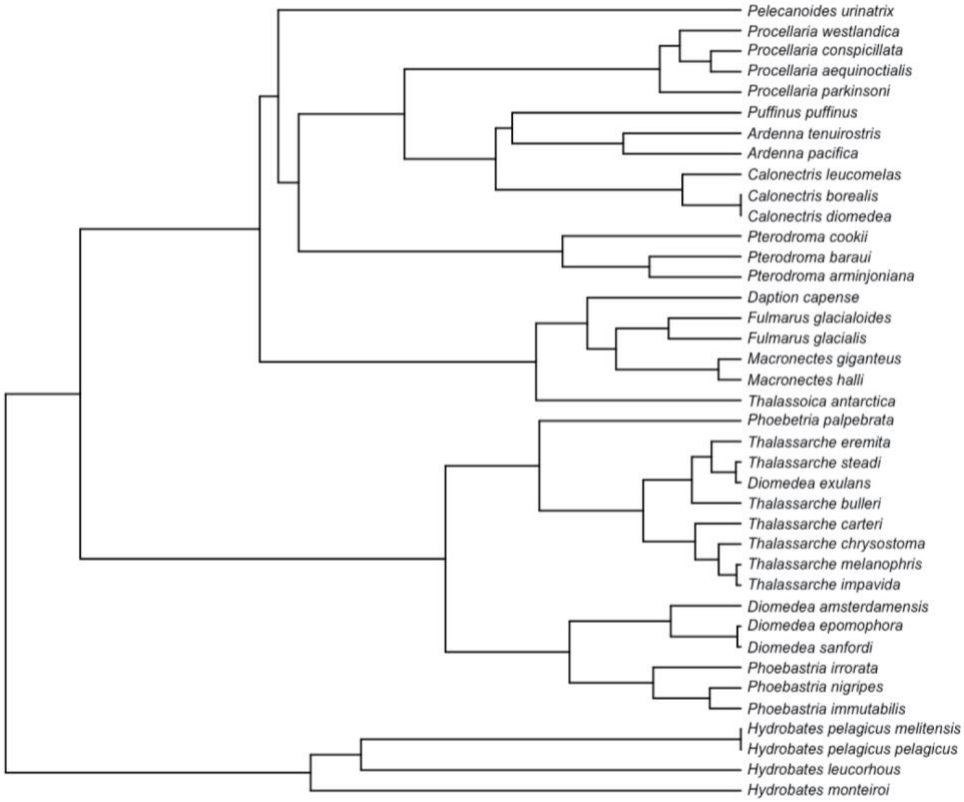


Figure 3. Maximum Clade Credibility tree for procellariiform species (Jetz *et al*., 2012) following the renaming of some species to be consistent with the scientific names used by BirdLife International, and the inclusion of extra nodes to incorporate additional species and subspecies. This phylogenetic tree only shows the species included in the comparative analysis. The unedited phylogenetic tree can be found in Appendix 3.

3. Results

3.1 Tag retrieval

Of the 6 tags deployed on storm petrels from Illauntannig, 5 tags were retrieved which represented an 83.33% retrieval rate. The data recorded by two tags did not meet the definition of a foraging trip and were removed from the analysis. Two trips were recorded for one tagged individual as the bird was not retrapped on its first return to its nesting site. The other tags recorded one foraging trip each. Therefore, the data analysed from this colony consisted of 4 trips from 3 storm petrels.

Data from 7 tags were obtained for High Island. Two of these tags did not record data consistent with the definition of a foraging trip and were removed. Two further tags were removed as the data showed long periods of time in both during which the tags were not operational (over 39 hours and 70 hours respectively). One of the remaining recorded trips was classified as incomplete as the tag stopped recording GPS locations before the bird returned to the colony. As a result, these tags produced 3 foraging trips (2 complete, 1 incomplete) from 3 storm petrels for analysis.

3.2 Impact of tag deployment

A slight mean mass loss (-0.23g, 0.78% mass loss; Table 1) was recorded for the deployment period of the three storm petrels breeding on Illauntannig, which were known to perform foraging trips. This loss in body mass may indicate that the additional weight of the GPS tag caused a reduction in their foraging efficiency; however, due to the small sample size, it was not possible to test if this loss in body mass was statistically significant. Two further individuals from this colony recorded a mass loss between tag deployment and recapture (Table 1); however, both of these individuals are thought to have returned to their nest shortly after the tag deployment and remained there until they were recaught trying to leave their nest the following night. In these cases, a loss in body mass would be expected. In any case, the apparent decline in mass was very small and unlikely to be detrimental.

Table 1. Body mass of European storm petrels from Illauntannig before and after the deployment of GPS tags. Birds 1-3 performed foraging trips but the other two remained at the colony after tag deployment.

Bird ID	Tag ID	Performed Foraging Trip	Pre-Deployment Body Mass (g)	Post-Deployment Body Mass (g)	Mass Gain/Loss (g)
1	449	Yes	30	31	1
2	453	Yes	27	27	0
3	414	Yes	31.7	30	-1.7
-	475	No	29	23	-6
-	901	No	28	24.5	-3.5

3.3 Characteristics of foraging trips

A total of 421 GPS locations were recorded from the 6 complete and 1 incomplete foraging trips (Figure 4). Following analysis of the 6 complete trips, the mean trip duration was calculated to be 37.86 hours (range 18.50 to 66.88 hours), the mean trip distance was 517.88 km (range 270.58 to 1113.26 km), and the mean foraging range was 169.87 km (range 78.95 to 336.36 km; Table 2). The mean speed was 14.59 km/h (range 9.43 to 17.75 km/h) and the maximum speed reached by a storm petrel on a foraging trip was 40.23 km/h (Table 2).

There were significant correlations between trip duration and distance ($r = 0.93$, $df = 4$, $p = 0.007$), and between trip distance and foraging range ($r = 0.94$, $df = 4$, $p = 0.006$). There was no significant relationship between trip duration and foraging range ($r = 0.77$, $df = 4$, $p = 0.073$), however, it was tending towards significance.

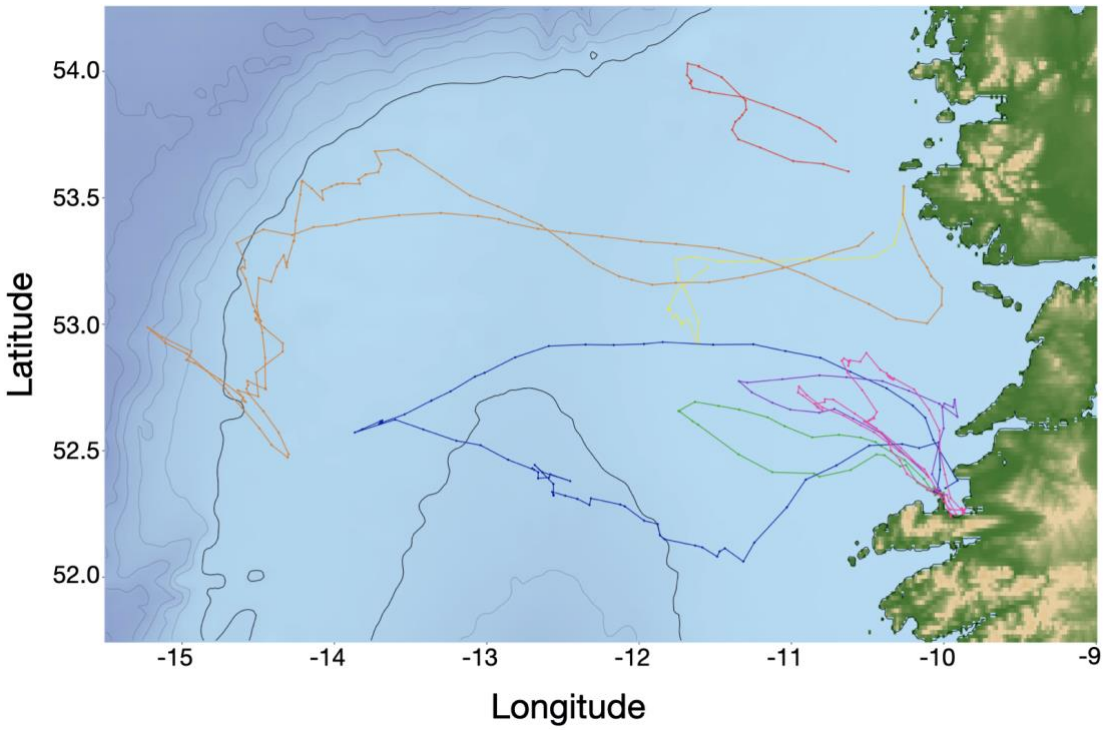


Figure 4. Complete and incomplete foraging trips performed by European storm petrels deployed with GPS tags from Illauntannig and High Island. The solid black line indicates the location of the continental shelf edge. Blue = bird 1, trip 1; Purple = bird 1, trip 2; Pink = bird 2; Green = bird 3; Orange = bird 4; Yellow = bird 5; Red = incomplete trip recorded from High Island.

Table 2. Foraging trip metrics of the six complete European storm petrel foraging trips recorded from the two breeding colonies (MI = Illauntannig, Magharee Islands, 2020; HI = High Island, 2016)

Colony	Bird ID	Trip No.	Trip Duration (h)	Total Distance (km)	Foraging Range (km)	Mean Speed (±SD) (km/h)	Max Speed (km/h)
MI	1	1	45.50	697.61	262.24	17.33 (± 10.42)	35.66
MI	1	2	18.50	270.58	102.58	17.75 (± 9.10)	33.05
MI	2	1	46.50	435.46	78.95	9.43 (± 8.68)	33.19
MI	3	1	26.00	278.00	122.31	15.23 (± 9.64)	33.78
HI	4	1	66.88 *	1113.26*	336.36	16.99 (± 9.56)	40.23
HI	5	1	23.80 *	312.34*	116.79	10.83 (± 9.49)	33.14
		Mean (±SD)	**37.86 (± 18.36)**	**517.88 (± 333.02)**	**169.87 (± 104.04)**	**14.59 (± 3.59)**	**34.84 (±2.82)**
		Max	**66.88**	**1113.26**	**336.36**	**17.75**	**40.23**

* underestimate due to delayed tag start time

3.4 Foraging energetics

The mean foraging range of short foraging trips (<36 hours) recorded in this study was 113.9km. The model predicted that in order to perform a short foraging trip with a balanced energy budget a storm petrel had to intake energy equivalent to approximately 5 full feeds (Figure 5). The mean foraging range of long foraging trips (>36 hours) recorded was 225.9km and to achieve a foraging range similar to this result with a balanced energy budget the model estimated that a storm petrel needed to feed 5-6 times (Figure 5). The maximum foraging range of a storm petrel recorded in this study was 336.4km (Table 2). This model predicted that this individual needed to consume approximately 173,200 Joules of energy in order to range this distance from the colony. This equates to around 8 feeding events (Figure 5). Adjusting other variables in the model, such as using maximum instead of mean flight speed, did not have a big impact on the foraging range.

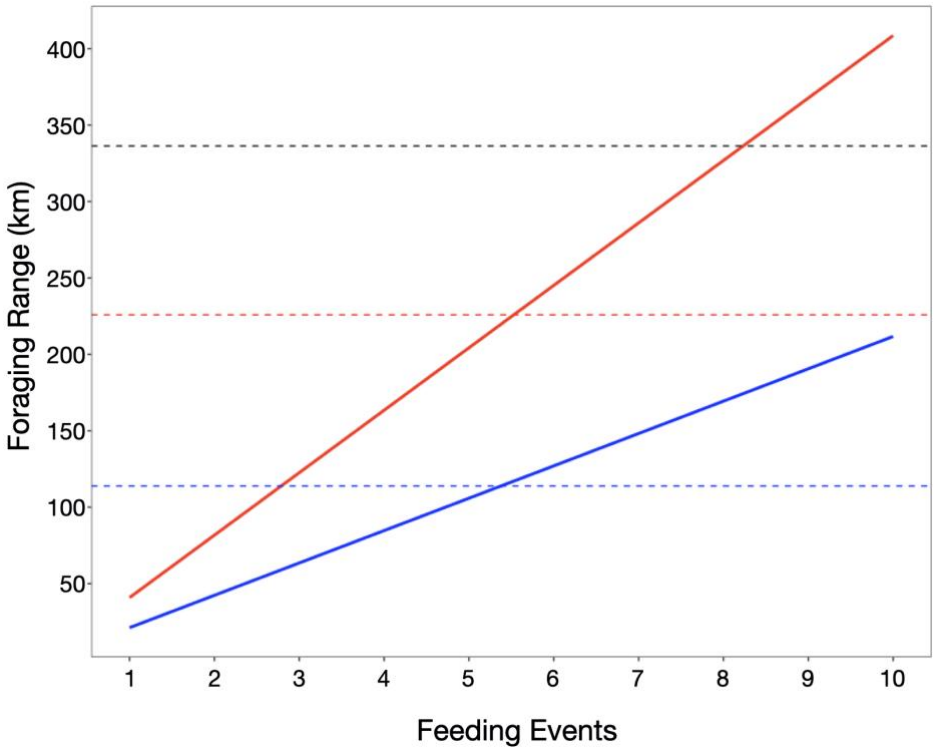


Figure 5. Foraging range estimated from the energetics model. The graph shows the foraging range for short foraging trips (blue) and long foraging trips (red) as a function of the number of feeding events. One feeding event equates to 21650 Joules of energy. The blue and red dashed horizontal lines indicate the mean foraging range of short (113.9 km) and long (225.9 km) foraging trips recorded in this study, respectively. The black dashed horizontal line indicates the maximum foraging range achieved by one of the tagged petrels (336.4 km).

3.5 Influence of prey distribution on storm petrel foraging distribution

According to the calculated AIC scores, the model for the High Island colony, which included the effect of monthly chlorophyll-*a* concentration, was preferred over the model without this covariate (Table 3). However, the model for the Illauntannig colony was stronger without the impact of chlorophyll-*a* concentration (Table 3). The preferred models clearly differentiated two behaviour states for both the Illauntannig and High Island populations (Appendix 4). 60.6% of the tracking points of storm petrels from High Island were determined to represent foraging behaviour, while 39.4% were assigned the transiting behaviour state. 59.2% and 40.8% of the Illauntannig tracking points were defined as foraging and transiting, respectively.

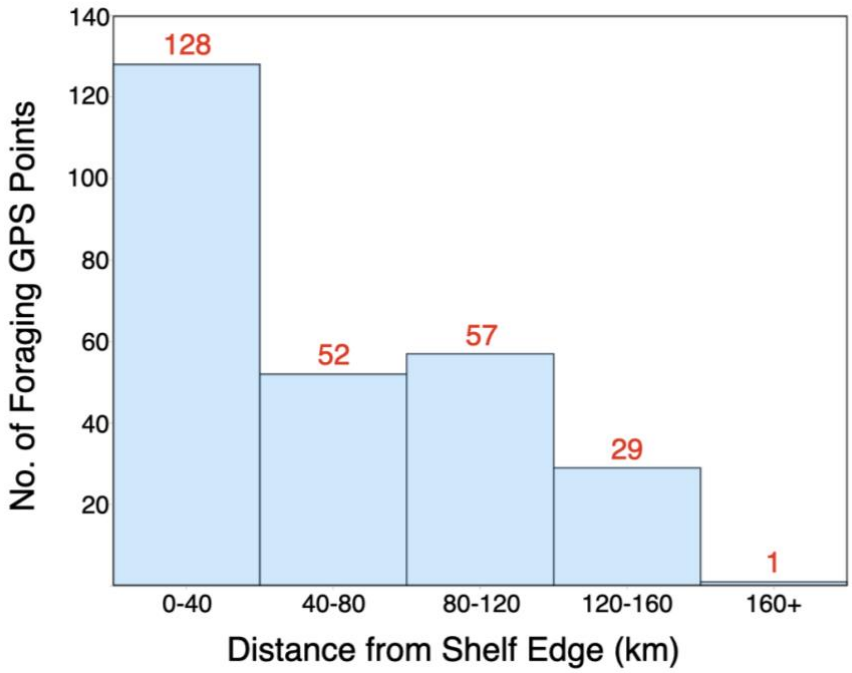
Table 3. Comparison of the AIC scores for the 2-state HMM models for each colony with and without the effect of the covariate (monthly chlorophyll-*a* concentration).

Model	**AIC**	**ΔAIC**
Illauntannig with covariate	5064.675	3.770
Illauntannig without covariate	5060.905	0.000
High Island with covariate	4408.796	0.000
High Island without covariate	4412.845	4.049

3.6 Influence of oceanographic features on storm petrel foraging distribution

There was a significant difference in the number of foraging GPS tracking points across the five distance intervals ($\mathcal{X}_4^2$ = 167.06, P < 0.001; Figure 6). 48% of the foraging points were found within 40km of the shelf edge.

a.



b.

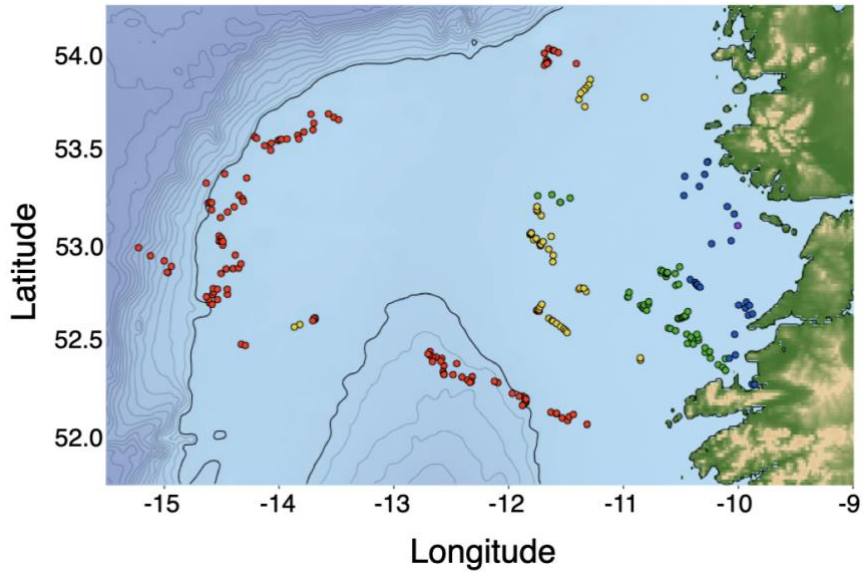


Figure 6. (a) Number of foraging GPS points in each distance interval ranging from the continental shelf edge. (b) Location of foraging GPS points in relation to the shelf edge. Red: 0-40km, Yellow: 40-80km, Green: 80-120km, Blue: 120-160km, Purple: 160+km.

3.7 Comparative analysis of foraging trip characteristics

Log-transformed body mass had statistically significant effects on the three foraging trip characteristics before correcting for phylogeny (Table 4). Figure 7 shows the relationship between body mass and the trip traits during both the incubation and chick-rearing phases of the breeding season. During the incubation stage, the storm petrel's trip duration, distance, and foraging range are below what would be expected for a procellariiform of its size; however, during chick-rearing, this species' foraging trip characteristics appear to conform with the general trend of procellariiform seabirds.

Table 4. Results of General Linear Models. Model formulas can be found in Appendix 2. In all models, body mass was log-transformed, latitude was squared, and 180 was added to all longitude values. P-values in bold indicate significance.

			Estimate	Std. Error	t value	P
GLM Model 1	Duration during Incubation phase	Intercept	0.5445	0.3470	1.569	0.123
		Mass	0.2650	0.0442	6.000	**<0.001**
		Latitude	0.0001	0.0001	0.839	0.406
		Longitude	-0.0019	0.0007	-2.649	**0.011**
GLM Model 2	Distance during Incubation phase	Intercept	5.8541	0.5901	9.920	**<0.001**
		Mass	0.3673	0.0744	4.934	**<0.001**
		Latitude	0.00005	0.0001	0.375	0.709
		Longitude	-0.0025	0.0013	-1.856	0.070
GLM Model 3	Range during Incubation phase	Intercept	5.5522	0.5754	9.649	**<0.001**
		Mass	0.2550	0.0757	3.368	**0.001**
		Latitude	0.00002	0.0001	0.176	0.861
		Longitude	-0.0037	0.0012	-2.986	**0.004**
GLM Model 4	Duration during Chick-rearing phase	Intercept	0.3912	0.5084	0.770	0.444
		Mass	0.1983	0.0601	3.297	**0.001**
		Latitude	-0.0002	0.0001	-3.666	**<0.001**
		Longitude	-0.0007	0.0007	-0.989	0.326
GLM Model 5	Distance during Chick-rearing phase	Intercept	5.0994	0.7499	6.800	**<0.001**
		Mass	0.3391	0.0892	3.802	**<0.001**
		Latitude	-0.00002	0.0001	-0.176	0.861
		Longitude	-0.0015	0.0011	-1.325	0.190
GLM Model 6	Range during Chick-rearing phase	Intercept	5.5192	0.6290	8.775	**<0.001**
		Mass	0.1646	0.0759	2.170	**0.033**
		Latitude	-0.0001	0.0001	-1.114	0.270
		Longitude	-0.0024	0.0010	-2.475	**0.016**

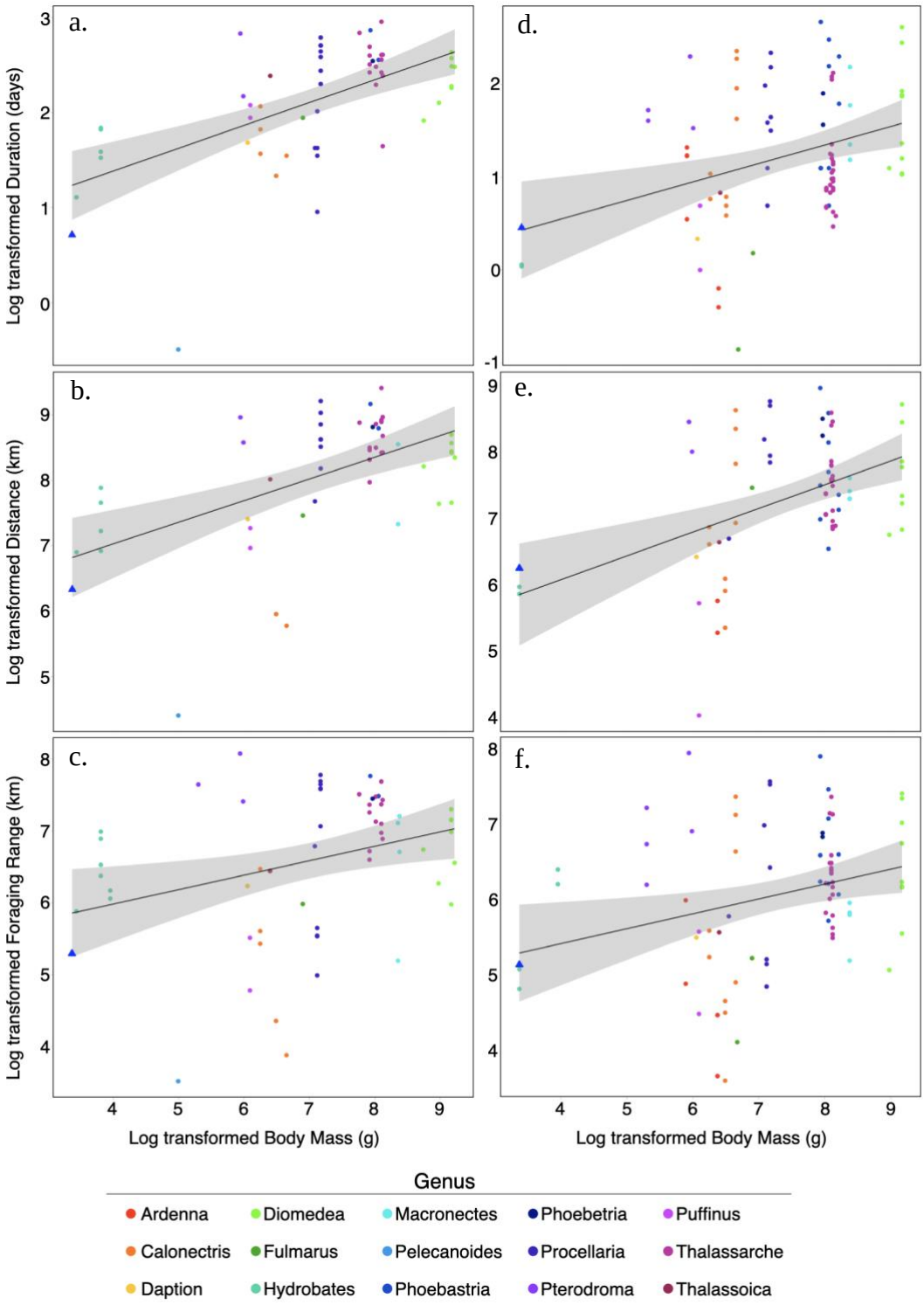


Figure 7. Relationship between log transformed body mass with (a) trip duration during incubation; (b) total distance travelled during incubation; (c) foraging range during incubation; (d) trip duration during chick-rearing; (e) total distance travelled during chick-rearing; and (f) foraging range during chick-rearing. The grey shaded area indicates the standard error. In a-c, the blue triangle shows the median of each trip characteristic of the European storm petrel according to Bolton (2020). In d-f, the blue triangle shows the mean of each trip characteristic of the European storm petrel according to this study.

However, after controlling for the non-independence resulting from evolutionary relatedness, body mass lost its statistical significance in all but one model (Table 5). Only in the model examining foraging trip duration during the chick-rearing phase did body mass remain significant after the inclusion of the phylogenetic tree. As body mass remained significant in this model, it is clear that this variable is a good predictor for foraging trip duration during the chick-rearing period of the breeding season for species belonging to the order Procellariiformes. In the other five MCMC models, the fact that body mass was no longer significant indicated that this factor is confounded with ancestry.

Table 5. Results of Markov Chain Monte Carlo (MCMC) models showing the posterior means, lower and upper 95% Credible Intervals, effective sample size, and pMCMC. Model formulas can be found in Appendix 2. In all models, body mass was log-transformed, latitude was squared, and 180 was added to all longitude values. pMCMC values in bold indicate significance.

			Posterior Mean	Lower 95% CI	Upper 95% CI	Effective Sample Size	pMCMC
MCMC Model 1	Duration during Incubation phase	Intercept	0.5818	-1.8670	3.2312	1777	0.638
		Mass	0.1906	-0.1701	0.5878	2232	0.296
		Latitude	-0.00001	-0.0002	0.0002	2000	0.917
		Longitude	0.0003	-0.0012	0.0019	2000	0.681
MCMC Model 2	Distance during Incubation phase	Intercept	6.0700	3.0469	8.9864	2000	**0.001**
		Mass	0.2527	-0.1401	0.6957	2000	0.238
		Latitude	-0.00004	-0.0003	0.0002	2000	0.753
		Longitude	0.000005	-0.0023	0.0021	2000	0.990
MCMC Model 3	Range during Incubation phase	Intercept	6.2612	2.7538	9.4998	2000	**<0.001**
		Mass	0.0560	-0.4347	0.5306	1865	0.817
		Latitude	-0.00006	-0.0004	0.0002	2000	0.704
		Longitude	-0.0007	-0.0031	0.0016	2000	0.542
MCMC Model 4	Duration during Chick-rearing phase	Intercept	-0.4693	-2.6580	1.3528	2000	0.672
		Mass	0.3340	0.0767	0.6097	2000	**0.004**
		Latitude	-0.0002	-0.0004	-0.00003	1749	**0.043**
		Longitude	-0.0008	-0.0021	0.0008	2000	0.288
MCMC Model 5	Distance during Chick-rearing phase	Intercept	4.8838	1.8416	8.0677	2171	**0.013**
		Mass	0.3752	-0.0264	0.8022	2259	0.058
		Latitude	-0.00003	-0.0004	0.0003	2133	0.847
		Longitude	-0.0011	-0.0035	0.0012	2000	0.322
MCMC Model 6	Range during Chick-rearing phase	Intercept	5.8827	3.5571	8.1932	2000	**0.001**
		Mass	0.1036	-0.2132	0.4302	2000	0.492
		Latitude	-0.00009	-0.0003	0.0002	2000	0.456
		Longitude	-0.0021	-0.0041	0.0001	2000	**0.046**

In the GLMs, latitude was statistically significant in the model for trip duration during the chick-rearing phase indicating that trip duration decreased as colony location moved from low to high latitudes (Table 4). Longitude was significant in the models for foraging range during both the incubation and chick-rearing periods, and for trip

duration during egg incubation (Table 4). This showed that, irrespective of breeding stage, foraging range decreased as the colony location moved from west to east. This was also the case for trip duration during incubation. After the inclusion of the phylogenetic tree in the MCMC models (Table 5), longitude lost its significance in the model exploring trip duration and foraging range during incubation, but maintained its significance in the range model during chick-rearing. Latitude remained significant in the model examining foraging trip duration during the chick-rearing phase (Table 5).

These MCMC models clearly suggest that there is a strong phylogenetic component determining the relationship between foraging trip traits with both the species' body mass and location of the breeding colony. This is supported by Lynch's phylogenetic heritability index as all MCMC models had a H^2 value close to 1 (Table 6), signifying that the foraging trip characteristics are evolving in accordance to Brownian motion.

Significant correlations were found between each of the procellariiform foraging characteristics for both breeding states (Figure 8).

Table 6. Lynch's phylogenetic heritability index (H^2) for each of the MCMC models. H^2 varies from 0 to 1, with a score of 0 indicating that the trait is evolving independently, and a score of 1 revealing that the trait is evolving in accordance to Brownian motion.

MCMC Model	Breeding Stage	Response Variable	H^2
1	Incubation	Duration	0.9988
2		Distance	0.9975
3		Range	0.9973
4	Chick-Rearing	Duration	0.9699
5		Distance	0.9789
6		Range	0.9476

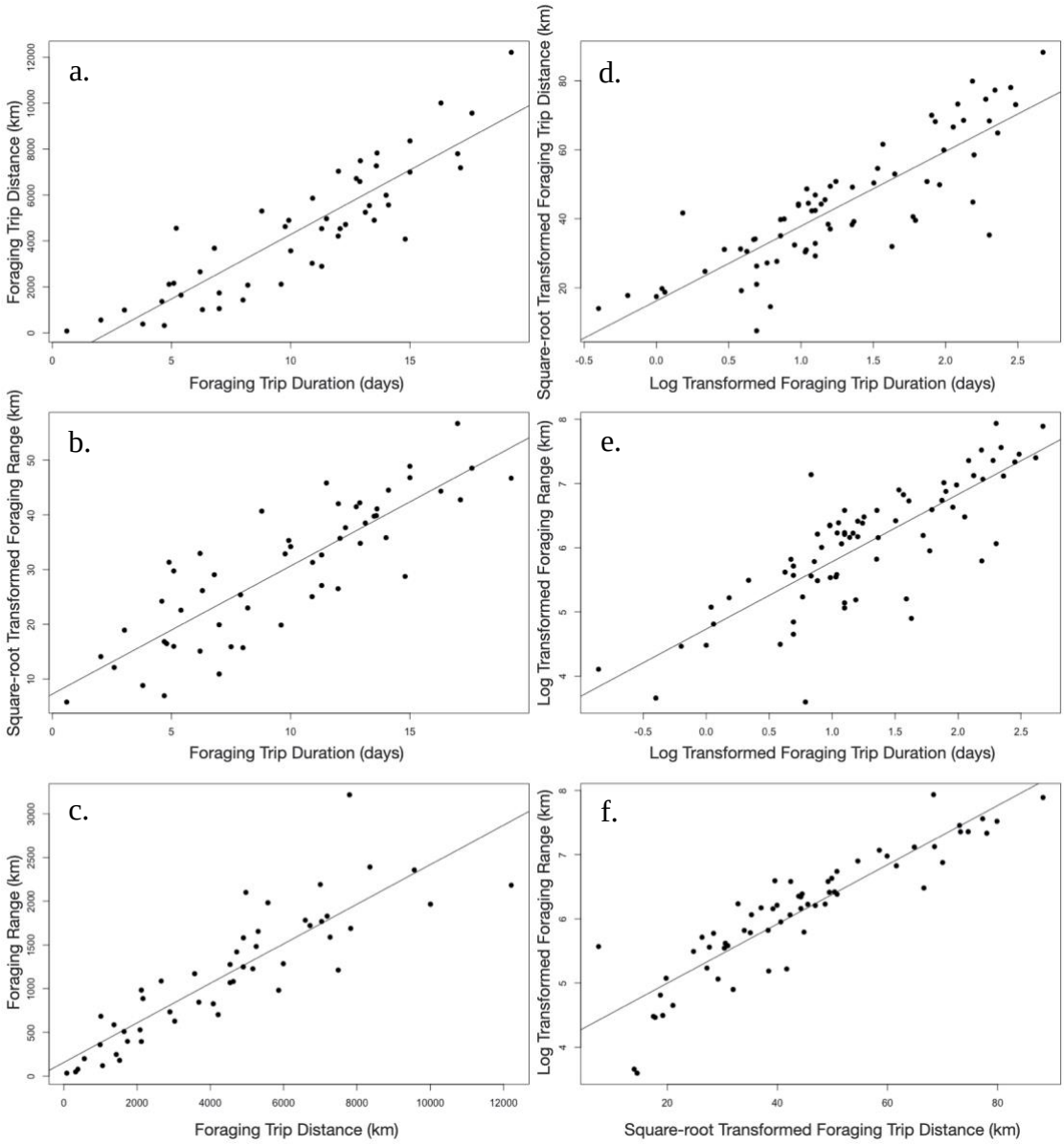


Figure 8. Strong linear relationships between each of the foraging trip characteristics in procellariiform species during the incubation and chick-rearing breeding phases. (a) Foraging trip duration ~ foraging trip distance during incubation ($r = 0.89$, $df = 47$, $p < 0.001$); (b) Foraging trip duration ~ square-root transformed foraging range during incubation ($r = 0.85$, $df = 52$, $p < 0.001$); (c) Foraging trip distance ~ foraging range during incubation ($r = 0.88$, $df = 47$, $p < 0.001$); (d) Log-transformed foraging trip duration ~ square-root transformed foraging trip distance during chick-rearing ($r = 0.85$, $df = 67$, $p < 0.001$); (e) Log-transformed foraging trip duration ~ log-transformed foraging range during chick-rearing ($r = 0.81$, $df = 73$, $p < 0.001$); and (f) Square-root transformed foraging trip distance ~ log-transformed foraging range during chick-rearing ($r = 0.90$, $df = 61$, $p < 0.001$).

4. Discussion

4.1 Foraging trip characteristics

This study presents the first GPS tracking data of the foraging movements of European storm petrels breeding in Ireland, the third anywhere in the world, and therefore is an important contribution to the limited GPS data collected for this species. In this study, the mean duration, distance and range of the storm petrel foraging trips were 37.86 h, 517.88 km, and 169.87 km, respectively. These results are very similar to Bolton's (2020) findings which is the only other GPS tracking study of the Atlantic subspecies to date (Table 7). Both this study and Bolton (2020) clearly demonstrate that, despite being the one of the smallest procellariiform species, the storm petrel is capable of travelling great distances for long durations while on foraging trips during the breeding season. These results also show that the storm petrel ranges far greater distances from the colony than the 65km estimate published by Thaxter *et al*. (2012). However, it appears that the Mediterranean subspecies travels for longer durations, longer distances and ranges further from the breeding colony on foraging trips than their Atlantic conspecifics (Rotger *et al*., 2020; Table 7).

Table 7. Mean/median and maximum foraging trip characteristics (trip duration, total distance travelled, and foraging range) of European storm petrels as determined in this study, Bolton (2020) and Rotger *et al*. (2020). This study's results are from the chick-rearing period for the Atlantic subspecies; the results from Bolton (2020) are from all the breeding stages combined for the Atlantic subspecies; and the results from Rotger *et al*. (2020) are from the incubation phase for the Mediterranean subspecies.

	This Study		**Bolton (2020)**		**Rotger *et al.* (2020)**	
	Mean	Max	Median	Max	Mean	Max
Duration (h)	37.86	66.88	27	73.5	72.72	114.96
Total Distance (km)	517.88	1088.28	391	958	992.47	1726.56
Foraging Range (km)	169.87	336.36	159	397	358.8	468.7

A strong linear relationship was found to exist between foraging trip duration and distance indicating that storm petrels which embark on foraging trips of long durations also travel further distances than individuals that spend a shorter period of time on foraging trips. In addition, a significant, strong linear relationship was identified

between trip distance and foraging range. This means that, not surprisingly, birds that travelled long distances also ranged further from the colony. The significant correlations between trip duration and distance, and between trip distance and range were also identified by Bolton (2020) for storm petrels breeding in Scotland and is consistent with the correlation results found in this study for procellariiform species (Figure 8). However, in this study, the relationship between trip duration and foraging range was not quite significant ($p = 0.073$). This does not match Bolton's (2020) results or the procellariiform correlations (Figure 8). In this study, one storm petrel (Table 2, Bird 2) embarked on a 46.5 hour foraging trip but only ranged 79km from the colony. After the removal of this outlier, the relationship between trip duration and foraging range became significant ($r = 0.988$, $df = 3$, $p = 0.0015$; Appendix 5), indicating that this outlier was decreasing the value of the correlation coefficient. It is also important to note that the small sample size of storm petrel foraging trips in this study means it is not possible to define correlations with much confidence.

4.2 Foraging energetics

The model used in this study predicted that a storm petrel would need to feed approximately 5-6 times in order to intake enough energy to enable it to perform a long foraging trip, which was assumed to be primarily for adult self-maintenance, or a short trip assumed to focus on chick provisioning. However, the number of times a storm petrel can feed during the course of a foraging trip to increase its energy reserves is limited by the time it takes to digest the prey. Using the Wilson's storm petrel as a proxy, gut passage time in European storm petrels is approximately 12 hours (Quillfeldt & Möstl, 2003). As a result, on short foraging trips, an adult can only intake energy equivalent to 2-3 feeding events in which the petrel consumes its maximum capacity of food. This is less than the 5 feeds the model predicts a storm petrel requires to perform a short foraging trip with a balanced energy budget. This suggests that storm petrels are operating at an energy deficit when performing short foraging trips to maximise the chick provisioning rate. This scenario has also been documented in other procellariiform species such as the Sooty shearwater (*Ardenna grisea*; Weimerskirch, 1998).

On long foraging trips, according to the mean trip duration of long trips recorded in this study, storm petrels could feed roughly 4-5 times, which is similar to the number

of feeds the model predicts it would require to intake enough energy to complete a long foraging trip with a balanced energy budget. However, this model assumes the energy density of the storm petrel's diet is the same for all foraging trips which is unlikely to be the case in reality. Many procellariiform species visit distant feeding grounds as they are more profitable than near-shore sites, therefore allowing for high energy acquisition (e.g. Short-tailed shearwaters, *Ardenna tenuirostris*; Weimerskirch & Cherel, 1998). Another limitation of this model is the lack of energetic data for the European storm petrel. In order for the model to be more accurate, it would be better to have actual energetic values for the European storm petrel and not be required to rely on other species as proxies. A third limitation is that this model assumes that storm petrels expend energy at the same rate on all foraging excursions. This has been shown to not be the case in some procellariiform seabirds such as the Blue petrel (*Halobaena caerulea*) which expends half as much energy per unit time on long foraging trips compared to short trips (Weimerskirch *et al*., 2003). While there are several limitations, this energetic model does provide insight into the foraging strategy employed by storm petrels from the two study colonies and suggests that storm petrels perform long foraging trips resulting in an energy surplus to compensate for the energy deficit suffered on short foraging trips.

4.3 Drivers of foraging distribution

Area-restricted search (ARS) is typically performed by seabirds when they enter a region known to be productive (Weimerskirch, 2007) and in procellariiforms, olfactory cues may be used to identify highly productive zones (Nevitt, 2008). The switch from transiting to ARS behaviour has been found to correlate with chlorophyll-*a* concentration for some seabird species (Kane *et al*., 2020; Sabarros *et al*., 2014). However, in this study, the two-state Hidden Markov Models (HMMs) did not confirm that chlorophyll-*a* concentration, or what it may infer (phytoplankton and zooplankton abundance and/or areas where DMS is present in high concentrations), acts as a cue for storm petrels to initiate ARS behaviour. The results for each colony differed with the High Island individuals being shown to begin foraging in areas of high chlorophyll-*a* concentration, but the association between foraging and chlorophyll-*a* concentration was not identified for the petrels from Illauntannig. Therefore, there is uncertainty whether the foraging distribution of storm petrels from these two colonies is influenced by prey distribution and abundance in the same manner. However, there

has been dispute over the use of environmental correlates to examine species distributions with one of the primary concerns being the potential for spatial or temporal disparities between lower and higher trophic organisms. Grémillet *et al.* (2008), for example, identified a spatial mismatch between phytoplankton and zooplankton distributions. More storm petrels need to be GPS-tagged to build a larger dataset so the analysis can be supported by a better sample size. In addition, a shorter GPS sampling interval would ensure that the behaviour states are applied to the foraging tracks with more accuracy. A short sampling interval, such as the 5-minute interval employed by Kane *et al.* (2020), would be preferable to the 30-minute interval used in this study.

The occurrence of ARS/foraging behaviour was not equally distributed across the distance intervals ranging from the continental shelf edge. The majority of foraging points were found near and beyond the shelf edge at the Porcupine Bank and the Porcupine Seabight implying that the shelf edge represents an important part of this species' foraging distribution. However, these foraging grounds were largely restricted to storm petrels performing long (>36 hour) foraging trips. From the energetics model it appears that storm petrels are operating at an energy deficit when performing short foraging trips and therefore, the highly productive waters of the shelf edge (Cox *et al.*, 2018) may be an essential component of the foraging distribution of this species, which they exploit on long foraging trips to replenish their energy reserves. This strategy is not unusual among procellariiform seabirds with recorded benefits of performing long foraging trips including access to areas of high prey abundance (Magalhães *et al.*, 2008). This may also be the case for storm petrels breeding along the west coast of Ireland as offshore areas have been found to be highly productive (Edwards *et al.*, 2001).

While the shelf edge is clearly an important foraging area for the storm petrel, diet analysis has also found evidence of foraging occurring in the intertidal zone (D'Elbée & Hémery, 1998). In addition, foraging near the coast has been observed both during the breeding season (Albores-Barajas *et al.*, 2011) and during migration (Thomas *et al.*, 2006). It is not understood to what extent the storm petrel relies on the intertidal zone as a foraging ground and this has not yet been examined using GPS tracking data. In this study, one of the storm petrels breeding on Illauntannig was recorded foraging

in Tralee Bay on two occasions during a 46.5 hour trip (Appendix 6). On the first occasion, the storm petrel entered Tralee Bay in the late evening and remained until just before sunrise. Almost exactly 24 hours later, the storm petrel returned to Tralee Bay, but this visit was much shorter, lasting less than 3 hours. None of the other tagged storm petrels were recorded foraging near the coast for protracted periods of time. Chlorophyll-*a* concentrations near the coast were found to be very high suggesting that inshore areas represent a beneficial foraging ground for storm petrels, which can be exploited at night to avoid detection by visual predators such as gulls (Oro *et al*., 2005). A larger sample of storm petrel foraging trips is required to gain a better understanding of how this species utilises coastal areas for foraging.

4.4 Comparative analysis of foraging trip characteristics

The Procellariiformes is an extremely diverse order in terms of body size. It includes one of the world's smallest seabird species, the European storm petrel, which weighs less than 30g, and the largest species, the wandering albatross (*Diomedea exulans*), which is capable of weighing in excess of 12kg. Several procellariiform seabirds have been shown to possess extraordinary foraging abilities in terms of the duration and distance travelled on foraging trips, and how far they can range from their breeding colony. The correlation between body mass and each of the foraging trip characteristics indicates that procellariiform species with a higher body mass tend to go on longer foraging trips, travel further distances, and range further from the breeding colony (Figure 7). This study, Bolton (2020), and Rotger *et al*. (2020) have all identified that the European storm petrel is capable of embarking on long-distance, multi-day foraging trips; but to date there has been no indication about whether the storm petrel's foraging characteristics surpass, align with, or are less than what would be expected for a procellariiform species of its size. When the foraging trip characteristics are compared to other species belonging to the order Procellariiformes, it becomes apparent that during the incubation phase, the European storm petrel's foraging characteristics are below what would be expected (Figures 7a-7c). In contrast, during the chick-rearing period, storm petrel foraging trip duration, distance and foraging range conform with the general trend of procellariiform species (Figures 7d-7f). The foraging movements of a larger sample of storm petrels, belonging to a greater range of breeding colonies, are needed to be examined as seabird foraging trip characteristics are heavily influenced by factors such as the proximity of the breeding

colony to feeding grounds (Lescroël & Bost, 2005); chick energetic requirements, which can change during the course of the breeding season (Bolton, 1995); adult body condition (Weimerskirch, 1998); and changing environmental conditions (Quillfeldt *et al*., 2010). Factors such as these vary between colonies and consequently a species' foraging distribution cannot be generalised according to the results of a small sample of breeding sites.

The GLMs used to investigate the relationship between each of the foraging trip characteristics with body mass and colony location revealed that body mass had a significant effect (Table 4). However, after controlling for the non-independence resulting from ancestral relatedness, body mass lost its significance in five of the six MCMC models (Table 5). It is clear that there is a strong phylogenetic component explaining the relationship between the foraging trip characteristics and the fixed effects. This does not mean that body mass is not important, but the high phylogenetic signal identified (Table 6) suggests that the body mass effect arises because of shared ancestry. Typically, similar morphological, behavioural and ecological traits are found in closely related species and so the phylogenetic effect on procellariiform foraging trip characteristics likely includes other taxon specific diversifications such as wing loading. Future research in this area should consider the possibility that a quadratic effect exists and not a linear one as assumed in this study. A very large body mass may in fact limit the duration and range of foraging trips, resulting in a drop or levelling of the relationship trendline. A second factor that should be considered is the sex of the tagged bird as some procellariiform species display sexual dimorphism in terms of body mass (e.g. Southern giant petrel, *Macronectes giganteus*; González-Solís *et al*., 2000). A third factor to note is that there was an apparent bias in the literature identified in this study toward larger species. This is no doubt due to the fact that miniature telemetry devices that can be deployed on small seabird species have only recently become commercially available. Only eleven species represented in this analysis had a body mass less than 500g, with only three being under 100g. A more extensive literature search should be conducted in the future, when there is a larger representation of smaller procellariiform species whose foraging movements have been studied using telemetry devices. Despite there being a need to conduct further research to explore the factors influencing the foraging trip characteristics of procellariiforms, it is clear that phylogenetic relatedness is a key component.

5. Conclusion

The results of this GPS-tracking study of the European storm petrel contribute to the limited but growing knowledge that currently exists on this species' foraging movements and are the first results from Ireland, which hosts a high proportion of the world population. Further research is required to answer the more complex questions highlighted in the topics addressed in this study. A larger database of European storm petrel foraging movements, consisting of data from a variety of breeding colonies is needed. It is clear that the foraging distribution of this species is influenced by a range of biological and environmental factors.

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Appendix 1a. Data used in comparative analysis of procellariiform foraging trip characteristics during the Incubation phase of the breeding season.

Species	Scientific Name	Foraging Trip Duration (d)	Foraging Trip Distance (km)	Foraging Range (km)	Colony Latitude	Colony Longitude	Body Mass (g)	Reference	Body Mass Reference
Amsterdam Albatross	*Diomedea amsterdamensis*	6.8	3685	845	-37.82	77.53	6270	Waugh & Weimerskirch (2003)	Jouventin et al. (1989)
Antarctic Petrel	*Thalassoica antarctica*	10.9	3027	628	-68.8	77.7	600	Dehnhard et al. (2020)	Descamps et al. (2016)
Barau's Petrel	*Pterodroma baraui*	17	7796	3216	-21.167	55.55	380	Pinet et al. (2012)	Pinet et al. (2012)
Black-browed Albatross	*Thalassarche melanophris*	5.2	4557	-	-51.3	-60.1	3357	Huin (2002)	Phillips et al. (2004)
Black-browed Albatross	*Thalassarche melanophris*	10.92	5862	981	-54	-38.05	3357	Phillips et al. (2004)	Phillips et al. (2004)
Black-browed Albatross	*Thalassarche melanophris*	13.62	7828	1689	-54	-38.05	3357	Phillips et al. (2004)	Phillips et al. (2004)
Black-footed Albatross	*Phoebastria nigripes*	12.9	6590	1782	23.87	-166.28	3150	Kappes et al. (2010)	Kappes et al. (2010)
Buller's Albatross	*Thalassarche bulleri*	13.5	4902	1581	-48.03	166.6	2746	Stahl & Sagar (2000)	Battam (2010)
Buller's Albatross	*Thalassarche bulleri*	12.3	4719	1419	-48.03	166.6	2746	Stahl & Sagar (2000)	Battam (2010)
Buller's Albatross	*Thalassarche bulleri*	11.3	2896	734	-48.03	166.6	2746	Stahl & Sagar (2000)	Battam (2010)
Buller's Albatross	*Thalassarche bulleri*	14.8	4081	827	-48.03	166.6	2746	Stahl & Sagar (2000)	Battam (2010)
Campbell Albatross	*Thalassarche impavida*	9.92	4898	1248	-52.54	169.145	3025	Sztukowski (2016)	Sztukowski (2016)
Campbell Albatross	*Thalassarche impavida*	12	7034	1768	-52.54	169.145	3025	Sztukowski (2016)	Sztukowski (2016)
Cape Petrel	*Daption capense*	5.4	1645	510	-68.8	77.8	425	Dehnhard et al. (2020)	Weidinger (1998)
Chatham Petrel	*Pterodroma axillaris*	-	-	2095	-44	-176.53	200	Rayner et al. (2012)	Rayner et al. (2012)
Common Diving Petrel	*Pelecanoides urinatrix*	0.61	81.8	33.7	-36.6	174.88	147	Zhang et al. (2019)	Navarro et al. (2013)
Cory's Shearwater	*Calonectris borealis*	4.7	322.2	48.4	35.18	-2.43	771	Afán et al. (2014)	Afán et al. (2014)
European Storm Petrel	*Hydrobates pelagicus pelagicus*	2.04	562	199	60	-1.17	29	Bolton (2020)	This study
European Storm Petrel	*Hydrobates pelagicus melitensis*	3.03	992.47	358.8	38.5	-0.13	31	Rotger et al. (2020)	Rotger et al. (2020)
Grey-headed Albatross	*Thalassarche chrysostoma*	12.92	7489	1211	-54	-38	3291	Phalan et al. (2007)	Phillips et al. (2004)
Grey-headed Albatross	*Thalassarche chrysostoma*	19.25	12210	2182	-46.9	37.75	3291	Nel et al. (2000)	Phillips et al. (2004)
Grey-headed Albatross	*Thalassarche chrysostoma*	13.59	7268	1589	-54	-38.05	3291	Phillips et al. (2004)	Phillips et al. (2004)
Grey-headed Albatross	*Thalassarche chrysostoma*	11.3	4539	1068	-54	-38.05	3291	Phillips et al. (2004)	Phillips et al. (2004)
Indian Yellow-nosed Albatross	*Thalassarche carteri*	17.12	7185	1829	-37.86	77.52	2350	Pinaud & Weimerskirch (2005)	Makhado et al. (2018)
Laysan Albatross	*Phoebastria immutabilis*	17.6	9564	2356	23.87	-166.28	2780	Kappes et al. (2010)	Kappes et al. (2010)
Leach's Storm Petrel	*Hydrobates leucorhous*	6.2	2659	1086	46.1	-65.53	45	Pollet et al. (2014)	Pollet et al. (2014)
Leach's Storm Petrel	*Hydrobates leucorhous*	6.3	1013	684	43.467	-65.733	45	Pollet et al. (2014)	Pollet et al. (2014)
Leach's Storm Petrel	*Hydrobates leucorhous*	4.9	2117	983	46.1	-65.53	45	Pollet et al. (2014)	Pollet et al. (2014)
Leach's Storm Petrel	*Hydrobates leucorhous*	4.6	1371	587	43.467	-65.733	45	Pollet et al. (2014)	Pollet et al. (2014)
Light-mantled Sooty Albatross	*Phoebetria palpebrata*	12.75	6719	1721.2	-54.5	154.9	2880	Weimerskirch & Robertson (1994)	Phillips et al. (2005)

Appendix 1a. Continued

Manx Shearwater	*Puffinus puffinus*	7	1058.5	119.2	54.68	-5.52	442	Dean et al. (2013)	Gray & Hamer (2001)
Manx Shearwater	*Puffinus puffinus*	8	1432.4	247.6	51.73	-5.28	442	Dean et al. (2013)	Gray & Hamer (2001)
Monteiro's Storm Petrel	*Hydrobates monteiroi*	-	-	479	39.059	-27.954	52	Paiva et al. (2018)	Paiva et al. (2018)
Monteiro's Storm Petrel	*Hydrobates monteiroi*	-	-	428	39.059	-27.954	52	Paiva et al. (2018)	Paiva et al. (2018)
Northern Giant Petrel	*Macronectes halli*	-	1524	180	-54.05	-38.6	4250	González-Solís et al. (2000b)	González-Solís et al. (2000a)
Northern Giant Petrel	*Macronectes halli*	-	5159	1226	-54.05	-38.6	4250	González-Solís et al. (2000b)	González-Solís et al. (2000a)
Northern Royal Albatross	*Diomedea sanfordi*	8.2	2081	529	-45.77	170.73	7922	Waugh et al. (2005)	Sugishita et al. (2017)
Scopoli's Shearwater	*Calonectris diomedea*	3.8	385.2	77.9	35.18	-2.43	657	Afán et al. (2014)	Afán et al. (2014)
Southern Fulmar	*Fulmarus glacialoides*	7	1738	397	-68.8	77.7	990	Dehnhard et al. (2020)	Weimerskirch (1990)
Southern Giant Petrel	*Macronectes giganteus*	-	-	818	-54.05	-38.6	4350	González-Solís et al. (2000a)	González-Solís et al. (2000a)
Southern Giant Petrel	*Macronectes giganteus*	-	-	1348	-54.05	-38.6	4350	González-Solís et al. (2000a)	González-Solís et al. (2000a)
Southern Royal Albatross	*Diomedea epomophora*	11.99	4213	703	-52.4	169.1	10100	Waugh & Weimerskirch (2003)	Waugh & Weimerskirch (2003)
Spectacled Petrel	*Procellaria conspicillata*	5.1	2161	886	-37.29	-12.68	1191	Reid et al. (2014)	Ryan (1998)
Streaked Shearwater	*Calonectris leucomelas*	4.8	-	272	39.3	141.97	516	Yamamoto et al. (2012)	Ochi et al. (2010)
Streaked Shearwater	*Calonectris leucomelas*	7.9	-	645	33.87	139.23	516	Yamamoto et al. (2012)	Ochi et al. (2010)
Streaked Shearwater	*Calonectris leucomelas*	6.2	-	228	38.45	139.22	516	Yamamoto et al. (2012)	Ochi et al. (2010)
Trindade Petrel	*Pterodroma arminjoniana*	8.79	5304.01	1654.97	-20.5	-29.32	398	Leal et al. (2017)	Kruger et al. (2016)
Wandering Albatross	*Diomedea exulans*	14	5991	1284	-46	51	9600	Weimerskirch et al. (1993)	Waugh & Weimerskirch (2003)
Wandering Albatross	*Diomedea exulans*	9.6	2118	395	-46	51	9600	Weimerskirch et al. (1993)	Waugh & Weimerskirch (2003)
Wandering Albatross	*Diomedea exulans*	12.07	4537.67	1275.33	-50.87	166	9600	Walker et al. (1995)	Waugh & Weimerskirch (2003)
Wandering Albatross	*Diomedea exulans*	13.13	5250	1483	-54	-38	9600	Phalan et al. (2007)	Waugh & Weimerskirch (2003)
Wandering Albatross	*Diomedea exulans*	9.77	4627	1081	-46.4	51.8	9600	Waugh & Weimerskirch (2003)	Waugh & Weimerskirch (2003)
Westland Petrel	*Procellaria westlandica*	2.6	-	147	-42.146	171.341	1235	Waugh et al. (2018)	Waugh et al. (2018)
Westland Petrel	*Procellaria westlandica*	4.7	-	284	-42.146	171.341	1235	Waugh et al. (2018)	Waugh et al. (2018)
Westland Petrel	*Procellaria westlandica*	7.5	-	253	-42.146	171.341	1235	Waugh et al. (2018)	Waugh et al. (2018)
Westland Petrel	*Procellaria westlandica*	5.1	-	255	-42.146	171.341	1235	Waugh et al. (2018)	Waugh et al. (2018)
White-chinned Petrel	*Procellaria aequinoctialis*	11.5	4970	2100	-54	-38.05	1300	Phillips et al. (2006)	Weimerskirch et al. (1999)
White-chinned Petrel	*Procellaria aequinoctialis*	10	3570	1170	-54	-38.05	1300	Phillips et al. (2006)	Weimerskirch et al. (1999)
White-chinned Petrel	*Procellaria aequinoctialis*	14.1	5569	1982	-54	-38.05	1300	Phillips et al. (2006)	Weimerskirch et al. (1999)
White-chinned Petrel	*Procellaria aequinoctialis*	13.3	5544	-	-54.05	38.6	1300	Berrow et al. (2000)	Weimerskirch et al. (1999)
White-chinned Petrel	*Procellaria aequinoctialis*	15	8355	2390	-46	52	1300	Weimerskirch et al. (1999)	Weimerskirch et al. (1999)
White-chinned Petrel	*Procellaria aequinoctialis*	15	6999	2190	-54	-38	1300	Weimerskirch et al. (1999)	Weimerskirch et al. (1999)
White-chinned Petrel	*Procellaria aequinoctialis*	16.3	10005.8	1965.7	-49.61	70.26	1300	Péron et al. (2010)	Weimerskirch et al. (1999)

Appendix 1b. Data used in comparative analysis of procellariiform foraging trip characteristics during the Chick-rearing phase of the breeding season.

Species	Scientific Name	Foraging Trip Duration (d)	Foraging Trip Distance (km)	Foraging Range (km)	Colony Latitude	Colony Longitude	Body Mass (g)	Reference	Body Mass Reference
Antarctic Petrel	*Thalassoica antarctica*	2.3	765	260	-68.8	77.7	600	Dehnhard et al. (2020)	Descamps et al. (2016)
Barau's Petrel	*Pterodroma baraui*	10	4674	2796	-21.167	55.55	380	Pinet et al. (2012)	Pinet et al. (2012)
Black Petrel	*Procellaria parkinsoni*	-	806.7	321.93	-36.183	175.417	695	Freeman et al. (2010)	Freeman et al. (2010)
Black-browed Albatross	*Thalassarche melanophris*	1.6	969	-	-51.3	-60.1	3357	Huin (2002)	Phillips et al. (2004)
Black-browed Albatross	*Thalassarche melanophris*	2.6	1050	-	-53.9	-59.18	3357	Huin (2002)	Phillips et al. (2004)
Black-browed Albatross	*Thalassarche melanophris*	2.68	-	253.3	-50	70	3357	Weimerskirch et al. (1997)	Phillips et al. (2004)
Black-browed Albatross	*Thalassarche melanophris*	2.42	-	241.4	-50	70	3357	Weimerskirch et al. (1997)	Phillips et al. (2004)
Black-browed Albatross	*Thalassarche melanophris*	8.37	4696.55	1242.45	-52.55	169.15	3357	Waugh et al. (1999)	Phillips et al. (2004)
Black-browed Albatross	*Thalassarche melanophris*	3.125	1959	474	-54	-38	3357	Phalan et al. (2007)	Phillips et al. (2004)
Black-browed Albatross	*Thalassarche melanophris*	2.36	1230	325	-54	-38.05	3357	Phillips et al. (2004)	Phillips et al. (2004)
Black-browed Albatross	*Thalassarche melanophris*	1.87	933	276	-54	-38.05	3357	Phillips et al. (2004)	Phillips et al. (2004)
Black-browed Albatross	*Thalassarche melanophris*	2.93	1789	429	-54	-38.05	3357	Phillips et al. (2004)	Phillips et al. (2004)
Black-browed Albatross	*Thalassarche melanophris*	3.21	2072	506	-54	-38.05	3357	Phillips et al. (2004)	Phillips et al. (2004)
Black-footed Albatross	*Phoebastria nigripes*	3	2198	497	23.87	-166.28	3150	Fernández et al. (2001)	Kappes et al. (2010)
Black-footed Albatross	*Phoebastria nigripes*	12	5341	1732	23.87	-166.28	3150	Fernández et al. (2001)	Kappes et al. (2010)
Black-footed Albatross	*Phoebastria nigripes*	2	692	303	23.87	-166.28	3150	Fernández et al. (2001)	Kappes et al. (2010)
Black-footed Albatross	*Phoebastria nigripes*	9	3424	1174	23.87	-166.28	3150	Fernández et al. (2001)	Kappes et al. (2010)
Campbell Albatross	*Thalassarche impavida*	2.36	1580.63	-	-52.54	169.145	3025	Sztukowski et al. (2018)	Sztukowski (2016)
Campbell Albatross	*Thalassarche impavida*	1.98	1165.72	-	-52.54	169.145	3025	Sztukowski et al. (2018)	Sztukowski (2016)
Campbell Albatross	*Thalassarche impavida*	1.96	1155	337	-52.54	169.145	3025	Sztukowski (2016)	Sztukowski (2016)
Campbell Albatross	*Thalassarche impavida*	2.42	1595	499	-52.54	169.145	3025	Sztukowski (2016)	Sztukowski (2016)
Cape Petrel	*Daption capense*	1.4	613	243	-68.8	77.7	425	Dehnhard et al. (2020)	Weidinger (1998)
Chatham Albatross	*Thalassarche eremita*	2.5	-	406	-44.417	-176.233	3213	Deppe et al. (2014)	Battam (2010)
Chatham Albatross	*Thalassarche eremita*	3.5	-	652	-44.417	-176.233	3213	Deppe et al. (2014)	Battam (2010)
Chatham Albatross	*Thalassarche eremita*	2.3	-	1260	-44.417	-176.233	3213	Deppe et al. (2014)	Battam (2010)
Chatham Petrel	*Pterodroma axillaris*	-	-	1354	-44	-176.53	200	Rayner et al. (2012)	Rayner et al. (2012)
Cook's Petrel	*Pterodroma cookii*	5.6	-	489	-36.18	175.07	200	Rayner et al. (2008)	Rayner et al. (2008)
Cook's Petrel	*Pterodroma cookii*	5	-	836	-46.18	167.63	200	Rayner et al. (2008)	Rayner et al. (2008)
Cory's Shearwater	*Calonectris borealis*	5.1	1021.7	134.3	35.18	-2.43	771	Afán et al. (2014)	Afán et al. (2014)
Cory's Shearwater	*Calonectris borealis*	7.09	2487.3	758.4	40	-31	771	Magalhaes et al. (2008)	Afán et al. (2014)
Cory's Shearwater	*Calonectris borealis*	10.6	4209.5	1233.5	39	-28	771	Magalhaes et al. (2008)	Afán et al. (2014)
Cory's Shearwater	*Calonectris borealis*	9.76	5573.8	1570.3	37	-25	771	Magalhaes et al. (2008)	Afán et al. (2014)
European Storm Petrel	*Hydrobates pelagicus pelagicus*	1.06	351	123	60	-1.17	29	Bolton (2020)	This study
European Storm Petrel	*Hydrobates pelagicus pelagicus*	1.04	391	160	60	-1.17	29	Bolton (2020)	This study

Appendix 1b. Continued

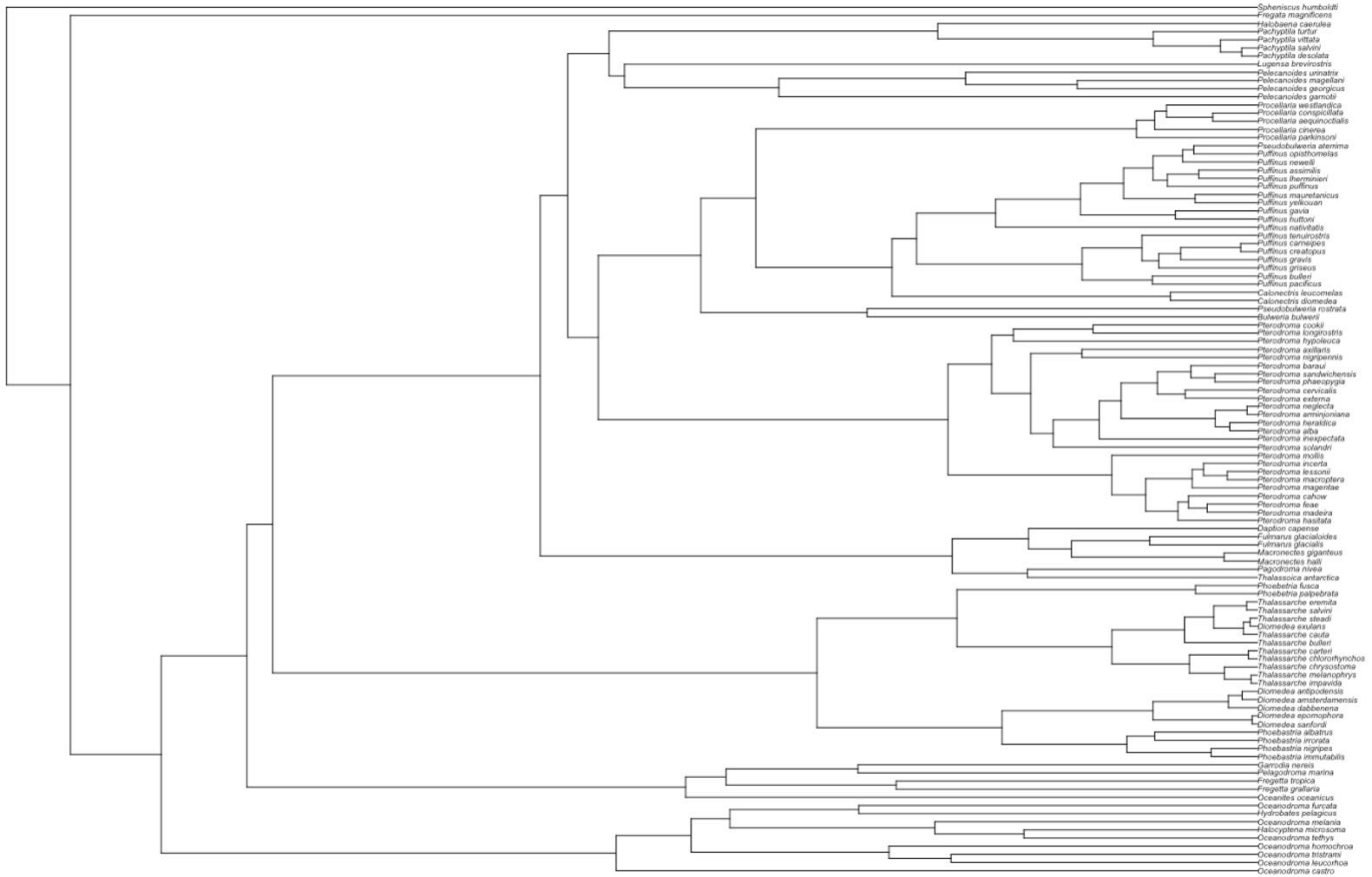
Grey-headed Albatross	*Thalassarche chrysostoma*	8.04	5366.6	1567.4	-52.55	169.15	3291	Waugh et al. (1999)	Phillips et al. (2004)
Grey-headed Albatross	*Thalassarche chrysostoma*	3.33	2445	610	-54	-38	3291	Phalan et al. (2007)	Phillips et al. (2004)
Grey-headed Albatross	*Thalassarche chrysostoma*	7.79	4436	652	-54	-38	3291	Phalan et al. (2007)	Phillips et al. (2004)
Grey-headed Albatross	*Thalassarche chrysostoma*	3.88	2420	722	-46.9	37.75	3291	Nel et al. (2000)	Phillips et al. (2004)
Grey-headed Albatross	*Thalassarche chrysostoma*	3.46	2585	592	-54	-38.05	3291	Phillips et al. (2004)	Phillips et al. (2004)
Grey-headed Albatross	*Thalassarche chrysostoma*	2.86	1980	595	-54	-38.05	3291	Phillips et al. (2004)	Phillips et al. (2004)
Grey-headed Albatross	*Thalassarche chrysostoma*	2.67	1960	568	-54	-38.05	3291	Phillips et al. (2004)	Phillips et al. (2004)
Grey-headed Albatross	*Thalassarche chrysostoma*	2.67	1924	574	-54	-38.05	3291	Phillips et al. (2004)	Phillips et al. (2004)
Laysan Albatross	*Phoebastria immutabilis*	3	1079	510	23.87	-166.28	2780	Fernández et al. (2001)	Kappes et al. (2010)
Laysan Albatross	*Phoebastria immutabilis*	14.5	7789	2675	23.87	-166.28	2780	Fernández et al. (2001)	Kappes et al. (2010)
Laysan Albatross	*Phoebastria immutabilis*	3	1799	722	23.87	-166.28	2780	Fernández et al. (2001)	Kappes et al. (2010)
Light-mantled Sooty Albatross	*Phoebetria palpebrata*	6.71	4901	970	-54	-38	2880	Phalan et al. (2007)	Phillips et al. (2005)
Light-mantled Sooty Albatross	*Phoebetria palpebrata*	4.79	3795	921	-54	-38.05	2880	Phillips et al. (2005)	Phillips et al. (2005)
Manx Shearwater	*Puffinus puffinus*	2	56.3	262.4	54.68	-5.52	442	Dean et al. (2013)	Gray & Hamer (2001)
Manx Shearwater	*Puffinus puffinus*	1	305.2	88.3	51.73	-5.28	442	Dean et al. (2013)	Gray & Hamer (2001)
Monteiro's Storm Petrel	*Hydrobates monteiroi*	-	-	493	39.059	-27.954	52	Paiva et al. (2018)	Paiva et al. (2018)
Monteiro's Storm Petrel	*Hydrobates monteiroi*	-	-	599	39.059	-27.954	52	Paiva et al. (2018)	Paiva et al. (2018)
Northern Fulmar	*Fulmarus glacialis*	0.425	-	60.8	74.367	19.167	790	Weimerskirch et al. (2001)	Phillips & Hamer (2000)
Northern Royal Albatross	*Diomedea sanfordi*	3	854	158	-45.77	170.73	7922	Sugishita et al. (2015)	Sugishita et al. (2017)
Scopoli's Shearwater	*Calonectris diomedea*	1.8	367.6	89.7	37.13	10.8	657	Grémillet et al. (2014)	Afán et al. (2014)
Scopoli's Shearwater	*Calonectris diomedea*	2	441.8	104.8	37.13	10.8	657	Grémillet et al. (2014)	Afán et al. (2014)
Scopoli's Shearwater	*Calonectris diomedea*	2.2	210.8	36.5	35.18	-2.43	657	Afán et al. (2014)	Afán et al. (2014)
Short-tailed Shearwater	*Ardenna tenuirostris*	0.67	195.6	38.8	-37.55	149.9	585	Berlincourt et al. (2015)	Berlincourt et al. (2015)
Short-tailed Shearwater	*Ardenna tenuirostris*	0.82	316.1	86.9	-38.37	142.22	585	Berlincourt et al. (2015)	Berlincourt et al. (2015)
Southern Fulmar	*Fulmarus glacialoides*	1.2	1738	185	-68.8	77.7	990	Dehnhard et al. (2020)	Weimerskirch (1990)
Southern Giant Petrel	*Macronectes giganteus*	5.9	1649.8	384.6	-45	-66	4350	Quintana et al. (2010)	González-Solís et al. (2000a)
Southern Giant Petrel	*Macronectes giganteus*	8.925	2009.6	328.3	-45	-66	4350	Quintana et al. (2010)	González-Solís et al. (2000a)
Southern Giant Petrel	*Macronectes giganteus*	3.28	1475.9	179.2	-54.66	-64.14	4350	Quintana et al. (2010)	González-Solís et al. (2000a)
Southern Giant Petrel	*Macronectes giganteus*	3.87	1468	337.7	-54.66	-64.14	4350	Quintana et al. (2010)	González-Solís et al. (2000a)
Spectacled Petrel	*Procellaria conspicillata*	7.3	3590	1073	-37.29	-12.68	1191	Reid et al. (2014)	Ryan (1998)
Streaked Shearwater	*Calonectris leucomelas*	2.15	740.1	187.6	39.4	141.98	516	Yoda et al. (2014)	Ochi et al. (2010)
Streaked Shearwater	*Calonectris leucomelas*	2.82	959.8	265.7	39.4	141.98	516	Yoda et al. (2014)	Ochi et al. (2010)
Trindade Petrel	*Pterodroma arminjoniana*	4.62	2981.93	992.24	-20.5	-29.32	398	Leal et al. (2017)	Kruger et al. (2016)

Appendix 1b. Continued

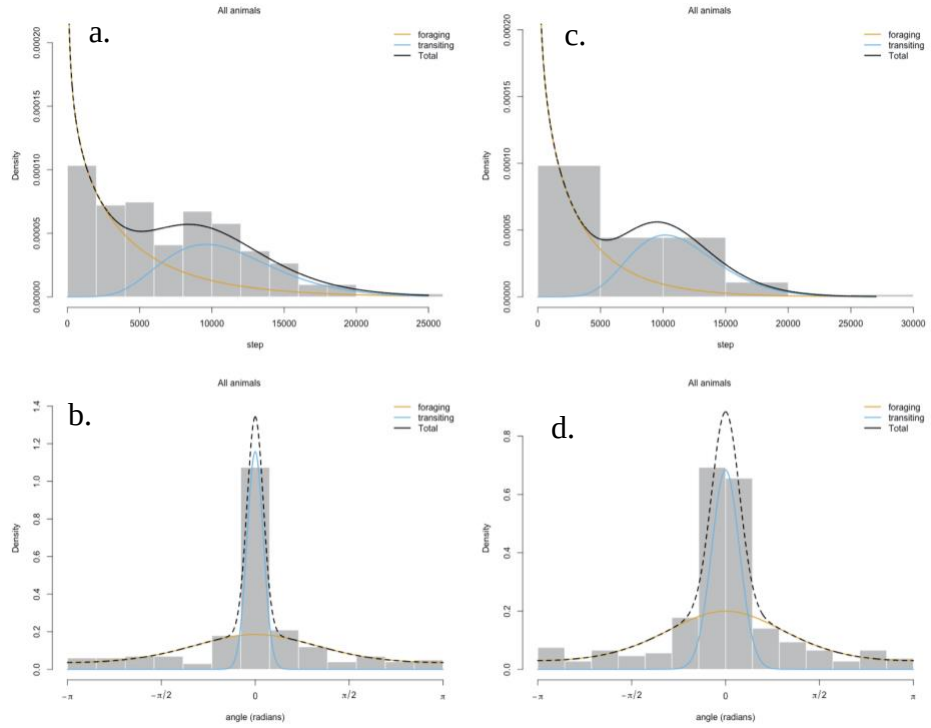
Wandering Albatross	*Diomedea exulans*	2.8	923	256	-46	51	9600	Weimerskirch et al. (1993)	Waugh & Weimerskirch (2003)
Wandering Albatross	*Diomedea exulans*	11.6	6091	1534	-46	51	9600	Weimerskirch et al. (1993)	Waugh & Weimerskirch (2003)
Wandering Albatross	*Diomedea exulans*	2.83	2369	508	-46	51	9600	Weimerskirch et al. (2007)	Waugh & Weimerskirch (2003)
Wandering Albatross	*Diomedea exulans*	6.88	4646	-	-54	-38.6	9600	Prince et al. (1992)	Waugh & Weimerskirch (2003)
Wandering Albatross	*Diomedea exulans*	3.33	1372	479	-50.87	166	9600	Walker et al. (1995)	Waugh & Weimerskirch (2003)
Wandering Albatross	*Diomedea exulans*	3.92	1536	472	-54	-38	9600	Phalan et al. (2007)	Waugh & Weimerskirch (2003)
Wandering Albatross	*Diomedea exulans*	6.5	2582	844	-54	-38	9600	Phalan et al. (2007)	Waugh & Weimerskirch (2003)
Wandering Albatross	*Diomedea exulans*	13.7	-	1638.2	-54	-38.6	9600	Xavier et al. (2004)	Waugh & Weimerskirch (2003)
Wandering Albatross	*Diomedea exulans*	6.6	-	1110.5	-54	-38.6	9600	Xavier et al. (2004)	Waugh & Weimerskirch (2003)
Waved Albatross	*Phoebastria irrorata*	10	1245	430	-1.37	-89.65	3678	Fernández et al. (2001)	Awkerman et al. (2005)
Waved Albatross	*Phoebastria irrorata*	6	1563	730	-1.37	-89.65	3678	Fernández et al. (2001)	Awkerman et al. (2005)
Wedge-tailed Shearwater	*Ardenna pacifica*	-	-	131.84	-4.21	55.66	362	Cecere et al. (2013)	Cecere et al. (2013)
Wedge-tailed Shearwater	*Ardenna pacifica*	3.75	-	398	-21.354	169.954	362	Weimerskirch et al. (2020)	Cecere et al. (2013)
Wedge-tailed Shearwater	*Ardenna pacifica*	1.73	-	-	-21.56	165.954	362	Weimerskirch et al. (2020)	Cecere et al. (2013)
Wedge-tailed Shearwater	*Ardenna pacifica*	3.42	-	-	-22.313	166.436	362	Weimerskirch et al. (2020)	Cecere et al. (2013)
Wedge-tailed Shearwater	*Ardenna pacifica*	3.44	-	-	-22.55	166.792	362	Weimerskirch et al. (2020)	Cecere et al. (2013)
Westland Petrel	*Procellaria westlandica*	3	-	171	-42.146	171.341	1235	Waugh et al. (2018)	Waugh et al. (2018)
Westland Petrel	*Procellaria westlandica*	4.9	-	182	-42.146	171.341	1235	Waugh et al. (2018)	Waugh et al. (2018)
Westland Petrel	*Procellaria westlandica*	2	-	127	-42.146	171.341	1235	Waugh et al. (2018)	Waugh et al. (2018)
White-capped Albatross	*Thalassarche steadi*	1.79	977.35	-	-50.83	165.9	3500	Torres et al. (2011)	Battam (2010)
White-chinned Petrel	*Procellaria aequinoctialis*	10.4	5973	1922	-54	-38.05	1300	Phillips et al. (2006)	Weimerskirch et al. (1999)
White-chinned Petrel	*Procellaria aequinoctialis*	4.5	2539	614	-54	-38.05	1300	Phillips et al. (2006)	Weimerskirch et al. (1999)
White-chinned Petrel	*Procellaria aequinoctialis*	5.2	2808	-	-54.05	38.6	1300	Berrow et al. (2000)	Weimerskirch et al. (1999)
White-chinned Petrel	*Procellaria aequinoctialis*	8.9	6381.8	1847.6	-49.61	70.26	1300	Péron et al. (2010)	Weimerskirch et al. (1999)

Appendix 2. Structure of the GLM and MCMC models

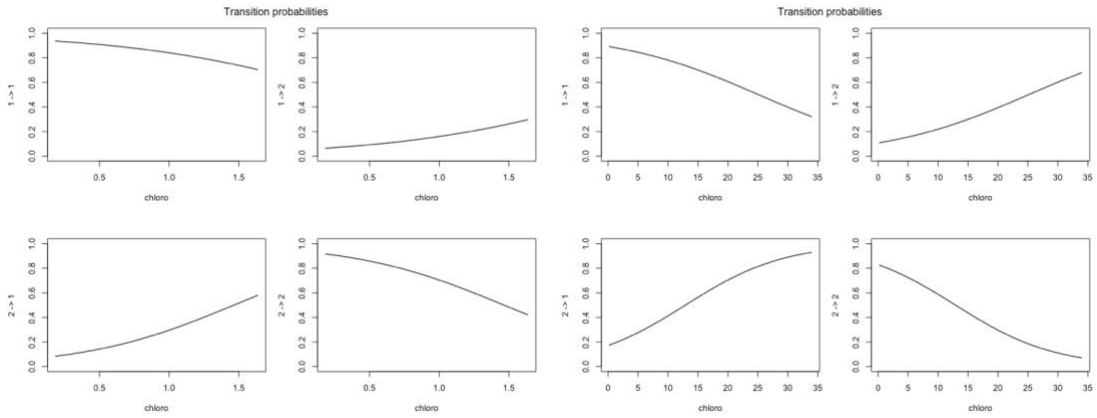
Model	Formula	GLM Models	MCMC Models
Foraging trip duration during Incubation phase	formula_1 <- log_duration ~ log_mass + sqrt_latitude_sq + longitude180	glm_mod_1 <- glm(formula = formula_1, family = "gaussian", data = myData1)	mod_mcmc_1 <- MCMCglmm(fixed = formula_1, random = ~animal, family = "gaussian", pedigree = tree_IncDur, data = data_IncDur, nitt = nitt, burnin = burnin, thin = thin, prior = prior)
Foraging trip distance during Incubation phase	formula_2 <- log_distance ~ log_mass + latitude_sq + longitude180	glm_mod_2 <- glm(formula = formula_2, family = "gaussian", data = myData2)	mod_mcmc_2 <- MCMCglmm(fixed = formula_2, random = ~animal, family = "gaussian", pedigree = tree_IncDist, data = data_IncDist, nitt = nitt, burnin = burnin, thin = thin, prior = prior)
Foraging trip range during Incubation phase	formula_3 <- log_range ~ log_mass + sqrt_latitude_sq + longitude180	glm_mod_3 <- glm(formula = formula_3, family = "gaussian", data = myData3)	mod_mcmc_3 <- MCMCglmm(fixed = formula_3, random = ~animal, family = "gaussian", pedigree = tree_IncRange, data = data_IncRange, nitt = nitt, burnin = burnin, thin = thin, prior = prior)
Foraging trip duration during Chick-rearing phase	formula_4 <- log_duration ~ log_mass + latitude_sq + longitude180	glm_mod_4 <- glm(formula = formula_4, family = "gaussian", data = myData4)	mod_mcmc_4 <- MCMCglmm(fixed = formula_4, random = ~animal, family = "gaussian", pedigree = tree_ChickDur, data = data_ChickDur, nitt = nitt, burnin = burnin, thin = thin, prior = prior)
Foraging trip distance during Chick-rearing phase	formula_5 <- log_distance ~ log_mass, latitude_sq + longitude180	glm_mod_5 <- glm(formula = formula_5, family = "gaussian", data = myData5)	mod_mcmc_5 <- MCMCglmm(fixed = formula_5, random = ~animal, family = "gaussian", pedigree = tree_ChickDist, data = data_ChickDist, nitt = nitt, burnin = burnin, thin = thin, prior = prior)
Foraging trip range during Chick-rearing phase	formula_6 <- log_range ~ log_mass + latitude_sq + longitude180	glm_mod_6 <- glm(formula = formula_6, family = "gaussian", data = myData6)	mod_mcmc_6 <- MCMCglmm(fixed = formula_6, random = ~animal, family = "gaussian", pedigree = tree_ChickRange, data = data_ChickRange, nitt = nitt, burnin = burnin, thin = thin, prior = prior)



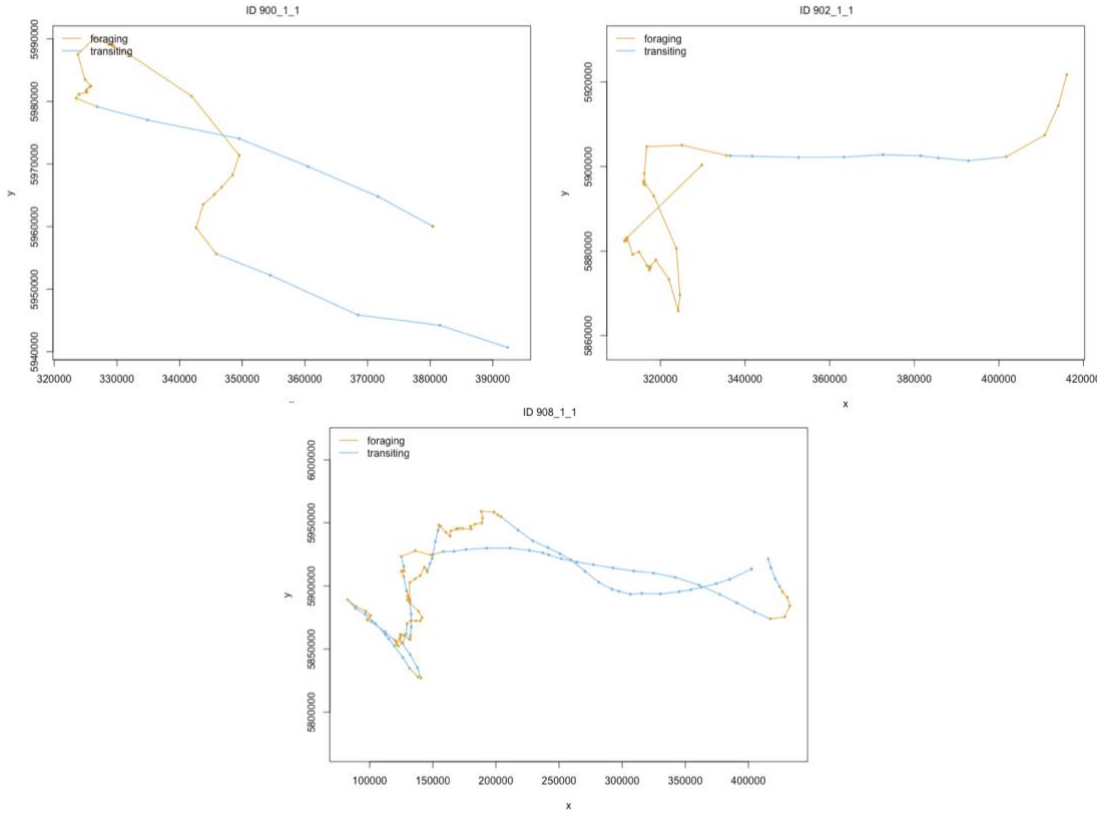
Appendix 3. Maximum Clade Credibility tree for procellariiform species (Jetz *et al*., 2012) prior to any adjustments being made



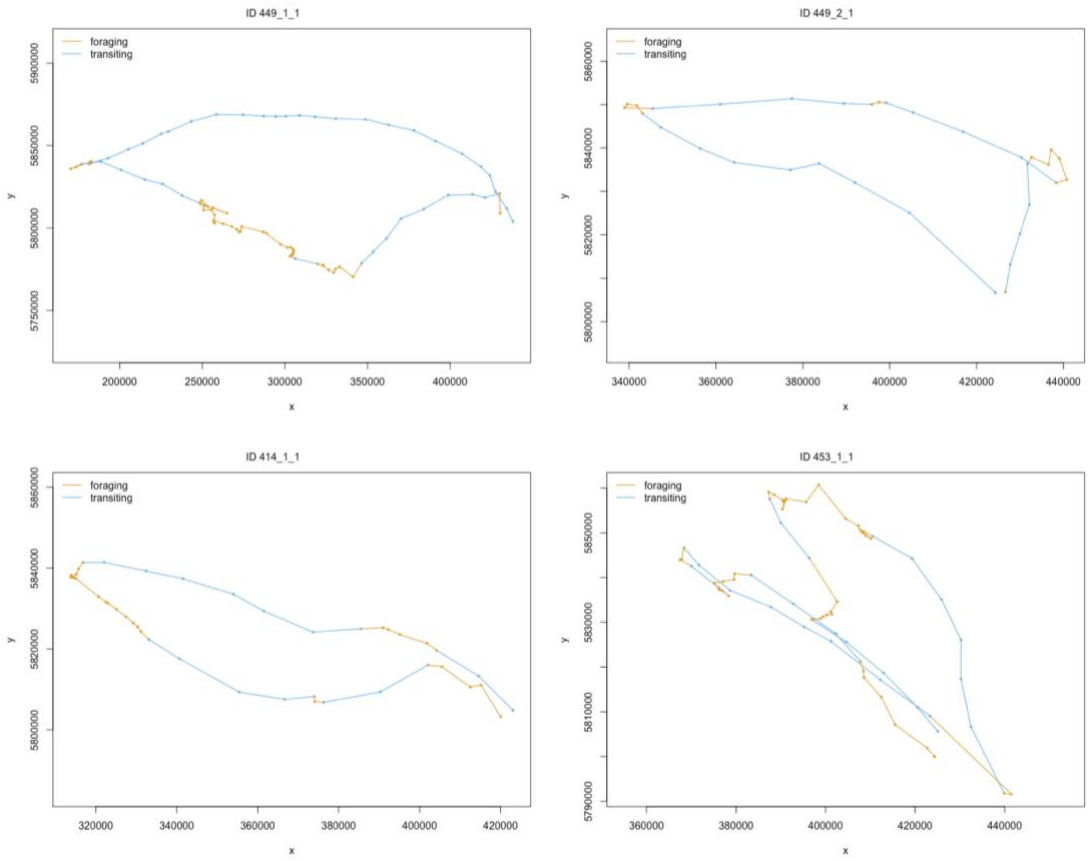
Appendix 4a. Plots from the two-state HMMs showing the state-dependent distributions of step lengths and turning angles for all birds from both breeding colonies which were interpolated to 30 minutes. Plots (a) and (b) show High Island storm petrels. Plots (c) and (d) show Illauntannig storm petrels.



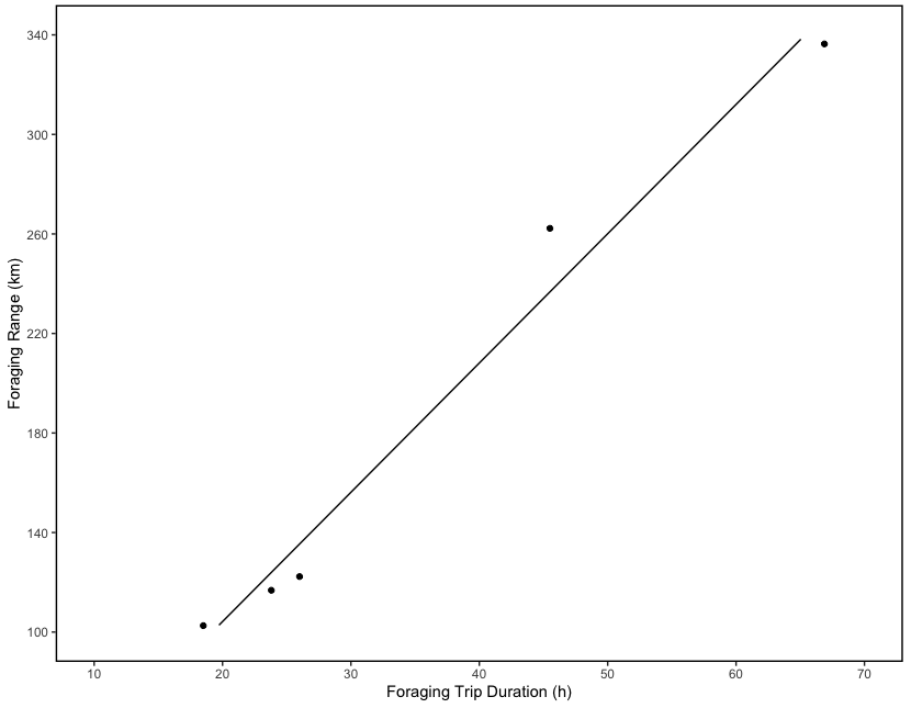
Appendix 4b. Plots of the transition probabilities between behaviour states as a function of monthly chlorophyll-*a* concentration for both colonies. Behaviour state 1 is foraging/ARS and behaviour state 2 is transiting. The four plots on the left are for High Island and the four plots on the right are for Illauntannig.



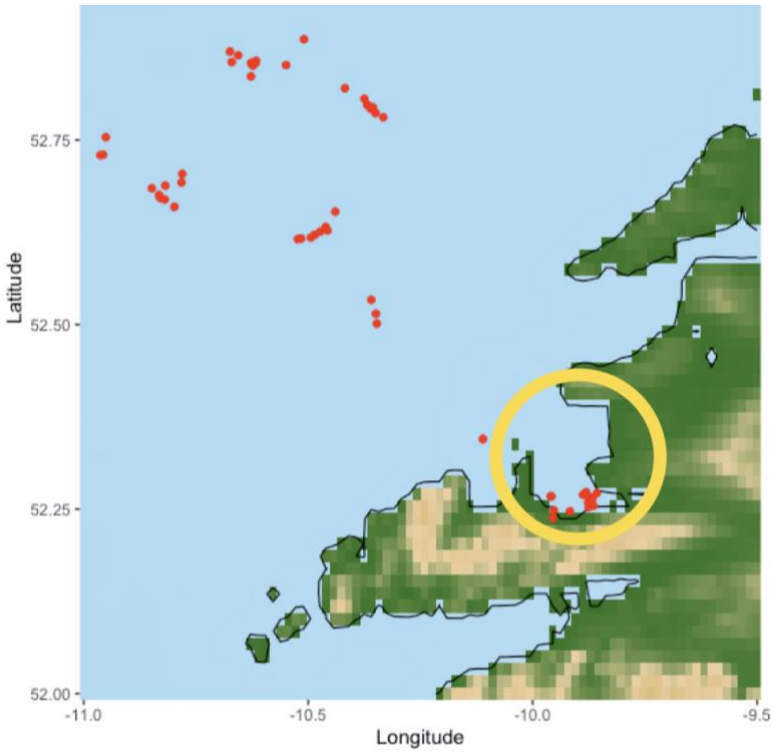
Appendix 4c. The foraging trips of storm petrels from High Island showing foraging and transiting behaviours determined by the preferred HMM model according to the AIC scores. The HMM with chlorophyll-*a* concentration included was preferred for the High Island colony.



Appendix 4d. The foraging trips of storm petrels from Illauntannig showing foraging and transiting behaviours determined by the preferred HMM model according to the AIC scores. The HMM with chlorophyll-*a* concentration excluded was preferred for the Illauntannig colony.



Appendix 5. Relationship between Foraging trip duration and Foraging range after the outlier (Table 2, Bird 2) was removed (r = 0.988, df = 3, p = 0.0015).



Appendix 6. The red points indicate the location of foraging behaviour performed by Bird 2 (Table 2) according to the preferred HMM model. This storm petrel spent time foraging in Tralee Bay, the location of which is marked by the yellow circle.

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