# Ecological drivers of population size and marine distribution of storm-petrels in the northeast Atlantic

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# Summary

The magnitude and causes of population change and marine distributions of very small seabirds have been difficult to study, but some populations appear to be in decline. It is important to understand the range of threats that these species face, to be able to identify potential conservation actions. In this thesis I use new developments in tracking technology and statistical analysis methods to address these issues in the two smallest North Atlantic seabirds: the European Storm-petrel *Hydrobates pelagicus* and the Leach's Storm-petrel *Hydrobates leucorhous*.

A census of two of the largest Leach's Storm-petrel colonies in the northeast Atlantic, analysed using both traditional and novel statistical methods, confirmed a continuing decline (68% across 19 years) on St Kilda, Western Isles, Scotland, and identified a substantial decline on Elliðaey, Vestmannaeyjar archipelago, Iceland (40–49% across 27 years).

Dissection of Great Skua *Stercorarius skua* pellets from St Kilda and Mousa, Shetland, quantified the number of pellets produced per individual storm-petrel consumed. This ratio varies between storm-petrel species and between sites. These data indicate that the number of Leach's Storm-petrels consumed by Great Skuas on St Kilda is higher than previously estimated using bioenergetics models, and represents a substantial proportion of the Leach's Storm-petrels present on St Kilda.

GPS tracking of European Storm-petrels breeding on Mousa indicates that their movements are driven primarily by avoidance of predation and intraspecific competition. Foraging areas differed between years, but in all years foraging trips were focused on the relatively shallow shelf waters to the southeast of Shetland.

These findings provide novel insights into the marine distributions, at-sea behaviours, foraging ecology, and population change among storm-petrels in the northeast Atlantic, and provide an important basis for identifying marine protected areas and conservation interventions on land.

# Licences

Work on Leach’s Storm-petrels on St Kilda was carried out under a Schedule 1 Disturbance Licence.

Permission to work on Mousa was granted by NatureScot, RSPB and the Bell family. All capture, handling and tagging of birds was conducted under appropriate licences issued by the BTO.

All fieldwork methods were designed to be compatible with Cardiff University ethical regulations and the ASAB Guidelines for the Treatment of Animals in Behavioural Research and Teaching (Buchanan et al., 2012).

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Although Skokholm didn’t end up as one of my PhD study sites, the island has featured prominently in my PhD years. I’m incredibly grateful to Rich and Giselle for their hospitality and for letting me loose on their precious stormies. I can’t wait to see what’s next for the Petrel Station and those little stars in box 64.

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# Table of Contents

# 1 General Introduction

Knowledge of the distribution and abundance of a species is fundamental to understanding its ecology and planning effective conservation management, but for some species, even this basic information is difficult to obtain. Storm-petrels are the smallest of the seabirds and belong to the Order Procellariiformes, one of the most threatened bird groups globally (Croxall et al., 2012). The behaviour and ecology of these species makes them especially challenging to study.

Due to their small size, storm-petrels are particularly vulnerable to predation by both mammalian and avian predators and so most species nest on remote islands, coming to land only under darkness and breeding out of sight in crevices or burrows (Davis, 1957; Scott, 1970; Warham, 1990). Obtaining accurate counts of breeding storm-petrels is notoriously difficult, and population estimates for these species are generally very imprecise (Mitchell et al., 2004). Where population declines have been detected, the drivers of those declines are sometimes unknown (e.g. Wilhelm et al., 2019).

Like all Procellariiformes, storm-petrels spend a large proportion of their lives at sea, so knowledge of their marine distributions and behaviour is key to understanding the threats they face. However, the small size of storm-petrels means that they are very difficult to detect in aerial or vessel-based surveys. It is only since the miniaturisation of tracking devices in recent years that we are now able to make significant advances in our understanding of the movements and behaviour of these tiny seabirds, and this is critical at a time when anthropogenic pressures on the marine environment are rapidly increasing.

I studied two species of storm-petrel at some of their largest colonies in the northeast Atlantic, with the aim of using state of the art methods to improve our knowledge of their population sizes, marine distributions and the range of threats, both natural and anthropogenic, that they may face.

## 1.1 Study species

### 1.1.1 European Storm-petrel

The European Storm-petrel *Hydrobates pelagicus* is the smallest Atlantic seabird, with an average body weight of just 26 g (Brooke, 2004). The species breeds on islands in the northeast Atlantic and Mediterranean, from Iceland and northern Norway to the Canary Islands. The largest colonies occur in the Faroe Islands, Ireland, Iceland and the UK (together holding around 90% of the global breeding population; BirdLife International, 2018). The Mediterranean population is recognised as a subspecies, *H. p. melitensis*, separate from the Atlantic population *H. p. pelagicus*, and breeds on islands off Italy, Malta, Greece and Spain (Cagnon et al., 2004; BirdLife International, 2018). Breeding colonies of both subspecies are almost always located on offshore islands free from non-native mammalian predators, although some colonies occur on islands with introduced mice (De León et al., 2006).

The global population of European Storm-petrels is estimated to be 1.3–1.5 million individuals (Brooke, 2004; BirdLife International, 2018), however, the difficulty of monitoring this species means that population estimates are uncertain. Currently the species is classified as ‘Least Concern’ on the IUCN Red List of Threatened Species (BirdLife International, 2017). The global population trend is unknown but surveys have indicated population declines at some colonies (Insley et al., 2014). The greatest threat to European Storm-petrels is thought to be the introduction of invasive non-native species, such as rats, to breeding islands (De León et al., 2006; Ratcliffe et al., 2009; Ruffino et al., 2009). Increases in populations of native avian predators such as gulls (*Larus* spp.), skuas (*Stercorarius* spp.) and owls (Strigiformes) at breeding sites can also lead to increased mortality of European Storm-petrels (Walmsley, 1986; Votier et al., 2006; Sanz-Aguilar et al., 2009).

### 1.1.2 Leach’s Storm-petrel

Leach’s Storm-petrel *Hydrobates leucorhous* is larger than the European Storm-petrel, weighing around 45 g. The species is widespread and breeds in burrows on islands across the Atlantic and Pacific Oceans. The global population is estimated at 6.7–8.3 million breeding pairs, but sharp declines have been detected at Atlantic colonies, leading to the species being up-listed from ‘Least Concern’ to ‘Vulnerable’ on the IUCN Red List in 2016 (BirdLife International, 2020).

Declines at some colonies have been attributed to increased predation, particularly by gulls (Stenhouse et al., 2000) and skuas (Newson et al., 2008; Miles, 2010), but this does not appear to be the case at the largest colony, on Baccalieu Island, Newfoundland, where the breeding population has declined significantly despite not being subjected to high predation pressure (Wilhelm et al., 2019).

In addition to predation, both species face a range of other potential threats, including changes to breeding habitat (Mitchell et al., 2004; Cadiou et al., 2010), impacts of climate change (Russell et al., 2015; Mauck et al., 2018), and collision with offshore structures such as oil and gas platforms as a result of light attraction (Wiese et al., 2001; Ronconi et al., 2015).

Despite their small size, storm-petrels are relatively long-lived species, with longevity records for both European and Leach’s Storm-petrel exceeding 30 years (Pollet et al., 2019a; Robinson et al., 2021). They have delayed maturation, with the average age of first breeding being four or five years (Okill and Bolton, 2005; Pollet et al., 2019a), and lay a single egg at each breeding attempt. As a result of these life history traits, reduced productivity or reduced survival of immatures may take a long time to become apparent in breeding populations, whereas reduced adult survival can have large and rapid effects on breeding population size.

## 1.2 Thesis outline

In **Chapter 2**, I use two methods of acoustic survey to estimate the population size of the largest Leach’s Storm-petrel colonies in the northeast Atlantic (St Kilda archipelago, Western Isles, UK and Elliðaey, Vestmannaeyjar archipelago, Iceland; Figure 1.1). I discuss the relative advantages and disadvantages of these techniques, as well as the possible causes of the identified population change.

Rationale:

Population estimates are essential for species conservation. Knowledge of population trajectories is used to assess the need for conservation management and to determine the efficacy of any interventions (Jones et al., 2016; Rodríguez and Chiaradia, 2019). Given the large declines detected at Leach's Storm-petrel colonies in the western Atlantic (Wilhelm et al., 2019; D'Entremont et al., 2020), and the recent up-listing of the species to 'Vulnerable' on the IUCN Red List (BirdLife International, 2020), there was a need to determine population trajectories for key colonies in the eastern Atlantic. Iceland's Vestmannaeyjar archipelago was thought to contain the largest Leach's Storm-petrel population in the eastern Atlantic, based on a single survey of the island of Elliðaey in 1991 (Hansen et al., 2009). St Kilda holds the majority of the UK's breeding Leach's Storm-petrels and the only previous whole-archipelago census was as part of the Seabird 2000 census of Britain and Ireland's seabirds in 1999/2000 (Mitchell et al., 2004), with a further census of the largest sub-colony in 2006 suggesting a 54% population decline (Newson et al., 2008).

Storm-petrels tend to be surveyed by 'grubbing', where surveyors reach into burrows to determine occupancy, the use of endoscopes to view burrow contents, or using acoustic playback techniques, where a recording of the species' call is played to elicit a response from occupied burrows (Ambagis, 2004; Wilhelm et al., 2019). Compared with grubbing and the use of an endoscope, the acoustic playback method is less invasive and has been shown to be more efficient and accurate (Ambagis, 2004), and is the primary census method used at eastern Atlantic colonies (Mitchell et al., 2004; Murray et al., 2008; Newson et al., 2008; Hansen et al., 2009). However, the playback method is still time-consuming and population estimates resulting from standard playback surveys are imprecise, resulting in a need for improvement in order to optimise the use of limited resources (Mitchell et al., 2004; Arneill, 2018; Bird et al., 2021). Advances in ecological modelling techniques expand the scope for census methods (Kéry and Royle, 2016), and the incorporation of predictive habitat modelling into the analysis of burrow-nesting seabird census data has been found to result in improved estimates of population size (Rayner et al., 2007; Stokes et al., 2021).

In **Chapter 3**, I re-examine a key element of the bioenergetics models used to estimate the rates of consumption of storm-petrels by Great Skuas. I use information from the dissection of 427 Great Skua pellets from two large storm-petrel colonies in Scotland (St Kilda, Western Isles and Mousa, Shetland; Figure 1.1) to provide empirical estimates of the number of pellets produced per European or Leach's Storm-petrel consumed, and how this varies between storm-petrel species and colonies.

Rationale:
Predation is a key threat to storm-petrels and native avian predators can become problematic if their populations increase or switch prey as a result of changes to other food resources (Votier et al., 2004b; Bicknell et al., 2013; Church et al., 2019). Rapid increases in Great Skua populations in Scotland over recent decades (Phillips et al., 1999a; Mitchell et al., 2004) and potential prey switching due to the Common Fisheries Policy discard ban (Votier et al., 2004b; Bicknell et al., 2013) may be exerting increased pressure on storm-petrel populations. Given the arrested growth of the European Storm-petrel population breeding on Mousa (Bolton et al., 2017) and the decline of Leach's Storm-petrels on St Kilda, which has been attributed to predation by Great Skuas (Newson et al., 2008; Miles, 2010), it is important to be able to accurately estimate predation rates.

In **Chapter 4**, I analyse GPS tracking data from European Storm-petrels breeding on Mousa, Shetland (Figure 1.1), to examine the broad-scale drivers of their marine distribution. I examine the influence of remotely-sensed environmental variables commonly used as proxies of prey availability, in addition to intraspecific competition and predation risk. I include GPS tracking data collected in 2018 as part of my PhD, in addition to data collected by Bolton (2021) in 2015–2017.

Rationale:

Knowledge of seabirds' marine movements and habitat use is an important first step in understanding their current threats and how they might be impacted by changes to the marine environment brought about by climate change and other anthropogenic pressures (Rodríguez and Chiaradia, 2019). Storm-petrels breeding in Shetland were assumed to be travelling to forage at the continental shelf edge, where prey availability is likely to be high but, using GPS tracking data, Bolton (2021) showed that birds breeding on Mousa are actually travelling in the opposite direction and remaining over the relatively shallow waters of the continental shelf to the southeast of Shetland. The reasons for their use of a restricted foraging area to the southeast of the colony are unclear, but may be multi-faceted. Many seabirds are top predators and their marine distributions are often examined in relation to the level of competition from conspecifics (Wakefield et al., 2011, 2013) and environmental variables that are likely to relate to prey availability (e.g. Wakefield et al., 2009; Scott et al., 2013; Grecian et al., 2016). However, due to their small size, storm-petrels are also vulnerable to predation at sea. To my knowledge, the influence of predation risk on the marine distribution of storm-petrels has not yet been examined, although several studies have investigated other ecological drivers of their marine habitat use (Hedd et al., 2018; De Pascalis et al., 2021; Wilkinson, 2021).

In **Chapter 5**, I use the same GPS tracking dataset to examine the marine distribution of breeding European Storm-petrels at a finer scale, by using hidden Markov models to classify the at-sea behaviour of the tracked birds. I investigate spatial and temporal patterns in behaviour and use the same biotic and abiotic environmental variables as in Chapter 4 to examine the drivers of foraging distributions.

Rationale:

While an understanding of the drivers of seabirds' general marine distribution is useful, the addition of behavioural data can improve our understanding of potential threats and the identification of important foraging areas and potential sites for

Marine Protected Area designation (Camphuysen et al., 2012). The ability to GPS-track even the smallest seabirds has led to the first tracking-derived insights into the at-sea behaviour of European Storm-petrels breeding in Ireland (Wilkinson, 2021) and the Mediterranean (De Pascalis et al., 2021; Rotger et al., 2021), but this is the first study to do the same for birds breeding in the UK.

In the General Discussion (**Chapter 6**) I explore the consequences of my main findings in terms of conservation of the two storm-petrel species, and identify priorities for future research.

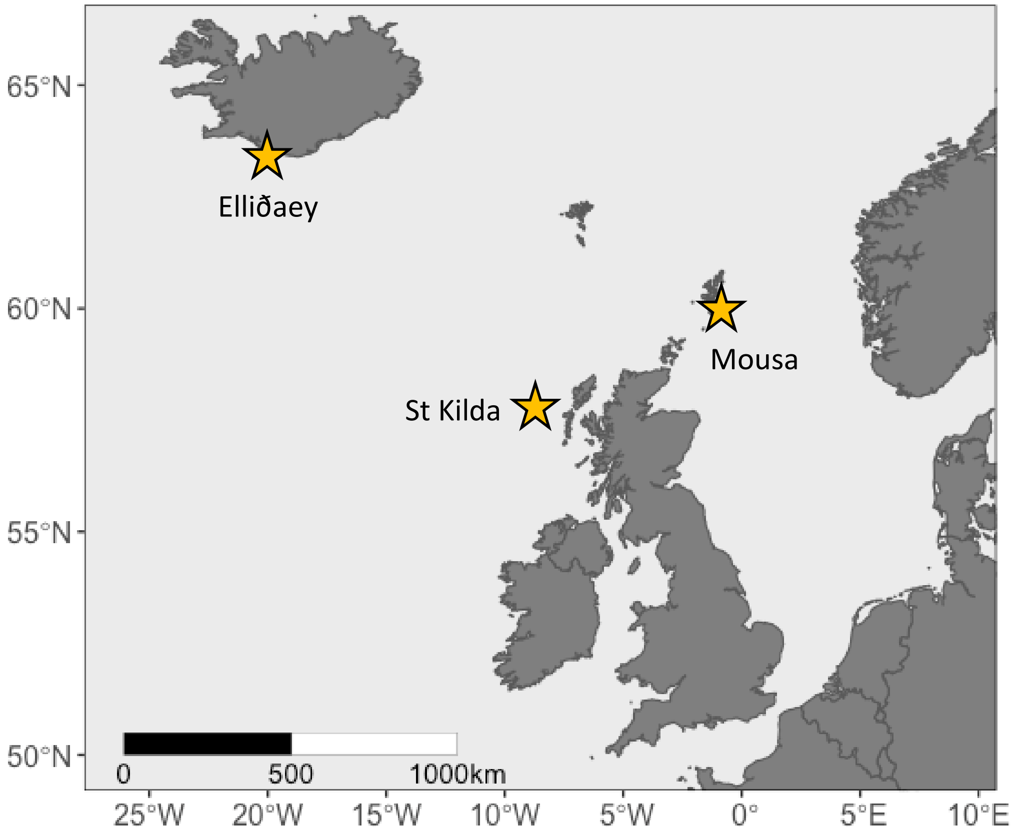

Figure 1.1. Study sites used in the four data chapters of the thesis.

# 2 Decline of Leach’s Storm-petrels at the largest colonies in the northeast Atlantic

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*Author contributions: MB, ESH and RL arranged fieldwork logistics. All authors except RJT, OP and RM contributed to fieldwork. ZD designed and performed the analysis and wrote the manuscript, with input from MB, RJT, RM, ESH, RL, MJW and OP.*

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## 2.1 Abstract

Leach’s Storm-petrel has undergone substantial population declines at North Atlantic colonies over recent decades, but censusing the species is challenging because it nests in burrows and is only active at colonies at night. Acoustic playback surveys allow birds present in nest sites to be detected when they respond to recordings of vocalisations. However, not all birds respond to playback on every occasion, response rate is likely to decline with increasing distance between the bird and the playback location, and the observer may not detect all responses. As a result, various analysis methods have been developed to measure and correct for these imperfect response and detection probabilities. I applied two classes of methods (calibration plot and

hierarchical distance sampling) to acoustic survey data from the two largest colonies of breeding Leach’s Storm-petrels in the northeast Atlantic: the St Kilda archipelago off the coast of northwest Scotland, and the island of Elliðaey in the Vestmannaeyjar archipelago off the southwest of Iceland. Our results indicate an overall decline of 68% for the St Kilda archipelago between 2000 and 2019, with a current best estimate of ~9,200 (95% CI: 8,100–10,500) pairs. The population on Elliðaey appears to have declined by 40–49% between 1991 and 2018, with a current best estimate of ~5,400 (95% CI: 4,300– 6,700) pairs. I also discuss the relative efficiency and precision of the two survey methods.

## 2.2 Introduction

Leach’s Storm-petrel is a widespread and highly pelagic seabird, breeding in burrows on islands across the Atlantic and Pacific Oceans. The global population is estimated at 6.7–8.3 million breeding pairs, but sharp declines have been detected at Atlantic colonies, leading to the species being up-listed from ‘Least Concern’ to ‘Vulnerable’ on the IUCN Red List in 2016 (BirdLife International, 2020). The main eastern Atlantic Leach’s Storm-petrel colonies are in Iceland and Scotland (Mitchell et al., 2004), but there are also up to 1,000 pairs breeding in Mykineshólmur in the Faroe Islands and smaller numbers breeding in Norway and Ireland (Bolton and Eaton, 2020).

The Vestmannaeyjar archipelago contains almost all of Iceland’s breeding Leach’s Storm-petrels and, based on extrapolation of the densities measured on Elliðaey Island in 1991, is believed to hold the largest population in the eastern Atlantic (Hansen et al., 2009). The 1991 survey of Elliðaey revealed a strong positive association between the occurrence of Leach’s Storm-petrel burrows and Atlantic Puffin *Fratercula arctica* (hereafter ‘Puffin’) habitat, which had been mapped across the whole of the Vestmannaeyjar archipelago (Hansen et al., 2009). Six other islands in the archipelago hold breeding colonies of Leach’s Storm-petrels: Bjarnarey, Álsey, and Suðurey, which contain similar-sized areas of Puffin breeding habitat to Elliðaey, and Brandur, Hellisey and Smáeyjar, which contain smaller areas of Puffin breeding habitat (Hansen et al., 2011). The density of Leach’s Storm-petrel Apparently

Occupied Sites (AOS; i.e. estimated breeding pairs) within surveyed areas of Puffin habitat on Elliðaey was extrapolated across the Puffin habitat on the other islands in the archipelago, to produce a whole-archipelago estimate of 178,900 (± 34,100) AOS, including 44,100 (± 9,100) AOS for Elliðaey Island (Hansen et al., 2009).

The Seabird 2000 census (Mitchell et al., 2004) included the first attempt to produce accurate population estimates for Leach’s Storm-petrels in Britain and Ireland. Mitchell et al. (2004) estimated the total British and Irish population of Leach’s Storm-petrels to be 48,357 AOS (95% CI: 36,742–65,193), with 94% of these in the St Kilda archipelago. The largest sub-colony on St Kilda was on the island of Dùn, with an estimated 27,704 AOS (95% CI: 20,430–38,506) in 1999/2000 (Mitchell et al., 2004). Further surveys of Dùn in 2003 and 2006 produced estimates of 14,490 (95% CI: 12,110–17,439) and 12,770 (10,046–17,086) AOS respectively, suggesting a decline of 54% on the island since the Seabird 2000 survey (Newson et al., 2008).

Previous censuses of Leach’s Storm-petrels in the northeast Atlantic have used the acoustic playback method described in Gilbert et al. (1998), which is based on techniques developed for surveying European Storm-petrels (Ratcliffe et al., 1998). The playback method involves playing recordings of storm-petrel calls, which elicit responses from birds in nest sites. Not all storm-petrels will respond to playback on every occasion, so the number of responses obtained during a survey is lower than the actual number of AOS in the surveyed area (Ratcliffe et al., 1998). Traditionally, storm-petrel playback censuses use a multi-stage method. Playback is performed within a calibration plot, in which the actual number of AOS is known or estimated, in order to estimate the response rate, and thus obtain a correction factor. The total population size is then estimated by applying the correction factor to the number of responses detected in the main survey across a much wider area. Various analytical methods have been used to estimate response rates from the calibration plot (Mitchell et al., 2004; Bolton et al., 2010), which all rely on the assumption that there is an equal probability of response from all nests in the calibration area. Typically, the calibration area is divided into very small sub-plots (quadrats), with playback conducted in each, to satisfy this condition. Here, I term this approach the ‘calibration plot method'.

Traditional acoustic playback methods for burrow-nesting seabirds are extremely time consuming. Detected response rate declines with increasing distance of AOS from the playback point (Ratcliffe et al., 1998) so, to maximise response rates, survey quadrats are typically very small (1–4 $m^2$). The ability to survey a larger area during each playback event, for example by using distance sampling methods which explicitly model the distance-detection function (i.e. the decline in detection probability as distance from the observer increases), has the potential to reduce the survey effort required to estimate a population size.

A key assumption of traditional distance sampling is that perfect detection occurs at distance = 0 (Buckland et al., 2001). However, the response rate of burrow-nesting seabirds to playback at distance = 0 tends to be substantially less than one, so there is a need to modify the method for these species. Hierarchical distance sampling (HDS) is a development of the distance sampling method that relaxes this assumption, by using repeat surveys of the same points to independently estimate (i) population density, (ii) detection probability and (iii) availability for detection (Sillett et al., 2012; Kéry and Royle, 2016). The HDS method assumes that the population is closed, so all individuals are always present within the survey area, but allows for individuals to be unavailable for detection on some occasions, for example, if individuals move to unobservable locations at certain times of the day, or under particular weather conditions. For storm-petrels, the probability of responding to playback can be treated as availability for detection, since it is not possible to detect birds when they do not respond. In traditional playback methods, the estimated 'response rate' is equivalent to the product of response rate (the probability of a bird responding to playback) and detection rate (the probability of the observer hearing an emitted response), but the HDS method estimates these components separately. As with the calibration plot method, HDS requires at least some points to be surveyed on more than one occasion, but it does not require individual AOS to be marked, as is the case with the calibration plot.

An additional advantage of HDS is that the density of birds can be modelled with respect to fine scale environmental covariates relating to habitat type. Although the calibration plot method can be used to estimate different densities in different habitat types, these tend to refer to broad areas, in which density is assumed to be homogeneous. A significant drawback of the calibration plot approach is that the colony area may be very difficult to delineate accurately, and errors in the assessment of colony area can hugely influence the resulting population estimate. This also applies to HDS to a degree, but an advantage of HDS is that models can incorporate covariates which explicitly represent the suitability of the habitat for the focal species.

In this study, the primary aim was to estimate current size and change of the largest Leach’s Storm-petrel populations in the northeast Atlantic. I present the results of a 2017–2018 survey of Leach’s Storm-petrels on Elliðaey, and a 2019 survey of Leach’s Storm-petrels in the St Kilda archipelago; the latter conducted as part of the fourth national breeding seabird census of Britain and Ireland, ‘Seabirds Count’. At both colonies we used two playback survey methods, in an attempt to optimise the accuracy and precision of estimates in the time available, while also enabling back-compatibility and direct comparisons with previous surveys. On Elliðaey, two transects were surveyed in 1991, covering approximately 1% of the island’s area. These transects were repeated in 2017 and 2018 and I also analysed data from a whole-island census based on a grid of sample points, using HDS. I used insights from these analyses to re-evaluate likely population size in 1991. For St Kilda, I used HDS but also analysed the survey data using the calibration plot method that was used in the previous censuses. I also evaluate the field and analysis methods in terms of their efficiency of data collection and precision of the resulting population estimates.

## 2.3 Methods

### 2.3.1 Fieldwork

#### *2.3.1.1 Field sites*

Elliðaey Island (63°28’N, 20°11’W) is a 45 ha uninhabited island of grass-covered volcanic tuff, with a maximum elevation of 145 m above sea level. Elliðaey is the northernmost island in the Vestmannaeyjar archipelago, lying approximately 7 km off the southwest coast of Iceland (Figure 2.1). The island is free of terrestrial mammals, except for sheep *Ovis aries* and visiting humans.

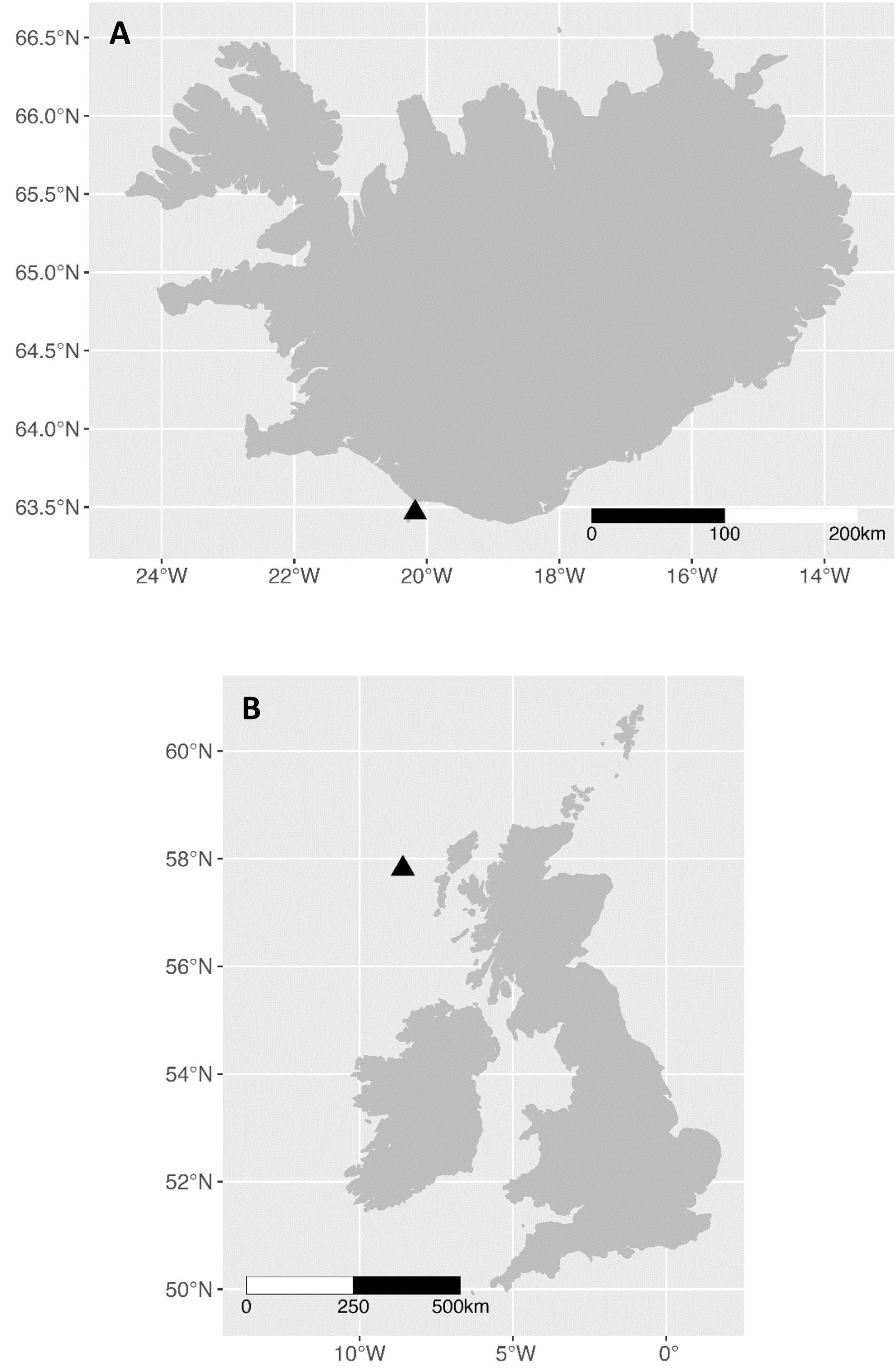


Figure 2.1. Maps showing (A) the location of the Vestmannaeyjar archipelago in relation to Iceland and (B) the St Kilda archipelago in relation to the British Isles.

The St Kilda archipelago (57°49’N 8°35’W) lies off the northwest coast of Scotland, 64 km west of North Uist (Figure 2.1). The four main St Kilda islands all hold breeding Leach’s Storm-petrels. The largest sub-colony is on the island of Dùn, where dense vegetation and scattered boulders cover the steep slopes, and the maximum elevation is 178 m. Large areas of Dùn are densely burrowed by Puffins, and the ground is mostly unconsolidated and fragile. Smaller sub-colonies of Leach’s Storm-petrels are found on the islands of Hirta, Boreray and Soay. All three of these islands are grazed by sheep and have far more consolidated ground, with steep slopes of short grass sward, rocky outcrops and boulder fields. Aside from visiting humans, the only other mammal on the islands is the endemic St Kilda Field Mouse *Apodemus sylvaticus hirtensis*, which is present on Hirta and Dùn. Harris and Murray (1978) report “a few pairs [of Leach’s Storm-petrel] on Levenish and an unknown number on Stac an Armin”, but these sea stacks are extremely difficult to access and these populations have never been systematically surveyed.

#### *2.3.1.2 Playback recording*

Leach’s Storm-petrels generally only respond to calls of the same sex when in the burrow (Taoka et al. 1989) and previous surveys of Leach’s Storm-petrels on both Elliðaey and St Kilda used only the male chatter call in playbacks (Mitchell et al., 2004; Hansen et al., 2009). In the current study we used calls of both sexes, in an attempt to increase response rates (Perkins et al., 2017). Pilot work indicated that we achieved slightly higher response rates using a recording containing two female calls followed by an interval and then two male calls, compared with either a recording with no interval between female and male calls, or where a single male call was followed by an interval and then a single female call. We therefore use the former recording throughout, with 10 second intervals after the calls of each sex in which to listen for responses. The total duration of the recording was 30 seconds, with a pure tone at the end to indicate the end of the survey period. Recordings were made on Elliðaey in 1991.

### *2.3.1.3 Playback method*

We performed the playback by holding a portable speaker (EasyAcc model LX-839) facing towards the ground, approximately one metre above the survey point, and playing the recording at maximum volume (c. 75 dB). We only recorded responses from Leach's Storm-petrels if they occurred within the 30-second survey period for each playback trial. Once this period had finished, the observer measured the approximate distance to each response using a string (on Elliðaey) or a bamboo cane (on St Kilda) marked at 50 cm intervals. We recorded responses in eight 50 cm distance bands, from 0 m to 4 m. We noted any responses beyond 4 m but did not measure beyond the 4 m radius. On a small number of occasions, a high number of responses made it difficult to accurately locate individual responses, so the observer played the call again to elicit another response, while taking care to only record those individuals that responded on the first playback. On St Kilda, we carried out playback surveys for three species, but at each survey point playback for Leach's Storm-petrel was always carried out first, and responses recorded, before playback for the other species.

### *2.3.1.4 Timing of surveys*

For both Elliðaey and St Kilda, we carried out fieldwork during the period when Leach's Storm-petrels were believed to be incubating, based on previous observations, so that an adult would normally have been present in every active burrow 24 hours a day (Mitchell et al., 2004; E.S. Hansen pers. obs.). Outside the incubation and brood-guard stage, the chick is usually left alone in the nest site, with adults making only brief nocturnal provisioning visits. Any burrows in which an egg had been laid but was not attended by an adult due to breeding failure or temporary egg neglect (Pollet et al., 2019a) would not have been detected in our surveys, which could induce a relatively small underestimation of the number of AOS. We performed distance sampling surveys between 0700 and 1900 hours, and only when weather conditions were considered unlikely to impact the detection of bird vocalisations or estimation of distances (i.e. not in strong wind, heavy rain or fog). Although response rates of storm-petrels to playback are generally higher at night (Ratcliffe et al., 1998; Mitchell et al., 2004), we performed the distance sampling surveys during daylight, as responses from birds in burrows can be difficult to distinguish from birds calling in flight at night and night surveys on rough terrain and near cliffs are more dangerous. We carried out the repeats of the 1991 survey transects on Elliðaey (described below) at night to replicate the previous survey method as closely as possible.

#### *2.3.1.5 Elliðaey surveys*

Four people performed the main census of Elliðaey on 24, 26 and 27 June 2018. We performed a point distance sampling survey across the whole island, using a predetermined grid of 1,362 points at 16 m intervals (see Figure 2.2). During fieldwork, 208 of these points were found to be inaccessible and were excluded from the survey, but most of these excluded points fell in habitat unsuitable for Leach's Storm-petrel nesting (i.e. bare rock). Each of the remaining 1,154 points was surveyed once.

##### *Calibration data*

Fieldwork on Elliðaey was cut short due to poor weather, before we had collected sufficient calibration data to analyse the survey data using a calibration plot method (i.e. by applying a correction factor). However, we also performed a trial to quantify time of day variation in response rates, as storm-petrel response rates are known to vary across the day (Ratcliffe et al., 1998). To do this, we surveyed 41 points every 3 hours between 0800 and 2300 (six times in total, during which a total of 31 nests were detected) on 27 June, using the same distance sampling method as the main survey. The calibration data showed no significant decrease in response rate across the first five daytime playbacks on the same day, suggesting there was no habituation effect to the playback (binomial repeated measures GLM, all pairwise comparisons with visit 1, $p > 0.342$). There was a significant increase in response rate on the sixth (night time) calibration playback (pairwise comparison between visit 1 and visit 6, $p < 0.0001$). The repeated playback at the same sites, combined with the distance sampling data collected in the main survey, therefore enabled us to analyse the survey data using the HDS method, although that had not been the original reason for the repeat samples.

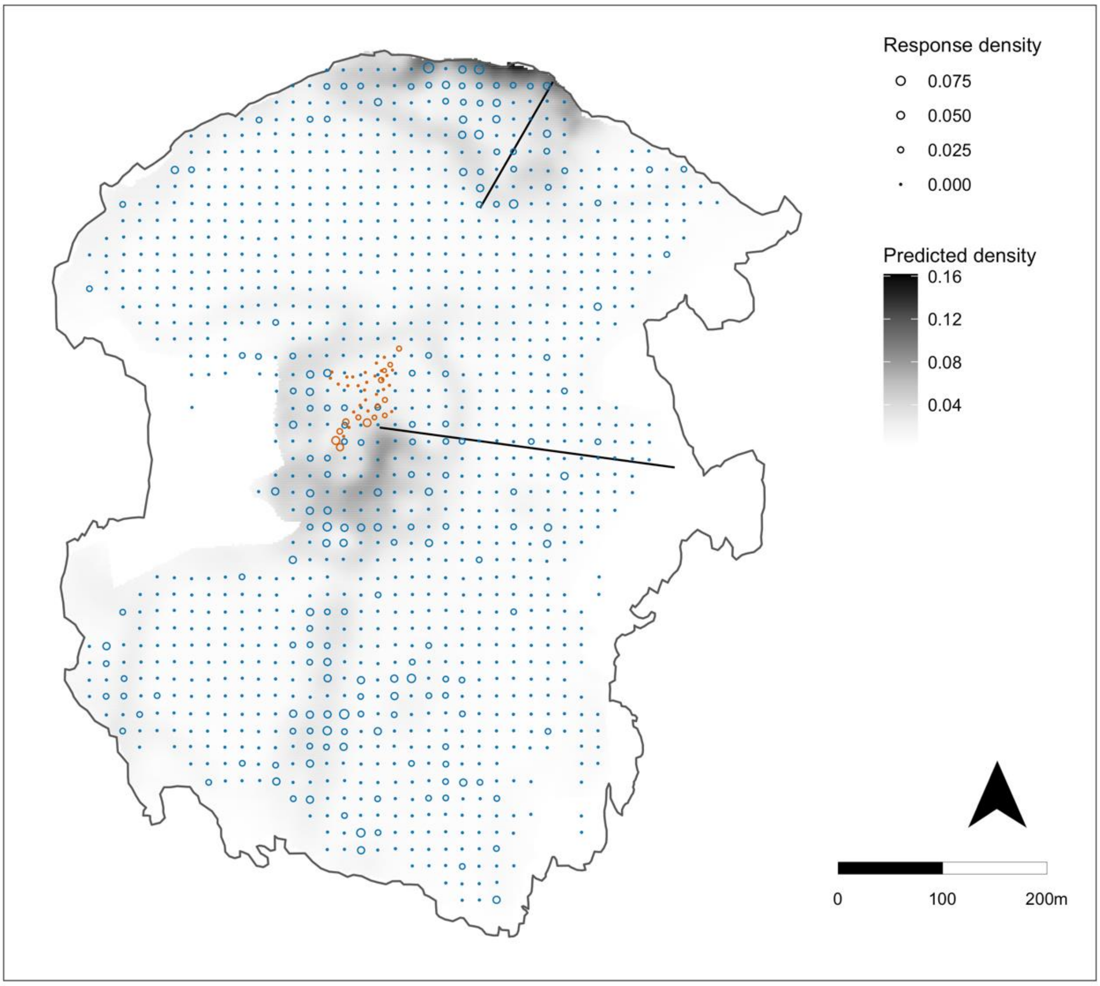


Figure 2.2. Map of Elliðaey island, Vestmannaeyjar archipelago, Iceland. Blue open circles represent mean response density per survey point. Orange open circles represent responses from points repeated during the time of day trial. Predicted density of Leach's Storm-petrel apparently occupied sites (AOS) from the top-performing hierarchical distance sampling model is shown. Black lines show the locations of the Hábarð (north) and Bunki (middle) transects, performed in 1991, 2017 and 2018. White areas without survey points are unsuitable habitat.

*Repeat of 1991 survey transects*

To enable a direct comparison with the previous Elliðaey population estimate, the survey method used in 1991 (30 June to 1 July) was repeated between 0000–0200 hours on 27–30 June 2017 and 30 June 2018. In 2017, playback was performed along the two strip transects used in the 1991 survey: Hábarð (10 m wide x 160 m long) and Bunki (10 m wide x 300 m long; Figure 2.2). Sheep displaced the Bunki transect lines in 2017, shortening the transect to the upper 70 m, which contained higher AOS densities than the rest of the transect in 1991. In 2018, we repeated only the Hábarð transect, and the final 10 m of the transect line were not surveyed. As in 1991, each of these transects was split into quadrats of 2.5 x 2.5 m and a single playback was performed in each quadrat, using the same recording of a single male Leach's Storm-petrel chatter call as in the 1991 survey. We recorded the number of birds responding from below ground within each quadrat.

#### *2.3.1.6 St Kilda surveys*

We surveyed Leach's Storm-petrel on Dùn, Hirta, Boreray and Soay between 18 June and 5 July 2019, alongside surveys for Puffins, Manx Shearwaters *Puffinus puffinus* and European Storm-petrels. We divided the islands into sectors of similar habitat based on those used in the Seabird 2000 census (Mitchell et al., 2000; following Harris and Murray, 1977) although sector maps were only available as low-resolution photocopies so boundaries were not identical. On all islands, we ran rope transects down the slope and established playback survey points at 10 m intervals along each transect (Figure 2.3). The area surveyed by each playback point was larger than that used in previous surveys (see Mitchell et al., 2000, Newson et al., 2008 for details).

*Dùn*

Five people surveyed Dùn (Figure 2.3A) on 27–29 June, and 3 and 5 July 2019. On the north-western section of Dùn (sector B), we laid transects at approximately 25 m intervals, and marked survey points with bamboo canes. We performed a playback survey at each point on each of the five survey days. On 3 July we laid out additional transects halfway between the original transects and on the remaining two survey days we also performed playback at points marked on these transects. The south-eastern sector of Dùn (sector D) is densely burrowed by Puffins and the terrain is extremely fragile. To avoid causing damage to the habitat and disturbance to the Puffin colony, we limited the number of survey points and playback occasions in this area. We performed playback once on five transects in this south-eastern sector on 27 June, alongside a Puffin census. We repeated a single transect in the south-eastern sector on each of the additional four survey days. We surveyed the neck between the north-western and south-eastern sections (sector C) on 28 June, with transects laid vertically down the slope at approximately 25 m intervals. On two transects in the main northwest survey area, we marked all responses with individually-numbered flags to enable estimation of response rate for the calibration plot method. Large numbers of Northern Fulmars *Fulmarus glacialis* nest on Dùn, with eggs and small chicks present during the survey period. To avoid excessive disturbance to the Fulmars, we excluded some potentially-accessible areas of the island from the survey. We surveyed additional points along the ridge of the north-western section of the island in an attempt to cover parts of this habitat, whilst avoiding areas occupied by nesting Fulmars. No attempt was made to visit the south-western side of Dùn because of difficulties with safe access.

### *Boreray*

Six people surveyed the island of Boreray (Figure 2.3B) on 18–22 June 2019. We performed playback along transects surveyed for Puffins. We laid out transects at 25 m intervals in areas of high Puffin density and less frequently in lower density areas. In the less accessible parts of the island (sectors BOR11 and BOR8) the number of transects was limited by time and safety constraints. On four transects, we marked survey points with metal pegs and repeated playback at these points on multiple days. On three transects, we marked responses with individually-numbered flags in order to obtain a response rate estimate for the calibration plot method. It became apparent that there were very few petrels on most of the island but that they were concentrated in the cleitean (drystone storage huts or bothies, originally ~3 x 6 m but now in varying states of disrepair). In addition to the transects we therefore surveyed each cleit on up to five occasions; on each occasion using a single playback with the speaker held above the centre of the structure. Access difficulties meant we did not systematically survey areas of rockfall on coastal fringes, but we elicited responses in some of these areas using *ad hoc* playback, suggesting that they warrant further investigation in future surveys. These responses are not included in our population estimates and, as far as we are aware, these areas were not included in previous censuses.

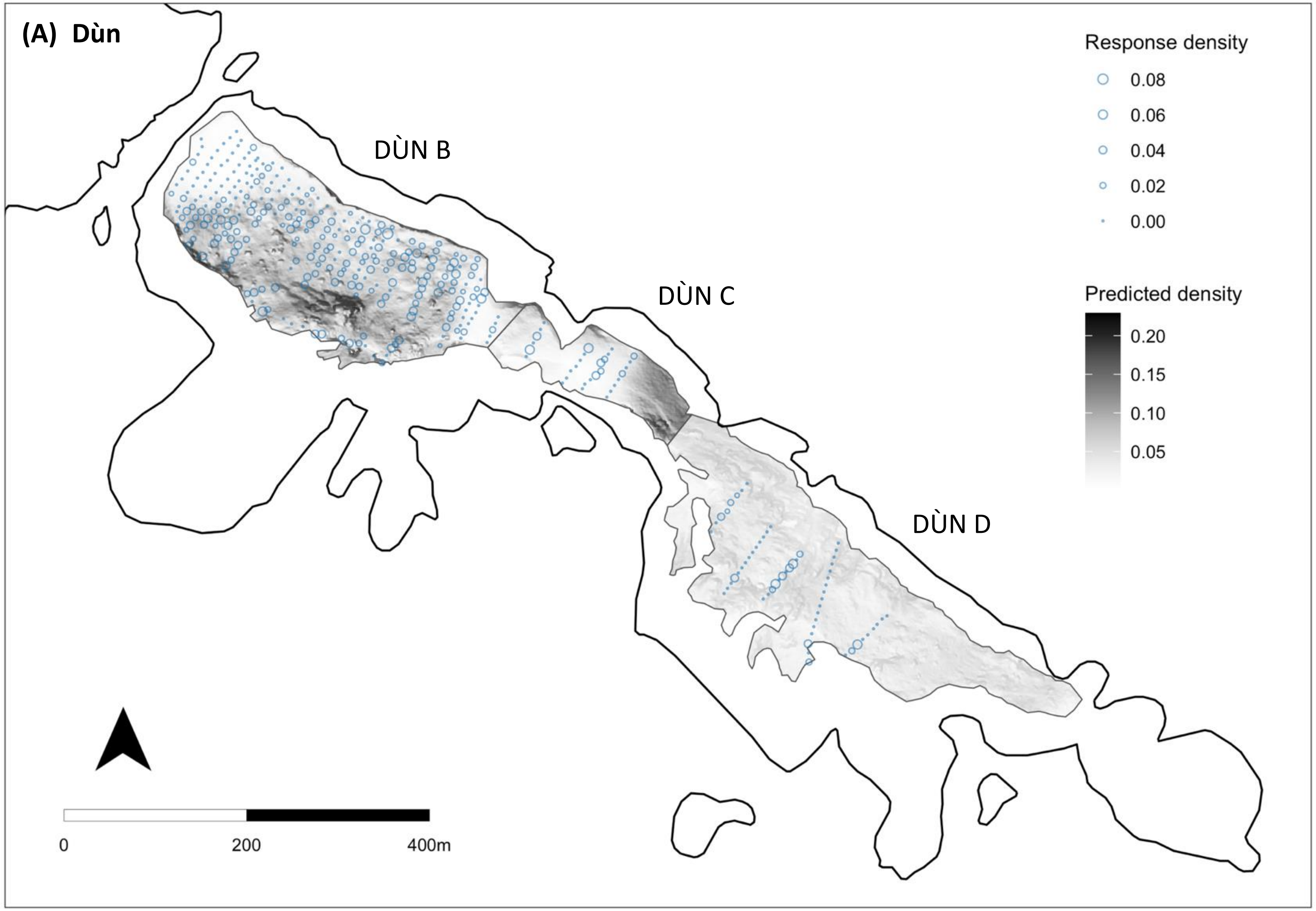
*Soay*

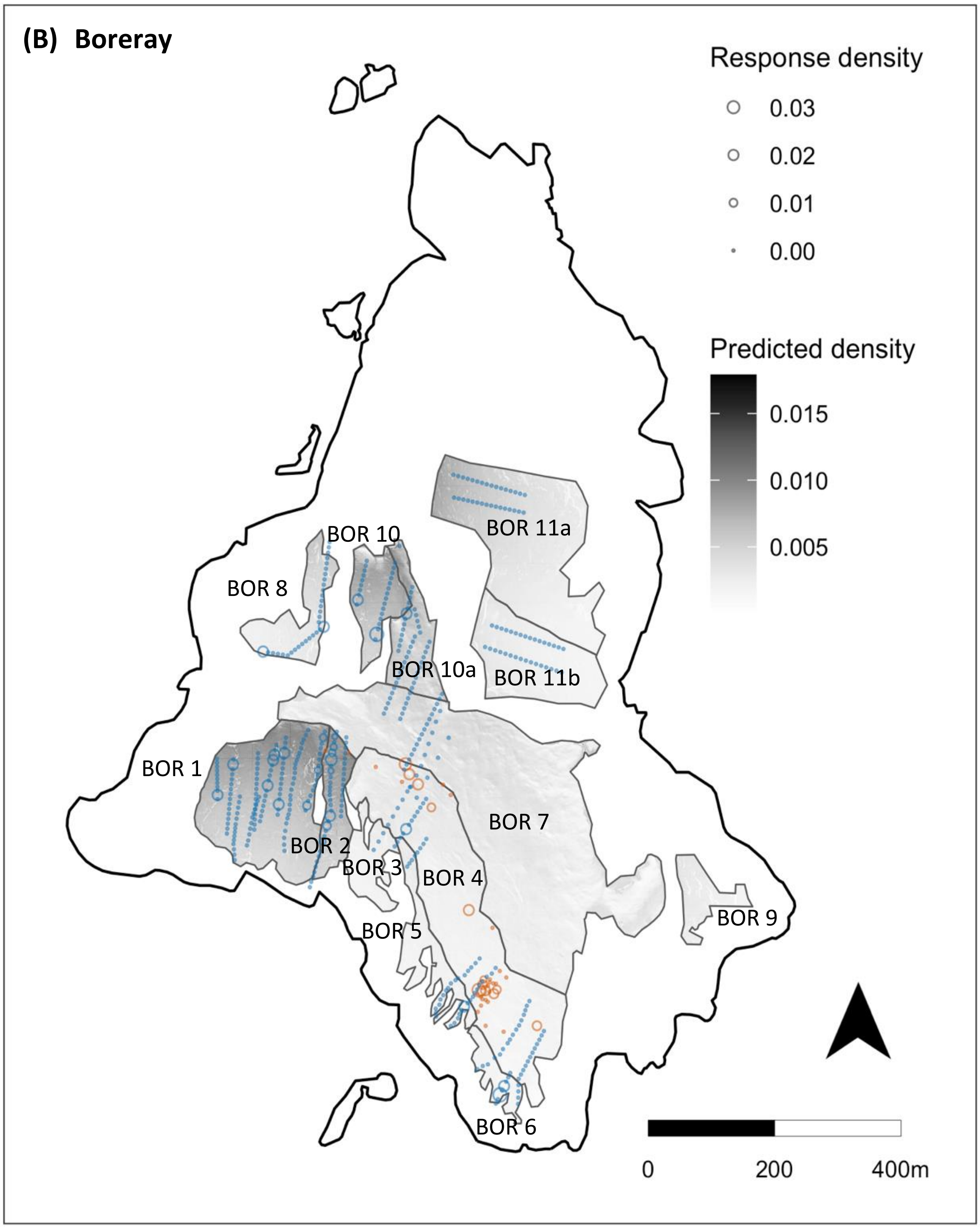
Due to time and weather constraints, six people surveyed Soay (Figure 2.3C) on a single visit on 23 June 2019. On the grassy slopes, we surveyed Leach’s Storm-petrels alongside Puffins, on six transects running down the slope. Five additional transects ran through the Tigh Dugan boulder field.

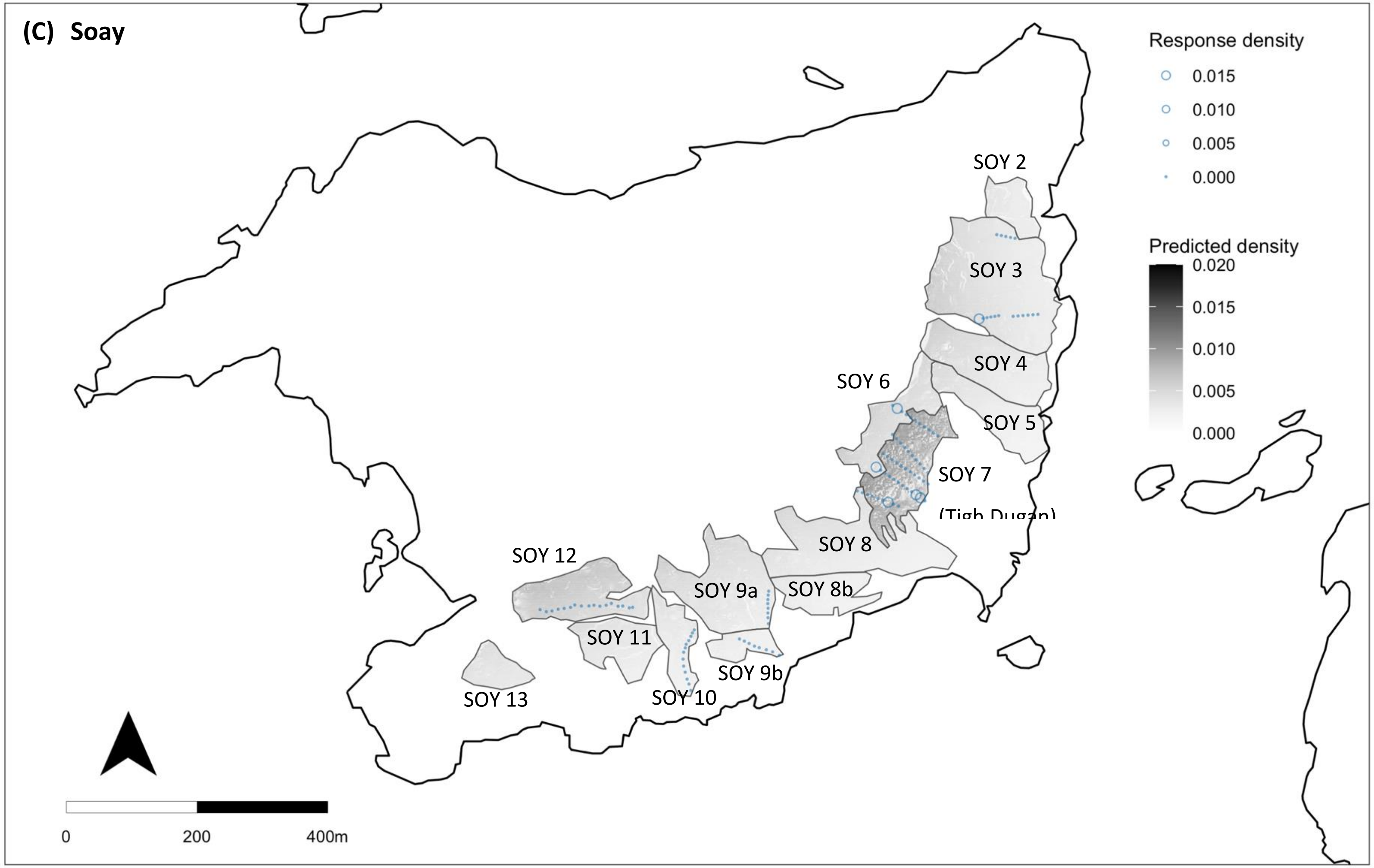
*Hirta*

In previous surveys of Hirta, the majority of Leach’s Storm-petrels were found to be in the Carn Mòr boulder field on the southwest of the island. We focused survey effort there in 2019, to make the most of the limited time available. Four people surveyed Carn Mòr (Figure 2.3D) on 25 June. We ran nine transects across the slope, parallel to the coastline, approximately 25 m apart. Two people surveyed three transects perpendicular to the coastline on the slopes adjacent to Carn Mòr on the same day. In an effort to determine presence/absence of Leach’s Storm-petrels elsewhere on Hirta, we performed playbacks approximately every 2 m along the walls and cleitean above the village on 1 July, and at least one playback was performed at each cleit, other stone structure and natural boulder pile in the valley of Gleann Mòr on 30 June, although conditions were poor, with very strong winds.

On some St Kilda transects, GPS location data were not recorded for every survey point. In these cases, I used a straight-line interpolation to determine the locations of missing survey points, based on adjacent points.


(A) Dùn
DÙN B
DÙN C
DÙN D
Response density
0.08
0.06
0.04
0.02
0.00
Predicted density
0.20
0.15
0.10
0.05
0
200
400m


(B) Boreray
Response density
0.03
0.02
0.01
0.00
Predicted density
0.015
0.010
0.005
BOR 1
BOR 2
BOR 3
BOR 4
BOR 5
BOR 6
BOR 7
BOR 8
BOR 9
BOR 10
BOR 10a
BOR 11a
BOR 11b
0
200
400m


(C) Soay
Response density
0.015
0.010
0.005
0.000
Predicted density
0.020
0.015
0.010
0.005
0.000
SOY 2
SOY 3
SOY 4
SOY 5
SOY 6
SOY 7
(Tigh Dugan)
SOY 8
SOY 8b
SOY 9a
SOY 9b
SOY 10
SOY 11
SOY 12
SOY 13
0
200
400m

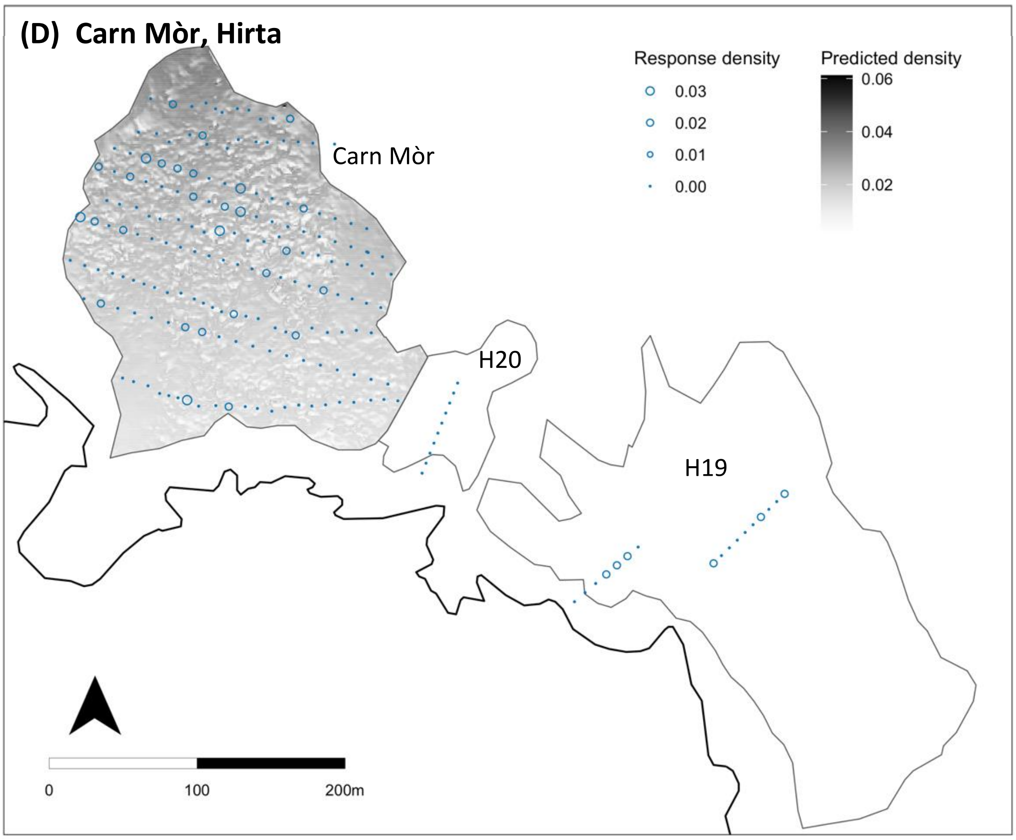


Figure 2.3. Maps of (A) Dùn, (B) Boreray, (C) Soay and (D) Carn Mòr, St Kilda, with sector outlines shown. Blue open circles represent mean response density per survey point. Orange open circles represent responses from cleitean (drystone storage huts or bothies) on Boreray, which were treated as a separate 'sector'. Predicted density of Leach's Storm-petrel apparently occupied sites (AOS) from the top-performing hierarchical distance sampling models is shown. Densities are based on topographical (3D) area.

### 2.3.2 Data Analysis

All analysis was performed using R (version 3.6.0; R Core Team, 2019), implemented in R-Studio (www.r-studio.com).

Due to time constraints, we were not able to survey every sector of every island on St Kilda, so to estimate whole-island populations I combined sectors of similar habitat and sufficient survey effort (Figure 2.3). Boreray was split into three 'combined sectors': (i) BOR1-2, which contained sectors BOR1 and BOR2, the terraced slopes with high Puffin density; (ii) BOR3+, which contained all other sectors; and (iii) the cleitean. Soay was split into (i) the Tigh Dugan boulder field (SOY7) and (ii) all other sectors (SOY), which generally comprised grassy slopes with scattered boulders. Dùn was split into (i) 'Puffin' (sector D) and (ii) 'non-Puffin' (sectors B and C) areas, due to the very high density of Puffin burrows in sector D. A small number of points fell outside the sector boundaries and these were allocated to the nearest sector by straight-line distance.

#### *2.3.2.1 Calibration plot method – St Kilda only*

##### *Estimating response rate*

In order to make direct comparisons of population size with the Seabird 2000 survey, I used the asymptote method to estimate response rate from the calibration transects, as described by Mitchell et al. (2004). The method involves fitting a curve to the cumulative number of AOS found on successive playback surveys of the calibration plot. The curve is fitted using an asymptotic regression model, of the form:

$$y = a(1 - e^{-b})$$

where $y$ is the number of AOSs detected on a visit, $a$ is the asymptote of the regression curve (equivalent to the total number of AOSs in the calibration plot) and $b$ is the exponential proportional rate of increase to the asymptote. I fitted the asymptotic regression model using the 'nls' function of the stats package (R Core Team, 2019).

I used the estimated value of $b$ and its standard error to describe a gamma distribution, from which I drew 10,000 samples. A gamma distribution was chosen, as a zero-bounded but continuous distribution, so that the sampled values of the parameter $b$ could not take negative values, reflecting the fact that the cumulative number of nests detected can only increase with further sampling, and not decrease. I converted these samples of $b$ to response rates using the equation $1 - \exp{(-b)}$, and took the 2.5 and 97.5 percentiles of these as the 95% confidence interval.

*Estimating response density*

I calculated mean response density (number of responses per m$^2$) for each combined sector of St Kilda and used the boot package (version 1.3–22; Davison and Hinkley, 1997; Canty and Ripley, 2019) to obtain 10,000 bootstrapped estimates of response density, which I used to calculate 95% confidence intervals.

*Population estimates*

I calculated population estimates for each combined sector by multiplying mean response density by the reciprocal of the mean response rate (i.e. the correction factor) and multiplying this value by the total area of the sector (Mitchell et al., 2004). For each combined sector I applied the 10,000 estimates of response rate to the 10,000 bootstraps of response density, to obtain confidence intervals for combined sector population estimates (Bolton et al., 2017).

I calculated whole-island population estimates by summing the estimates for each combined sector within an island. I obtained whole-island confidence intervals by summing randomly-combined population estimate bootstraps for each combined sector within an island. Similarly, I obtained the whole-archipelago population estimate by summing the estimates for each island, and its confidence interval by summing randomly combined bootstrap population estimates for each island.

#### *2.3.2.2 Hierarchical Distance Sampling (HDS) models – all islands*

I built HDS models using the 'gdistsamp' function of the unmarked package (version 0.12–3; Fiske and Chandler, 2011). I modelled Elliðaey separately from St Kilda due to differences in habitat types and the availability of covariate data. Since HDS requires at least some survey points to be surveyed more than once, I combined the main survey and time of day calibration data for the Elliðaey HDS models. For St Kilda, since the island of Dùn had a relatively high survey effort, I first built models for the Dùn data alone. For the rest of the St Kilda archipelago, I used data for all islands – including Dùn – in the models, since survey effort was not sufficient to model the other islands individually. While it is not currently possible to incorporate spatial autocorrelation effects within the unmarked package, the potential biases are believed to be small, particularly if habitat covariates have good explanatory power (Kéry and Royle, 2016).

For point distance sampling, it is recommended that the outermost ~10% of observations are truncated before analysis, to improve the estimation of the detection function (Buckland et al., 2001). I truncated our distance sampling data to 4 m, excluding any responses detected beyond this distance, which excluded 8.84% of detections for Dùn and 8.57% for St Kilda as a whole, but 21.71% for Elliðaey. This suggests that birds could more readily be detected beyond 4 m on Elliðaey than on St Kilda.

I initially constructed null models to test whether the hazard rate, half-normal, exponential or uniform detection functions best described the detection process, and whether a Poisson or negative binomial distribution best described abundance. I then used an information-theoretic approach to select the best-performing null models, based on Akaike's Information Criterion (AIC; Burnham and Anderson, 2004).

### Model covariates

#### *Elliðaey*

I extracted altitude, slope and aspect values for each survey point from a 2 m resolution digital elevation model (DEM) of Elliðaey (ArcticDEM version 2.0; Porter et al., 2018).

The dense tussocks of Red Fescue *Festuca rubra* that both Puffins and Leach's Storm-petrels nest in on Elliðaey are readily identifiable from satellite imagery. I classified all land on Elliðaey as either 'tussock' or 'non-tussock' habitat, using random forest supervised classification in the caret package (version 6.0–84; Kuhn, 2019). I extracted RGB colour values from polygons of known areas of tussock and non-tussock habitat that I identified visually from Bing Maps satellite imagery (dated 25 July 2016) to train the classifier, and then classified the whole of Elliðaey as either tussock or non-tussock habitat. I calculated the proportion of tussock habitat within 4 m, 8 m, 25 m and 50 m buffers around each survey point.

*St Kilda*

I used the 'grid_terrain' function of the lidR package (Roussel et al., 2020) to create a digital terrain model (DTM) from 0.5 m resolution LiDAR data for the St Kilda archipelago (LiDAR data from Historic Environment Scotland). I then extracted altitude, slope and aspect values from the DTM for each survey point.

For Dùn, I used the caret package (Kuhn, 2019) to classify the habitat for each 1 m x 1 m pixel as 'rock', 'grass' or 'herb', based on RGB values from LiDAR imagery. I calculated the proportion of each habitat for 4 m, 8 m, 25 m and 50 m buffers around each survey point. The 'rock' category included cliffs, slabs and boulders. I used the term 'grass' for areas of more consolidated ground, observed in the field to be dominated by Red Fescue and Yorkshire Fog *Holcus lanatus*. I used the 'herb' category for areas of taller vegetation, observed in the field to be dominated by Sea Mayweed *Tripleurospermum maritimum* and Common Sorrel *Rumex acetosa,* where the ground tended to be tussocked. (Note that Red Fescue covers most of Elliðaey, including the tussocked areas, whereas on Dùn Red Fescue is more commonly found in non-tussocked areas.)

I classified the southeast sector of Dùn (sector D) as 'Puffin' habitat due to its extremely high density of nesting Puffins (Luxmoore et al., 2018). Although Puffins nest elsewhere on Dùn, for modelling purposes I classified the rest of the island as 'non-Puffin' habitat, since Puffin burrows occur at much lower densities and are generally restricted to areas of boulders and the tops of the north-eastern cliffs.

For St Kilda, I acquired daily wind speed data for the survey period, averaged across three weather stations on Hirta. Wind speed and direction can vary greatly around the archipelago, so it is important to recognise that the averaged values from Hirta may not be completely representative of the weather experienced at the time and location of each survey.

To help with model computation, I scaled all numerical covariates by subtracting the mean and dividing by the standard deviation, giving a standardised mean value of 0 and a standard deviation of 1.

## Model structure

### *Elliðaey*

I included altitude (linear and quadratic), slope (linear and quadratic), aspect (linear), and proportion of tussock habitat at 4 m, 8 m, 25 m and 50 m radius from each survey point as potential covariates of storm-petrel abundance in the Elliðaey model set. I included time of day (linear and quadratic) as a covariate of availability for detection. I did not include date as a covariate of availability since the models use repeat sampling of the same sites to estimate availability and no sites on Elliðaey were sampled on more than one day. I included observer ID and date (linear, quadratic and categorical) as possible effects on detection probability. I included date as a detection covariate to account for differences in weather conditions between days, in the absence of weather data.

### *St Kilda*

I included the following covariates as abundance effects for the Dùn-only model: Puffin/non-Puffin sector (categorical), altitude (linear and quadratic), slope (linear and quadratic), proportion of rock, grass, and herb habitat at 4 m, 8 m, 25 m and 50 m radius from each survey point (linear and quadratic). The all-island models included altitude (linear and quadratic), slope (linear and quadratic), island (categorical) and sector (categorical) as possible abundance effects. The set of all-island models also included a 'combined sector' effect on abundance, thereby reducing the total number of sectors in the model. Habitat was not included in the all-island models since habitat availability varied greatly between islands and the habitat with the highest density of Leach's Storm-petrels differed between islands. I included time of day (linear and quadratic), date (linear, quadratic and categorical), and wind speed (linear and quadratic) as covariates of availability for the Dùn-only and all-island model sets. For both model sets, I included wind speed (linear and quadratic) and observer ID as effects that may influence the detection probability. I included wind speed as an effect on both availability (i.e. response rate) and detection, since higher wind speeds could affect both the ability of a bird to hear the playback (and therefore the likelihood of it responding) and the ability of the observer to detect a response from the bird.

### Model selection

Due to the large number of possible covariate combinations, I used a sequential approach to model selection (Arnold, 2010; Sillett et al., 2012; Olsen et al., 2017). First, I tested univariate models for each of the abundance, availability and detection covariates, while holding the other parameters constant. I retained covariates that ranked better than the null model by AIC. I checked variables for pairwise multicollinearity and where Pearson's r was > 0.7, I retained the variable with the lower univariate AIC.

Next, I combined the selected variables into additive, multivariate models. I started by testing detection models, while holding the availability and abundance components constant. I then used the top-performing detection model to test combinations of availability variables. Next, I tested combinations of abundance variables using the top-performing detection and availability models. Finally, I kept the top-performing combination of abundance covariates and removed a single variable at a time from the detection and availability components, to check whether the addition of abundance covariates made any other variables redundant. I evaluated goodness of fit of the overall top-performing model by parametric bootstrapping (Sillett et al., 2012). I used the 'parboot' function of the unmarked package to simulate 100 new data sets from the model, refitting the model to each data set and calculating the Freeman-Tukey fit statistic for each iteration.

I used the top-performing model to predict Leach's Storm-petrel abundance for every 2 m x 2 m grid cell on Elliðaey and every 1 m x 1 m grid cell in each sector of the St Kilda archipelago, reflecting the resolution of the covariate data. I used the sum of the expected abundance in all cells as the total population estimate for Elliðaey and at the levels of (i) sector, (ii) island and (iii) archipelago for St Kilda. The large number of cells made bootstrapping confidence intervals for sectors and islands unfeasibly time-consuming, so I calculated variances for combined abundance estimates (at the sector or island level) using the 'deltavar' function of the embdbook package (version 1.3.12; Bolker, 2008, 2020). Since confidence intervals for individual cells were asymmetric, I constructed confidence intervals for combined abundance estimates using a log-normal approach:

$$\lambda_{LCL} = \lambda / C$$

and

$$\lambda_{UCL} = \lambda * C$$

where $\lambda$ is the mean abundance estimate, and

$$C = \exp\{1.96 * \sqrt{log_e(1 + [cv(\lambda)]^2)}\}$$

#### *2.3.2.3 Area calculations*

Due to the steepness of the terrain across the islands, the slope-corrected (topographic) surface area was often much greater than the horizontal planar area, with an increase in area of more than 50% for some St Kilda sectors. I used the sp package (version 1.3–1; Pebesma and Bivand, 2005; Bivand et al., 2013) to calculate surface area from the DEM for Elliðaey and from the DTM for the St Kilda sectors. Where area estimates were given in previous analyses, I also used these values to produce current population estimates that are as comparable as possible, although I note that the area of available breeding habitat can change over time (Pollet and Shutler, 2018).

## 2.4 Results

### 2.4.1 Elliðaey

#### *2.4.1.1 Repeat of 1991 survey*

Response density for the top 70 m of the Bunki transect was 67.5% lower in 2017 than 1991 (Table 2.1). For the Hábarð transect, response density in 2017 and 2018 was 46.0% and 39.8% lower than in 1991, respectively. Overall, there was a decline in response density of 48.8% between 1991 and 2017 and 39.8% between 1991 and 2018.

Table 2.1. Results from playback surveys on the Bunki and Hábarð Leach's Storm-petrel transects on Elliðaey, Iceland, in 1991, 2017 and 2018. Response densities (number of Apparently Occupied Sites responding per m$^2$) are given ± SE.

| **Date** | **1991**<br>30 June to 1 July | | | **2017**<br>27–30 June | | | | **2018**<br>29 June | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| **Transect** | **Area (m$^2$)** | **Responses** | **Response density** | **Area (m$^2$)** | **Responses** | **Response density** | **Change (%)** | **Area (m$^2$)** | **Responses** | **Response density** | **Change (%)** |
| **Bunki** | 2,975 | 110 | 0.037<br>± 0.0057<br>(0.057)* | 700* | 13 | 0.019<br>± 0.0064 | -67.5* | – | – | – | – |
| **Hábarð** | 1,600 | 257 | 0.161<br>± 0.0123 | 1,600 | 139 | 0.087<br>± 0.0108 | -46.0 | 1,500 | 145 | 0.097<br>± 0.0077 | -39.8 |
| **Total** | 4,575 | 367 | 0.080<br>± 0.0065<br>(0.129)* | 2,300 | 152 | 0.066<br>± 0.0080 | -48.8 | 1,500 | 145 | 0.097<br>± 0.0077 | -39.8 |

*To estimate the change in the Bunki transect between 1991 and 2017, only the top 70 m are used in 1991 for comparability (see Methods).

Table 2.2. Top five hierarchical distance sampling models by AIC for Leach's Storm-petrels on Elliðaey, Dùn and the St Kilda archipelago as a whole. As recommended by Arnold (2010), I have excluded models containing uninformative covariates from the model lists. Where quadratic effects are included, the model also included the corresponding linear effect. 'Tussock50' refers to the proportion of habitat classified as "tussock" within a 50 m radius of the survey point. 'Puffin habitat' is a binary variable, specifying whether a survey point was within the area of the island containing a very high density of Puffins. 'herb25' refers to the proportion of habitat classified as "herb" within a 25 m radius of the survey point.

| **Model rank** | **Covariates** | | | **No. of parameters** | **ΔAIC** | **Cumulative weight** |
|---|---|---|---|---|---|---|
| | **Abundance** | **Availability** | **Detection** | | | |
| **ELLIĐAEY** | | | | | | |
| 1 | Altitude + Tussock50$^2$ | Time$^2$ | linear date | 10 | 0.00 | 0.91 |
| 2 | Altitude + Tussock50$^2$ | Time$^2$ | – | 9 | 4.61 | 1.00 |
| 3 | Altitude + Tussock50$^2$ | – | linear date | 8 | 13.43 | 1.00 |
| 4 | Altitude$^2$ + slope$^2$ | Time$^2$ | linear date | 11 | 24.28 | 1.00 |
| 5 | Altitude$^2$ + slope | Time$^2$ | linear date | 10 | 25.02 | 1.00 |
| **DÚN** | | | | | | |
| 1 | Puffin habitat + herb25$^2$ + slope$^2$ | Time$^2$ + linear date$^2$ + wind speed | Observer | 21 | 0.00 | 0.27 |
| 2 | Puffin habitat + herb25$^2$ + slope$^2$ | Time$^2$ + linear date$^2$ | Observer | 20 | 0.05 | 0.54 |
| 3 | Puffin habitat + herb25$^2$ + slope$^2$ | Time$^2$ + linear date$^2$ | Observer + wind speed | 21 | 1.23 | 0.69 |
| 4 | Puffin habitat + herb25$^2$ + slope | Time$^2$ + linear date$^2$ | Observer | 19 | 3.02 | 0.75 |
| 5 | Puffin habitat + herb25$^2$ + slope$^2$ | Time$^2$ + linear date + wind speed | Observer | 20 | 3.15 | 0.81 |
| **ST KILDA** | | | | | | |
| 1 | Combined sector + altitude + slope$^2$ | Time$^2$ | Observer + wind speed | 27 | 0.00 | 0.80 |
| 2 | Combined sector + altitude + slope$^2$ | Time$^2$ | Observer | 26 | 3.45 | 0.94 |
| 3 | Sector + altitude$^2$ + slope$^2$ + aspect | Time$^2$ + linear date$^2$ | Observer + wind speed | 49 | 5.69 | 0.98 |
| 4 | Combined sector + slope$^2$ | Time$^2$ + linear date$^2$ | Observer + wind speed | 28 | 10.83 | 0.99 |
| 5 | Combined sector + altitude$^2$ + slope | Time$^2$ + linear date$^2$ | Observer + wind speed | 29 | 11.46 | 0.99 |

#### *2.4.1.2 HDS method*

In the main survey, we detected a total of 339 responses during 1,400 playbacks at 1,195 survey points on Elliðaey.

A half-normal detection function and negative binomial distribution for abundance produced the lowest AIC of all the null models, and were used in the subsequent model set. The full model set consisted of 72 models, in addition to the null models. The top five models are given in Table 2.2. The best-performing model for Elliðaey contained a linear effect of altitude and a quadratic effect of tussock habitat at a 50 m radius on abundance, a quadratic effect of both time of day on availability, and a linear effect of date on detection probability. Graphs of covariate effects are provided in Appendix 1 (Figures A1.1–A1.3). The Freeman-Tukey *P*-value for the best-performing model was 0.537, suggesting an adequate fit to the data. The total population estimate was 5,356 (95% CI: 4,296– 6,678) AOS.

### 2.4.2 St Kilda

We detected a total of 973 responses during 2,231 playbacks at 1,231 survey points on St Kilda. The size of each survey sector, the number of survey points and the number of playback responses for each combined sector are given in Table 2.3. Additional detail on the number of survey points and the number of repeated playbacks for each sector is provided in Appendix 1 (Table A1.1). Table 2.4 gives the results for the calibration plot and HDS methods for each of the surveyed St Kilda islands.

#### *2.4.2.1 Calibration plot method*

On Boreray, we only identified nine AOS on the calibration transects, which was not sufficient to reliably calculate a response rate. We identified a total of 52 AOS within a 4 m radius during the five playback occasions at the calibration sites on Dùn. I had intended to use only responses from a 1 m radius for the calibration plot method, but too few responses were obtained at this distance to produce a sufficiently precise response rate. I therefore used responses within a 3.5 m radius, since this produced narrower confidence intervals relative to the mean population estimates than any other radius (see Appendix 1, Table A1.2). The response rate calculated from the asymptote method was 0.208 (95% CI: 0.096–0.344). This represents the response rate calculated across all AOS within a 3.5 m radius of the playback point and the resulting correction factor was applied to response densities calculated for responses within 3.5 m of each survey point. The response rate from Dùn was used for the calibration plot method for all St Kilda islands.

On Hirta, no responses were obtained from the cleitean and walls above the village or in Gleann Mòr. Our survey effort for areas on Hirta other than Carn Mòr was not sufficient to estimate the population for the rest of the island, but based on the rate of decline observed at Carn Mòr, I estimate that other areas of Hirta currently contain fewer than 500 AOS.

#### *2.4.2.2 HDS method*

I removed 60 survey points from the HDS analysis for St Kilda, as the GPS data recorded were not sufficiently accurate (> +/- 5 metres) to extract environmental covariates for their locations and I could not reasonably interpolate their location from other points.

As for Elliðaey, for the St Kilda dataset a half-normal detection function and negative binomial distribution for abundance produced the lowest AIC of all the null models, for both the Dùn-only dataset and the all-island dataset, and I used these for the rest of the models in both sets.

The full model sets contained 133 models for Dùn and 114 models for all islands, in addition to the null models. The best Dùn-only model contained an effect of Puffin sector and quadratic terms for the proportion of herb habitat at a 25 m radius and slope on storm-petrel abundance; quadratic effects of time of day and date, and a linear effect of wind speed on availability (i.e. the probability of a bird responding if it is present); and an observer effect on detection (Table 2.2). The best all-island model contained the following effects on abundance: 'combined sector', a linear effect of altitude and a quadratic effect of slope; a quadratic effect of time of day on availability; a linear effect of wind speed and an observer effect on detection probability (Table 2.2). Graphs of covariate effects are provided in Appendix 1 (Figures A1.4–A.10). The top-performing models for Dùn and St Kilda had Freeman-Tukey *P*-values of 0.366 and 0.238, respectively, suggesting adequate fits to the data.

Table 2.3. Summary of the areas, number of surveyed points, number of playbacks at those points (note that we surveyed some points multiple times), and number of responses (from all survey occasions, so including multiple responses from some AOS) in each sector on St Kilda. Area refers to the topographical area. Seabird 2000 area is the area used in the previous survey, where available (Mitchell et al., 2000). For Dùn, the Seabird 2000 area of 147,396m$^2$ has been divided between the sectors based on their proportion of the total area calculated in this study. Number of responses are given for a 4 m radius and 3.5 m radius as these are the radii used in the HDS and calibration plot methods, respectively. Numbers in brackets are those used in the HDS analysis, after some survey points were excluded due to GPS inaccuracies.

| | **Area (m$^2$)** | **Seabird 2000 area** | **No. of survey points** | **No. of playbacks** | **No. of responses** | |
|---|---|---|---|---|---|---|
| | | | | | **4 m radius** | **3.5 m radius** |
| **DÙN** | | | | | | |
| **Dùn B+C** | 81,352 | 77,578 | 356 (314) | 1,034 (983) | 805 (767) | 747 |
| **Dùn D** | 73,214 | 69,818 | 59 | 91 | 38 | 38 |
| **BORERAY** | | | | | | |
| **BOR1-2** | 59,715 | | 184 | 352 | 33 | 29 |
| **BOR3+** | 353,113 | | 305 | 324 | 11 | 11 |
| **Cleitean** | | | 40 (37) | 143 (135) | 46 (45) | 46 |
| **SOAY** | | | | | | |
| **Tigh Dugan boulder field (SOY7)** | 18,067 | | 44 | 44 | 3 | 3 |
| **Other areas (SOY)** | 227,796 | | 72 | 72 | 3 | 3 |
| **HIRTA** | | | | | | |
| **Carn Mòr** | 56,827 | 32,375 | 171 | 171 | 34 | 31 |

Table 2.4. Leach's Storm-petrel population estimates resulting from the calibration plot and hierarchical distance sampling (HDS) methods for each of the St Kilda islands surveyed in 2019. For each sector or combination of sectors, density of Apparently Occupied Sites (AOS) is given, along with population estimates for topographical area and, where available, the area used in the Seabird 2000 census (Mitchell et al., 2000). Seabird 2000 population estimates are given for comparison. For each island, the population change since the Seabird 2000 census is calculated using the estimate that is most comparable with the Seabird 2000 estimate.

| | **CALIBRATION PLOT METHOD** | | | **HDS METHOD** | | **SEABIRD 2000** | |
|---|---|---|---|---|---|---|---|
| | **AOS per m$^2$** | **Total no. AOS** | **Total no. AOS Seabird 2000 area** | **Mean AOS per m$^2$** | **Total no. AOS** | **AOS per m$^2$** | **Total no. AOS** |
| **DÙN** | | | | | | | |
| Dùn B+C | 0.082<br>(0.049– 0.175) | 6,675<br>(3,974–14,203) | 6,365<br>(3,450–14,286) | 0.051<br>(0.045–0.058) | 4,148<br>(3,649–4,714) | | |
| Dùn D | 0.052<br>(0.023–0.121) | 3,777<br>(1,688–8,891) | 3,601<br>(1,151–7,072) | 0.030<br>(0.022–0.042) | 2,204<br>(1,586–3,063) | | |
| **Dùn total** | 0.068<br>(0.045–0.127) | **10,452**<br>**(6,899–19,614)** | **9,967**<br>**(6,569–18,506)** | | **6,351**<br>**(5,507–7,324)** | 0.188<br>(0.137–0.260) | **27,704**<br>**(20,430–38,506)** |
| **Dùn population change (%)** | **-64%** | | **-64%** | | | | |

| | **CALIBRATION PLOT METHOD** | | | **HDS METHOD** | | **SEABIRD 2000** | |
|---|---|---|---|---|---|---|---|
| | **AOS per m$^2$** | **Total no. AOS** | **Total no. AOS Seabird 2000 area** | **Mean AOS per m$^2$** | **Total no. AOS** | **AOS per m$^2$** | **Total no. AOS** |
| **BORERAY** | | | | | | | |
| BOR1-2 | 0.007<br>(0.003–0.017) | 419<br>(175–1,008) | | 0.006<br>(0.004–0.008) | 328<br>(232–463) | | |
| BOR3+ | 0.004<br>(0.002–0.011) | 1,589<br>(554–4,021) | | 0.003<br>(0.002–0.004) | 928<br>(598–1,438) | | |
| Cleitean | 1.358<br>(0.623–3.163)<br>(per cleit) | 57<br>(26–133) | | 0.975<br>(0.673–1.414)<br>(per cleit) | 41<br>(28–59) | | |
| BOR1[a] | 0.006<br>(0.002–0.015) | | | | | 0.045<br>(0.028–0.062) | |
| BOR4[a] | 0.002<br>(0.000–0.008) | | | | | 0.110<br>(0.081–0.148) | |
| **Boreray total** | | **2,065**<br>**(1,024–4,634)** | | | **1,297**<br>**(934–1,803)** | | **12,093**<br>**(9,283–15,671)** |
| **Boreray population change (%)** | BOR1 -87%<br>BOR4 -98% | **-83%** | | | | | |

| | **CALIBRATION PLOT METHOD** | | | **HDS METHOD** | | **SEABIRD 2000** | |
|---|---|---|---|---|---|---|---|
| | **AOS per m$^2$** | **Total no. AOS** | **Total no. AOS Seabird 2000 area** | **Mean AOS per m$^2$** | **Total no. AOS** | **AOS per m$^2$** | **Total no. AOS** |
| **SOAY** | | | | | | | |
| Tigh Dugan boulder field (SOY7) | 0.009 (0.000–0.026) | 154 (0–465) | | 0.006 (0.003–0.013) | 104 (48–227) | | |
| Other areas | 0.005 (0.000–0.016) | 1,184 (0–3,626) | | 0.003 (0.001–0.006) | 609 (283–1,314) | | |
| **Soay total** | | **1,338 (170–3,780)** | | | **713 (362–1,405)** | | **2,031 (1,839–2,296)** |
| **Soay population change (%)** | | **-34%** | | | | | |

| | **CALIBRATION PLOT METHOD** | | | **HDS METHOD** | | **SEABIRD 2000** | |
|---|---|---|---|---|---|---|---|
| | **AOS per m$^2$** | **Total no. AOS** | **Total no. AOS Seabird 2000 area** | **Mean AOS per m$^2$** | **Total no. AOS** | **AOS per m$^2$** | **Total no. AOS** |
| **HIRTA** | | | | | | | |
| Carn Mòr | 0.023<br>(0.009–0.070) | 1,285<br>(662–2,902) | 732<br>(377–1,653) | 0.015<br>(0.012–0.020) | 871<br>(655–1,158) | 0.073<br>(0.052–0.109) | 2,386<br>(1,680–3,527) |
| **Carn Mòr population change** | **-68%** | | **-69%** | | | | |
| Other areas | not surveyed | | | | | | 1,219<br>(1,077–1,398) |
| **Hirta total** | | | | | | | **3,605**<br>**(2,758–4,925)** |
| **St Kilda total** | | **15,140**<br>**(11,315–25,412)** | **14,102**<br>**(10,454–23,554)** | | **9,233**<br>**(8,148–10,462)** | | **45,433**<br>**(34,310–61,398)** |
| **St Kilda population change** | | | **-68%**[b] | | | | |

[a] Densities are given for sectors BOR1 and BOR4 for comparison with those from Seabird 2000, but these sectors are included in the combined sectors BOR1–2 and BOR3+, respectively.

[b] The overall population change for St Kilda is based on the difference between the total for the Seabird 2000 area in 2019 and the St Kilda total from Seabird 2000 minus the 'other areas' of St Kilda which were not surveyed in 2019.

## 2.5 Discussion

I estimate the breeding population of Leach's Storm-petrels on Elliðaey to be in the region of 5,400 (95% CI: 4,300–6,700) pairs (based on the HDS estimate), following a decline of between 40–49% since 1991 (based on the repeats of the transects performed in 1991). The population in 1991 was therefore likely to have been in the region of 9,000–10,600 pairs; substantially lower than the previous estimate of 44,300 pairs, from the island-wide habitat-based extrapolation (Hansen et al., 2009). Results from the 2018 whole-island survey show that the 1991 transects at Hábarð and Bunki were positioned in the two densest areas of the colony (Figure 2.2), inflating the mean density and biasing the 1991 population estimate correspondingly. I also detected declines on all four of the main St Kilda islands, with reductions in AOS of 34–83% since the Seabird 2000 survey (Mitchell et al., 2004). Whilst I note that the field survey methods we used were not identical to those used in previous surveys (Mitchell et al., 2000; Newson et al., 2008), the population estimate for the entire St Kilda archipelago, derived from the same analytical methods used in 2000, is approximately 14,100 (95% CI: 10,500–23,600) pairs. This indicates an overall decline of 68% across surveyed areas since 1999. The HDS method produced a lower, but substantially more precise, estimate of 9,200 (95% CI: 8,100–10,500 AOS. Since the HDS approach accounts for the effects of several 'nuisance variables' on the likelihood of storm-petrels responding to playback and detection of responses given, I consider the estimate derived from the HDS approach to be the more reliable of the two estimates.

### 2.5.1 Assessment of population change

The results from Elliðaey suggest the number of Leach's Storm-petrels breeding on the island in 2018 is much lower than the 1991 estimate. Our survey was much more extensive than the playback transects performed in 1991, since we surveyed points across the whole island, and is therefore likely to have produced a more accurate result. Our repeat in 2018 of the Hábarð transect surveyed in 1991 was performed on a single night of extremely poor weather, and the results of this should be treated with caution. Nevertheless, the 2017 survey of the 1991 transects produced similarly low estimates to that in 2018.

Since the previous population estimate for Leach's Storm-petrels breeding across all of the islands in the Vestmannaeyjar archipelago was entirely based on extrapolation of the 1991 Elliðaey survey results, the 2018 Elliðaey survey results indicate that the population of the archipelago is likely to be substantially lower than the previously estimated 178,900 pairs. Based on the assumptions used to produce the whole-archipelago estimate in 1991, we might expect the entire Vestmannaeyjar population to now be in the region of 21,900 pairs. However, Leach's Storm-petrel densities and habitat preferences may vary between islands within the same archipelago, as we found on St Kilda, so surveys of the other Vestmannaeyjar islands will be necessary to produce a more reliable estimate for this population, which is likely still the largest in the northeast Atlantic.

There also appear to have been significant declines in the number of Leach's Storm-petrels breeding in the St Kilda archipelago. Results suggest a decline of 22% on Dùn since the previous survey there in 2006 (Newson et al., 2008); a reduction of 2,800 pairs. While the reduction in breeding pairs since Seabird 2000 is large, the exponential rate of decline on Dùn appears to have slowed, from 15% per year between 1999 and 2003, to 2% per year if we compare our estimate of 9,967 AOS (which uses the closest method to previous surveys) to the 2006 estimate of 12,770 (Newson et al., 2008). However, the wide confidence intervals for the asymptote estimates on which these population estimates are based, suggest that the statistical power to detect within-island population changes is low.

### 2.5.2 Causes of population declines

As for many Leach's Storm-petrel colonies, the reasons for the apparent decline on Elliðaey are unclear. Until 2008, when human harvesting of Puffins ceased on Elliðaey, Herring *Larus argentatus* and Lesser Black-backed Gulls *Larus fuscus* were controlled, reducing the gull population to < 10 breeding pairs, but snapshot counts during the Leach's Storm-petrel survey in 2018 estimated substantial numbers of gulls on the island (28 individual Herring Gulls and 135 Lesser Black-backed Gulls; Hey et al., 2019). Pellet analysis suggests that gulls on Elliðaey may consume approximately 200 Leach's Storm-petrels annually, although it is not known whether the predated storm-petrels are predominantly breeding or non-breeding birds (Hey et al., 2019).

On St Kilda, predation by Great Skuas *Stercorarius skua* is a likely cause of the Leach's Storm-petrel decline (Votier et al., 2006; Miles, 2010). The number of Great Skuas in the archipelago increased from 10 to 271 pairs between 1971 and 1997 (Phillips et al., 1999a), although the population has subsequently declined (Mitchell et al., 2004; Lawrence, 2019). In 2019 we identified five Great Skua Apparently Occupied Territories with medium to large chicks in the northwest ('non-Puffin') sector of Dùn; one more pair than in 2007–2009 (Miles 2010). I cleared one Great Skua territory of pellets and prey remains on 29 June and four days later found the remains of a minimum of three Leach's Storm-petrels (plus two Puffins and one Manx Shearwater) in the same territory. St Kilda's Great Skua population was estimated to consume 15,000 Leach's Storm-petrels in 1996 (Phillips et al., 1999b) and 21,000 a year in 2007–09 (Miles, 2010; but see Chapter 3), but with Dùn's Leach's Storm-petrel population apparently stabilising somewhat between 2003 and 2006 (Newson et al., 2008), it was assumed that the majority of predated individuals were non-breeders (Miles, 2010).

The endemic St Kilda Field Mouse is present on Hirta and Dùn. Seabirds form a significant part of the diet of Field Mice in Carn Mòr, but it is unclear whether these are predated or scavenged (Bicknell et al., 2009, 2020). The 2019 census results suggest declines in Leach's Storm-petrel populations on Soay and Boreray, where there are no Field Mice, so they are unlikely to be a major cause of population change in the archipelago and it seems likely that predation by Great Skuas has a much greater impact.

While large population declines at other Leach's Storm-petrel colonies have been attributed to predation pressure (Stenhouse et al., 2000; Wilhelm et al., 2015), the world's largest population (1.95 ± 0.42 (SE) million pairs) on Baccalieu Island, Newfoundland, is not subject to intense predation, yet has declined by 42% in 29 years (Wilhelm et al., 2019). Apparent adult survival rates in the western Atlantic and on Elliðaey are low (< 0.80; Fife et al., 2015; Greg Robertson & E.S. Hansen, unpublished data 1983–2018) compared with those in the Pacific (0.975; Rennie et al., 2020), and reproductive success is high at some colonies and variable at others (Mauck et al., 2018; Wilhelm et al., 2019). It is likely that non-breeders make up a large proportion of the Leach's Storm-petrels depredated at colonies, since they tend to spend more time above ground than breeding adults, prospecting for nest sites and displaying to potential mates (Furness, 1987). There is evidence of movement between populations within the Atlantic, and high levels of dispersal from natal colonies (Bicknell et al., 2012, 2014). The loss of large numbers of non-breeders through predation and other causes of population declines at the biggest colonies in the western Atlantic may therefore reduce the ability of compensatory recruitment to buffer against high mortality in eastern Atlantic colonies (Votier et al., 2008).

Several other threats may be causing or contributing to Leach's Storm-petrel declines. Storm-petrels can be disorientated by artificial lights, and significant numbers may be killed in collisions with offshore oil and gas platforms and their gas flares (Ronconi et al., 2015), which are present in the recently-described foraging ranges of Leach's Storm-petrels from several declining colonies in the western Atlantic (Hedd et al., 2018). Storm-petrels are also at risk from oil spills and discharges from such platforms, but the extent of overlap with the marine distribution of Leach's Storm-petrels from the studied colonies is unknown, and monitoring of the interactions between seabirds and these structures is currently very limited (Ronconi et al., 2015). Climate change is also likely to affect Leach's Storm-petrels, through impacts on prey distribution and abundance, direct impacts of severe weather events on foraging success and adult survival, and reduced reproductive success (Mauck et al., 2018). Leach's Storm-petrels in the northwest Atlantic have high mercury levels (Bond and Diamond, 2009), although no association was found between mercury levels and reproductive success or survival (Pollet et al., 2017). The role of disease in the population dynamics of storm-petrels is currently unknown, but infectious diseases have been implicated in the decline of other Procellariiform species

(Weimerskirch, 2004).

The widespread decline of Leach's Storm-petrels across the Atlantic, and the extensive movement of birds within the ocean basin, suggest that the Atlantic's Leach's Storm-petrels should be viewed as a meta-population, and that any conservation actions for this highly mobile and dispersive species must take this into account. The foraging and migratory movements of Leach's Storm-petrels breeding in the northeast Atlantic are poorly known, but winter isotope values are similar to those from Baccalieu Island, Newfoundland (Hedd and Montevecchi, 2006; Roscales et al., 2011) and preliminary data from Elliðaey in 2020 indicate that their winter distribution overlaps with birds tracked from the western Atlantic (Pollet et al., 2014, 2019b; A. Hedd et al. unpublished data). Further tracking of birds from Elliðaey is underway and could reveal important information on the threats they face at sea. Continued monitoring and demographic studies of breeding Leach's Storm-petrels on both Elliðaey and St Kilda, such as the ongoing monitoring of birds breeding in nest boxes on St Kilda, are also vital to improve our understanding of the processes causing the population declines.

### 2.5.3 Assessment of field and analytical methods

Accurately censusing burrow-nesting seabirds is challenging due to the generally low and variable rates of response to playback. Consequently, confidence intervals around population estimates tend to be large. We aimed to make population estimates as accurate and precise as possible, by optimising the type and amount of data that could be collected in the time available. We did this by using a distance sampling method, which enables a larger area to be surveyed for each playback than the calibration plot method (i.e. based on Ratcliffe et al., 1998), which assumes constant response and detection rates across the survey plot, meaning plots are necessarily small (typically < 4 $m^2$; Gilbert et al., 1998). It is important to note that implementation of the HDS analysis is far more complex and time-consuming than the calibration plot method and is unlikely to be practical in all survey situations.

Our field methods were largely optimised for the HDS analysis method, and this is reflected in the larger confidence intervals of the population estimates from the calibration plot method. Further assessment of the use of HDS to census burrow-nesting seabirds would, however, be useful, to ensure that the assumptions of this relatively complex type of model are met. For example, are there directionality effects in which observers are less likely to detect or accurately measure a response from a nest site behind them? For playback surveys, the probability that a bird responds to a playback is likely to decline with distance from the playback speaker, because the further a bird is from the stimulus, the less likely it is to hear it. While the 'gdistsamp' function of the unmarked package does not enable 'availability' (i.e. the likelihood of a bird responding) to vary with distance from the observer, the models appear to be robust to situations where availability varies between individual animals based on their spatial distribution (Fiske and Chandler, 2011; see Appendix 1, Figure A1.11). Simulated datasets with known population size, response rates and detection rates, may be useful to confirm that this holds true for playback surveys.

It is not possible to give specific recommendations about sampling density, the number of points that should be repeated, or the number of occasions on which points should be repeated. The optimal survey design will depend on the extent of variation in the density of birds and in the magnitude and variation (in both time and space) in response rate. Simulations or the collection of pilot data could inform the most appropriate sampling strategy.

The accuracy of the population estimates obtained from the calibration plot method would be improved by surveying a greater number of points surveyed once with close-range playback (i.e. with a smaller survey radius) and island-specific or sector-specific calibration, but these were not feasible in the time available in the field. Although I had originally intended to use only the responses within a 1 m radius for the calibration plot method, the low density of birds meant that insufficient responses were detected within that range for the asymptote to be estimated reliably. Therefore, responses from up to 3.5 m from the speaker were used to estimate the asymptote, even though the HDS analysis revealed that response rate (i.e. 'availability') may vary substantially across that distance. However, using data from different radii resulted in widely different population estimates. The density calculated using a 2 m radius was three times the density from a 3.5 m radius (see Appendix 1, Table A1.2), and the effect of survey radius for playback studies deserves further investigation. Given the diagnostics of the models fitted to the data collected, I believe that the HDS estimates are the most accurate assessment of the current Leach’s Storm-petrel populations on Elliðaey and St Kilda, but that the calibration plot method estimates for St Kilda are most directly comparable with those from previous surveys. Estimates from the calibration plot method for St Kilda are higher than those for the HDS method, but the HDS estimates fall within the 95% confidence intervals of the respective estimates from the calibration plot method for each of the combined sectors.

Field methods for the HDS approach allowed us to cover more ground by increasing the survey radius for each playback. On Dùn, where the ground is unconsolidated and storm-petrels often nest under vegetation, rather than in burrows, the distance sampling approach may have reduced the risk of trampling birds or nests, as surveyors remained on transect lines and did not need to walk over large areas, as was required in previous surveys where playback was performed every metre across 5 m x 5 m quadrats.

It is important that daytime playback surveys are performed when Leach’s Storm-petrels are incubating or brooding small chicks, as this is the only period of the year when active nest sites will be consistently occupied by adults during the day, and therefore available to respond to playback. A mis-timed survey may result in an underestimate of the breeding population. In 2019, approximate laying dates were estimated for eight Leach’s Storm-petrel pairs breeding in artificial nest boxes on Hirta. Nests were checked approximately weekly prior to laying and the laying date was taken as the median date between the date the egg was first seen and the date of the previous nest check. These estimated laying dates spanned a protracted period, from 1 June to 22 July, with a mean of 20 June (Lawrence, 2019), so timing a survey when all birds are incubating or brooding would not be possible. Our surveys were performed between 18 June and 5 July and I found no evidence of a change in response rate with date for the islands overall, although the top Dùn model included a quadratic effect of date on availability (i.e. response rate). This date effect could, however, be a result of changes in weather conditions, rather than changes in the number of birds incubating.

An important consideration for future surveys is establishing colony extent. The limited fieldwork time available in this study and the difficulties of access meant that we could not survey every island in its entirety or attempt to determine the extent of the Leach’s Storm-petrel distribution. Since the estimated densities are scaled up to the area of apparently suitable habitat, the size of habitat areas is important in estimating population sizes. The areas I used are based on apparently suitable habitat identified from aerial imagery. For St Kilda, sector boundaries were based on those used in the Seabird 2000 survey (Mitchell et al., 2000), although only poor-quality photocopies of the original sector maps were available. My estimates of sector areas are slightly larger than those used by Mitchell et al. (2000) (Table 2.3). These differences can partially be explained by differing methods of estimating surface area on steep, rough topography, but may also be due to differences in delineating colony extent, or habitat change (Pollet and Shutler, 2018). It is almost inevitable that areas outside of those identified as suitable habitat will contain at least some Leach’s Storm-petrels. This is especially the case on St Kilda, where habitats form a complex matrix, and many areas are inaccessible. However, using the same areas in future surveys will enable population change to be assessed in a standardised manner. Provided remotely-sensed environmental data are available, all habitat types are sampled and models fit well, the HDS approach may be less susceptible to inaccuracies in estimation of habitat extent.

Notwithstanding the analytical challenges, and associated costs, of application of an HDS approach, the efficiency savings in terms of fieldwork effort, and improved precision of population estimates, suggest that HDS should be considered wherever possible for future surveys. However, the HDS models require more data than the traditional methods so the feasibility of collecting sufficient data should be considered when designing a survey.

# 3 Assessment of Great Skua pellet composition to inform estimates of storm-petrel consumption from bioenergetic models

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## 3.1 Abstract

Generalist predators may exert levels of predation on particular prey that result in, or contribute to, decline of that prey species. Bioenergetics models have been used to estimate the rates of consumption of Leach's Storm-petrels and European Storm-petrels by Great Skuas on St Kilda (Western Isles, UK) and Hermaness (Shetland, UK). The models require estimates of the number of indigestible pellets produced from each individual storm-petrel consumed, which have previously been determined by captive feeding trials or examination of pellets cast by free-living birds, but which have not discriminated between the two storm-petrel species. Here, I use information from dissection of 427 Great skua pellets collected on Hirta, St Kilda, and Mousa, Shetland, to provide empirical estimates of the pellet:prey ratios for Leach's and European Storm-petrels separately. I found that pellet:prey ratios were similar for collections of the 'standing crop' of pellets accumulated over the entire breeding season and samples of pellets cast within the preceding five days. However, pellet:prey ratios of both Leach's and European Storm-petrel were considerably lower than reported previously. Furthermore, I found that the pellet:prey ratio for European Storm-petrels consumed on St Kilda was 80% higher than the value for the same species on Mousa. These results suggest that the use of a single generic value for the pellet:prey ratio for both species and all locations may lead to inaccuracies in

estimation of consumption rates, and I recommend further work to understand the causes of such variation.

## 3.2 Introduction

Bioenergetics models have been widely used for many years in seabird ecology to estimate rates of prey consumption at scales ranging from individual colonies to ocean basins (e.g. Guinet et al., 1996; Barrett et al., 2006). Such models can shed light on a range of processes from large-scale patterns of energy flux across ecosystems (Hunt et al., 2005) to the extent of competitive interactions between particular top predator species and fishery activity (Bunce, 2001). Here I focus on the application of bioenergetic models to assess rates of predation by seabirds on other seabird species. Quantifying rates of predation on specific prey types is important for understanding population dynamics, particularly where changes in predator or prey numbers are apparent or where conservation management may be required.

Numbers of Great Skuas have rapidly increased in Scotland during the last century, likely due to reduced persecution, increased availability of food from fishery discards and prey-switching, including direct predation of other seabirds (Mitchell et al., 2004; Votier et al., 2004b). Great Skuas are generalist predators and their diet includes fish, birds and invertebrates (Bayes et al., 1964; Furness, 1987). Many of the seabird species that Great Skuas prey upon are declining in the UK (JNCC, 2021) and the implementation of the Common Fisheries Policy discard ban is predicted to result in an increase in predation on seabirds as the availability of discarded fish decreases (Reeves and Furness, 2002; Votier et al., 2004b; Bicknell et al., 2013).

Storm-petrels are vulnerable to predation due to their small size and relative immobility on land. The breeding ecology of storm-petrels is strongly influenced by predation risk: nest sites are located in crevices and burrows on islands free from mammalian predators and adult birds are active at the colony only at night. Despite these adaptations, storm-petrels remain vulnerable to avian predators such as gulls and skuas (Watanuki, 1986; Stenhouse and Montevecchi, 1999; Stenhouse et al., 2000; Oro et al., 2005; Votier et al., 2006).

Traditionally, a range of methods have been used to study seabird diet, including identification of prey from feeding observations, pellets, prey remains, spontaneous regurgitates and stomach flushing (Votier et al., 2003). These techniques give broadly similar results, but there are biases associated with each (Votier et al., 2003). More recent advances include the extraction and identification of prey DNA from predator faeces or regurgitates (Bowser et al., 2013) which may reduce such bias but are costly and time-consuming to implement at large scale. In contrast, pellets of regurgitated, indigestible prey remains are easy to collect and can provide large sample sizes to determine the proportions of different prey types consumed (Votier et al., 2003). However, pellet analysis tends to overestimate indigestible material and any pellets produced away from the colony are not available for analysis, leading to uncertainty regarding the absolute quantities of prey consumed (Votier et al., 2003).

Pellet analysis can be combined with bioenergetics modelling to quantify consumption rates of different prey types without the need to estimate rates of pellet production. Such models have been used to calculate levels of storm-petrel predation by Great Skuas at two large colonies in the UK (Phillips et al., 1999b; Votier et al., 2004a; Miles, 2010). The models firstly estimate the total energy requirement of the entire breeding and non-breeding population over the breeding season, then use the proportion, energy content and assimilation efficiency of each prey type to estimate its relative contribution to the total energy budget. The proportion of each prey type may be assessed by pellet analysis. Typically, each pellet comprises a single prey type, and the model requires for each prey type: (i) an estimate of the size (in prey mass or number of individuals) of an average “meal” (i.e. the quantity of food present in a bird’s proventriculus on its return from a foraging trip; Phillips et al., 1999b), and (ii) the number of pellets that are produced from a single meal. From these two quantities the number of pellets produced from each prey individual consumed (i.e. the pellet:prey ratio) is calculated, which is used as a so-called “correction factor” (Phillips et al., 1999b) in the model. Although European and Leach’s Storm-petrels differ considerably in size (25 g and 45 g respectively), Phillips et al. (1999b) considered that a single storm-petrel of either species constituted a single meal, and "*on the evidence of groups of pellets found together on breeding territories clearly consisting of combinations of wings, whole legs or body feathers, it was estimated that at least three pellets result from a meal of a single individual*" of either species. Phillips et al. (1999b) therefore used a correction factor of 3.0 pellets produced per storm petrel consumed, and concluded that in 1996 Great Skuas on St Kilda consumed 7,450 European Storm-petrels and 14,850 Leach's Storm-petrels. Votier et al. (2004a) used a similar bioenergetics model to estimate the number of European Storm-petrels consumed annually by Great Skuas at Hermaness, Shetland, using a pellet:prey ratio of 2.5 pellets per European Storm-petrel consumed, as estimated by Votier et al., (2001). The ratio was obtained by feeding 11 storm-petrel carcasses, as six separate meals, to captive, full-grown Great Skua fledglings (Votier et al., 2001 Tables 2 & 3, though note the methods section of that study incorrectly states that eight storm-petrels were fed to the captive skuas). Since carcasses of European Storm-petrels were not available, a variety of larger-bodied storm-petrel species from the austral Oceanitidae family were used (S. Votier pers. comm.). A total of 28 pellets were cast from the 11 storm-petrels consumed, giving a pellet:prey ratio of 2.5 (Votier et al*.,* 2001, Table 3). Pellets produced by Great Skuas held in captivity or produced from the consumption of large austral storm-petrel species may not be entirely representative of pellets of European and Leach's Storm-petrels produced by free-living Great Skuas. Votier et al. (2004a) concluded that Great Skuas at Hermaness consumed 215 European Storm-petrels in 2001.

Here I use dissection of Great Skua pellets collected at two colonies and containing remains of both European and Leach's Storm-petrels to quantify the pellet:prey ratios for each prey species. For each sample of pellets, I calculated the minimum number of storm-petrels consumed from the number of the most frequently occurring body part. For example, since each storm-petrel has only one furcula, a sample of pellets that contains five storm-petrel furculae represents the remains of a minimum of five storm-petrels. I calculated pellet:prey ratios by dividing the number of pellets in a sample by the minimum number of storm-petrels represented in that sample. For example, a sample of ten pellets that contained a total of five storm-petrel furculae would give a pellet:prey ratio of 2:1, and a correction factor of 2 in a bioenergetics model. Specifically, I compare the pellet:prey ratios (i) for Leach's and European Storm-petrels; (ii) for European Storm-petrels at two different colonies and (iii) for samples collected as the "standing crop" of pellets accumulated over an extensive (and unknown) period of time with those collected from an area cleared of pellets five days previously.

## 3.3 Methods

### 3.3.1 Sampling for comparison of pellet:prey ratios for Leach's and European Storm-petrels

I analysed archived Great Skua pellets from Hirta, St Kilda, to compare pellet:prey ratios for European and Leach's Storm-petrels. The St Kilda archipelago supports 94% of the British and Irish population of Leach's Storm-petrels, with 45,433 apparently occupied sites (AOS) in the Seabird 2000 census (but see Chapter 2), as well as an estimated 1,121 European Storm-petrel AOS (Mitchell et al., 2004). Pellets were collected from a Great Skua club site in August 2015, 2016 and 2017. Club sites are areas where non-breeders congregate and are rarely, if ever, attended by breeding skuas (Klomp and Furness, 1992). All pellets at the site were collected during a single visit each year, so represent the standing crop of pellets deposited by predominantly non-breeding Great Skuas over an unknown period of time. Each year's standing crop is unlikely to include intact pellets from the previous breeding season, however, because winter storms cause pellets to disintegrate. In addition, pellets collected in 2016 and 2017 could not be more than one year old as all pellets had been removed from the site in the previous August.

### 3.3.2 Sampling for comparison of pellet:prey ratios for European Storm-petrels at two colonies

To compare pellet:prey ratios for European Storm-petrels between colonies, I collected Great Skua pellets on Mousa, Shetland (60°00'N, 01°11'W), in August 2018. Mousa supports an estimated 10,778 breeding pairs of European Storm-petrels (Bolton et al. 2017), the largest colony in the UK, but is not known to support breeding Leach's Storm-petrels. To maximise the sample size of pellets containing storm-petrel remains, I focussed search effort in areas where storm-petrel predation had been noted previously (M. Bolton, pers. obs.). Table 3.1 summarises the areas searched and the number of pellets found in each area. I collected and dissected all pellets to identify their contents.

Table 3.1. Summary of the remains of European Storm-petrels found in Great Skua pellets collected at five sites on Mousa, Shetland, UK in August 2018. Estimates of the number of pellets produced per European Storm-petrel consumed are calculated by dividing the number of pellets containing the species by the minimum number of individuals in those pellets (i.e. the highest count of either furculae, left humeri or right humeri). For samples from all sites, the most frequently occurring body part was the right humeri, so this was used to represent the minimum number of individuals. Area A was sampled twice to test for differences between the 'standing crop' and freshly cast pellets.

| Area | Date searched | No. of pellets collected | No. of pellets containing storm-petrel remains | Furculae | Left humeri | Right humeri | Pellets per storm-petrel |
|---|---|---|---|---|---|---|---|
| A | 1 Aug | 55 | 53 | 65 | 62 | 65 | 0.82 |
| A | 6 Aug | 32 | 32 | 40 | 34 | 41 | 0.78 |
| B | 6 Aug | 18 | 13 | 14 | 14 | 17 | 0.76 |
| C | 14 Aug | 20 | 19 | 31 | 32 | 32 | 0.59 |
| D | 9 Aug | 42 | 28 | 26 | 26 | 29 | 0.97 |
| E | 14 Aug | 4 | 0 | 0 | 0 | 0 | - |
| **Total** | | **171** | **145** | **176** | **168** | **184** | **0.79** |

### 3.3.3 Sampling for comparison of pellet:prey ratios for standing crop and freshly deposited pellets

Pellets containing only feathers may disintegrate faster than pellets containing hard parts. Such differential pellet degradation would reduce the estimate of the number of pellets produced per storm-petrel consumed. To assess this potential bias, I sampled area A twice, five days apart, to test for differences in the composition of standing crop and freshly cast pellets. Although I may have overlooked some pellets on the first visit, pellets collected on the second visit to area A largely represent those deposited in the previous five days.

### 3.3.4 Pellet analysis

Storm-petrel remains were easily identifiable from feathers and bone morphology (Votier et al., 2006). I compared prey remains with reference material and classified pellets as containing storm-petrel remains if I found any of the following diagnostic features: skull, keel, humerus, pelvis, furcula, bill, legs, feet, remiges or retrices, or any fully diagnostic contour feather (such as a tail covert). I distinguished between remains of European and Leach's Storm-petrels based on size, with the above diagnostic features of Leach's Storm-petrels being obviously larger than those of European Storm-petrels. Pellets from St Kilda that comprised dark contour feathers but none of the above diagnostic features often contained bones of other avian prey, such as auks, and so I considered them not to contain storm-petrel remains.

For the initial sample of 55 pellets from area A on Mousa, I retained and counted multiple easily-identifiable body parts (furcula, humeri, keel, skull, synsacrum, feet and wings) to determine which were found at the highest frequency and were therefore most representative of the total number of storm-petrels consumed. I then counted the most frequently occurring body parts in this initial sample in the full sample of pellets from both Mousa and St Kilda.

### 3.3.5 Data analysis

Below I compare the pellet:prey values obtained from my dissection of pellets collected on St Kilda with those from Mousa and also with values used in earlier studies of skua consumption of storm-petrels. Since pellet:prey ratios are incorporated into bioenergetics models as a correction factor, to account for non-parity between the number of individuals consumed and pellets produced, their effect on model estimates of prey consumption depends on their absolute magnitude. I therefore focus my analysis on the magnitude of the differences in estimates of the ratio, rather than on any statistical significance of differences.

## 3.4 Results

A total of 256 pellets were collected on St Kilda: 71 in 2015, 84 in 2016 and 101 in 2017. Within the entire sample, I identified storm-petrel remains in 26 pellets (Table 3.2). Seventeen of these pellets contained European Storm-petrel remains and nine contained Leach's Storm-petrel remains. A single pellet (from 2016) contained storm-petrel remains that could not be identified to species level. Nine pellets containing storm-petrel remains (five of European, three of Leach's and one of unknown storm-petrel species) each contained one additional food item: fish (n = 2), auk (Alcidae sp.; n = 1), unidentified bird species (n = 2), mammal (n = 1), goose barnacle *Lepus* sp. (n = 2) and unidentified mollusc (n = 1). A further three pellets containing storm-petrel remains (one of European and two of Leach's Storm-petrel remains) contained two additional food items: fish + goose barnacle (n = 1), auk + mollusc (n = 1), mammal + vegetation (n = 1).

On Mousa, I collected a total of 171 pellets, of which 145 contained European Storm-petrel remains (Table 3.1). Of these, six pellets contained one additional item: fish (n = 3), Common Starling *Sturnus vulgaris* (n = 1), seaweed (n = 1) and grass (n = 1). One additional pellet contained both fish and auk remains alongside storm-petrel remains. No remains of Leach's Storm-petrel were found.

In the initial sample of 55 pellets from area A on Mousa, furculae (n = 65), left humeri (n = 62) and right humeri (n = 65) were the most frequently found body parts (Figure 3.1). Since these three bones were found at similar frequencies in the first sample of pellets examined, I counted all three in the full sample of pellets from both colonies.

Table 3.2. Summary of the remains of European Storm-petrels (ESP) and Leach’s Storm-petrels (LSP) found in Great Skua pellets collected at a club site on Hirta, St Kilda, UK in 2015, 2016 and 2017. For each species, estimates of the number of pellets produced per storm-petrel consumed are calculated by dividing the number of pellets containing the species by the minimum number of individuals in those pellets (i.e. the highest count of either furculae, left humeri or right humeri).

| **Year** | **No. of pellets collected** | **No. of pellets containing storm-petrel remains** | **European Storm-petrel (ESP)** | | | | | **Leach’s Storm-petrel (LSP)** | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | **No. of pellets** | **Furculae** | **Left humeri** | **Right humeri** | **Pellets per ESP** | **No. of pellets** | **Furculae** | **Left humeri** | **Right humeri** | **Pellets per LSP** |
| 2015 | 71 | 6[a] | 5 | 3 | 3 | 2 | 1.67 | 0 | 0 | 0 | 0 | - |
| 2016 | 84 | 9[b] | 6 | 5 | 5 | 4 | 1.20 | 4 | 2 | 2 | 1 | 2.00 |
| 2017 | 101 | 11 | 6 | 3 | 4 | 4 | 1.50 | 5 | 3 | 2 | 2 | 1.67 |
| **Total** | **256** | **26** | **17** | **11** | **12** | **10** | **1.42** | **9** | **5** | **4** | **3** | **1.80** |

[a] 1 pellet from 2015 contained storm-petrel feathers that were not identified to species level.

[b] 1 pellet from 2016 contained remains of both ESP and LSP.

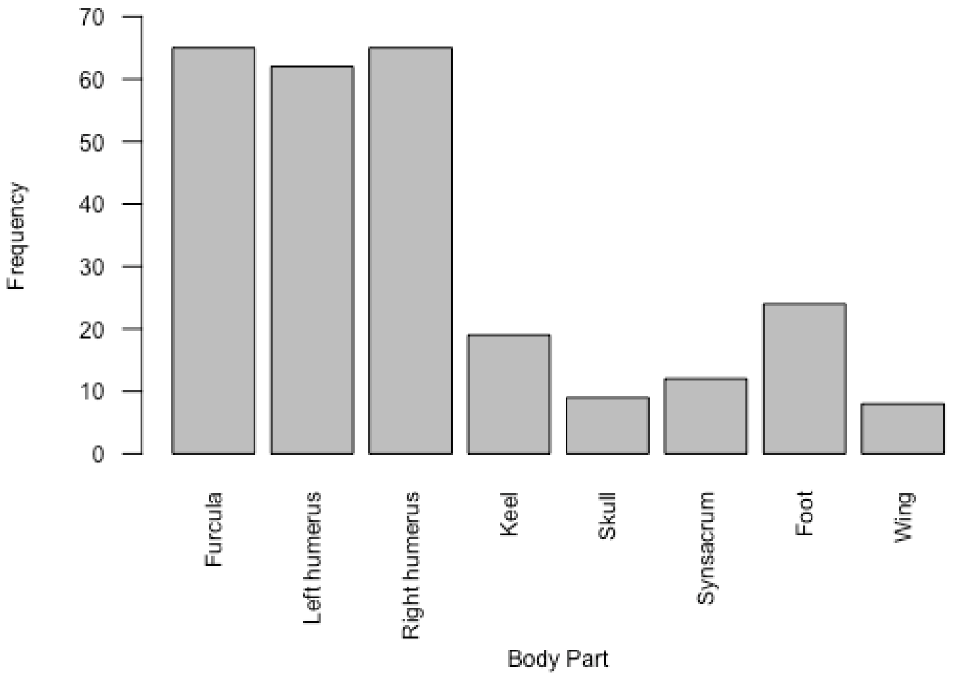


Figure 3.1. Frequency of occurrence of European Storm-petrel body parts in 55 Great Skua pellets found on Mousa, Shetland in August 2018.

### 3.4.1 Comparison of pellet:prey ratios for Leach's and European Storm-petrels on St Kilda

In the full sample of pellets from St Kilda I found 11 furculae, 12 left humeri and 10 right humeri from European Storm-petrels and five furculae, four left humeri and three right humeri from Leach's Storm-petrels (Table 3.2). The majority of pellets from St Kilda containing storm-petrel remains included parts from just one storm-petrel of either species (i.e. no more than one furcula, left humerus or right humerus). Two pellets (one from 2016 and one from 2017) contained body parts of a minimum of two European Storm-petrels. A single pellet from 2016 contained body parts from a minimum of two European Storm-petrels and one Leach's Storm-petrel. The mean number of pellets produced per European Storm-petrel ingested was 1.42. For Leach's Storm-petrel this value was 27% higher, at 1.80.

### 3.4.2 Comparison of pellet:prey ratios for European Storm-petrels at two colonies

In the combined sample of 171 pellets from Mousa, I found 173 furculae, 168 left humeri and 184 right humeri, giving a minimum estimate of 184 European Storm-petrels (Table 3.1). The number of each of these body parts found in a single pellet ranged from zero to five. The right humerus was the most commonly found body part in the samples from each area. Within the sample of pellets that contained storm-petrel remains (n = 145), the mean number of right humeri per pellet was 1.27. This value equates to 0.79 pellets produced per storm-petrel consumed, compared with 1.42 pellets per European Storm-petrel from the St Kilda sample. The pellet:prey ratio for European Storm-petrels on St Kilda was therefore 80% higher than that for Mousa.

### 3.4.3 Comparison of pellet:prey ratios for standing crop and freshly deposited pellets

In the initial sample (standing crop) from area A on Mousa I found 65 right humeri in 53 pellets containing storm-petrel remains, giving an estimate of 0.82 pellets per storm-petrel (Table 3.1). In the second sample (freshly cast pellets), I found 41 right humeri in 32 pellets containing storm-petrel remains, giving an estimate of 0.78 pellets per storm-petrel. The standing crop estimate was therefore just 5% higher than that for the freshly cast pellets.

## 3.5 Discussion

Bioenergetics models offer a means of quantifying prey consumption and require estimates of multiple parameters, such as prey energy content and ratios of pellets:prey. Here, I aimed to improve the accuracy of one of the input parameters for future Great Skua bioenergetics models by determining pellet:prey ratios for European and Leach’s Storm-petrels consumed by wild-living skuas.

This analysis of Great Skua pellets collected in Shetland and on St Kilda shows that field estimates of pellet:prey ratios may be somewhat variable. Estimates of the ratios for European Storm-petrels from different sampling areas on Mousa ranged from 0.59 to 0.97, and the estimate for European Storm-petrels consumed on St Kilda (1.42) was 80% greater than the estimate from the combined samples from Mousa (0.79). The reason for this difference is unclear but could be related to the rate of storm-petrel consumption by individual skuas, and the extent to which storm-petrels were inter-mixed with other prey types. If a skua feeds exclusively on multiple storm-petrels in a night, it is likely to produce pellets containing remains of multiple individuals. However, if storm-petrels are taken only occasionally, there is little opportunity for multiple birds to be contained within a single pellet. Additional food items were found alongside storm-petrel remains in a greater proportion of pellets from St Kilda (0.46) than from Mousa (0.05), which may reflect differences in the temporal pattern of storm petrel ingestion, alongside other prey, at the two colonies. In addition, pellets from St Kilda were collected from primarily non-breeding skuas over three years, while pellets from Mousa were from breeding territories and were collected in only one year. Skua breeding status and inter-annual differences may have contributed to the differences in pellet:prey ratios found here.

On St Kilda, the estimate of the pellet:prey ratio for Leach's Storm-petrels (1.80) was 27% greater than that for European Storm-petrels (1.42). Previously, a common correction factor was used for both species (Phillips et al., 1999b), despite Leach's Storm-petrels being approximately 80% larger than European Storm-petrels. My results suggest that a single correction factor is unlikely to be appropriate for all studies of Great Skua predation on European and Leach's Storm-petrels.

Previous estimates of generic storm-petrel pellet:prey ratios (Phillips et al., 1999b; Votier et al., 2001) are 76–280% higher than my field-based estimates for European Storm-petrels and 39%–67% higher than my estimates for Leach's Storm-petrels. Phillips et al. (1999b) based their pellet:prey ratio on the presence of wings, legs and body feathers found in groups of pellets, and this may explain their higher estimate. In the sample of pellets from Mousa where all body parts were counted, I found 24 feet/legs and eight wings in 53 pellets containing storm-petrel remains (Figure 3.1). Based on these body parts, I would have estimated a minimum of 12 storm-petrels in 53 pellets, giving a pellet:prey ratio of 4.42. This is considerably higher than the ratio of 0.82 estimated using the number of furculae or right humeri (n = 65 for both body parts) found in this sample. I am unable to quantify the effects of these lower pellet:prey ratios on Great Skua bioenergetics models since previous sensitivity analyses do not state the effects of changes to this correction factor (Phillips et al., 1999b; Miles, 2010). Given the size of the differences between my estimates and those used previously, it is likely that values from the current study would have a large impact on the estimated numbers of storm-petrels consumed.

There was only a 5% difference between the pellet:prey ratios for the samples from the initial and repeat visits to area A on Mousa, suggesting that sampling pellets from the standing crop does not bias estimates of the number of pellets produced per storm-petrel consumed. However, standing crop samples could not be used to determine the proportion of diet that consists of storm-petrels since pellets containing different prey types disintegrate at different rates (Furness and Hislop, 1981). Fish would generally be under-represented in the standing crop since pellets of fish bones may begin to disintegrate within two days, while pellets containing feathers can remain intact for ten days or more (Furness and Hislop, 1981).

From this study it is not possible to assess the level of predation of storm-petrels by Great Skuas on Mousa, since pellets were not collected systematically and known predation hotspots were targeted. In addition, I collected pellets during what may be the peak period for storm-petrel predation, since skuas were feeding large chicks and large numbers of non-breeding storm-petrels were prospecting for nest sites, making them vulnerable to predation as they spend more time above ground. However, ring recovery data suggests breeding storm-petrels were also consumed. I recovered twenty-six European Storm-petrel rings from the Great Skua pellets I collected on Mousa during this study, of which 11 rings were from birds ≥ 3 years old, including nine from birds ≥ 4 years old. Since European Storm-petrels begin breeding at age three or four (Okill and Bolton, 2005), these birds are likely to have been breeders.

Given the large number of individual storm-petrels found in pellets after modest search-effort, there is a need for quantification of predation levels at this colony. The

European Storm-petrel population on Mousa more than doubled between surveys conducted in 1996 and 2008 (Bolton et al., 2010) but growth had ceased by the most recent survey in 2015 (Bolton et al., 2017). Great Skua numbers on Mousa increased from 20–24 pairs between 2001 and 2005 to 30–40 pairs between 2008 and 2015; an average annual increase of around 4% (RSPB, unpublished data). There is scope for further work to identify the extent of storm-petrel predation by Great Skuas on Mousa so that any population-level impacts can be determined.

While I have identified considerable differences in pellet:prey ratios for storm-petrels consumed by Great Skuas, the causes of those differences are unclear. The sample sizes of pellets containing storm-petrels remains from St Kilda are small and the breeding status and stage of the skuas that produced the pellet samples are unknown. I encourage further extensive sampling of Great Skua pellets across sites, years and breeding stages, and also consideration of co-occurrence of other prey types, in order to establish the causes of variation in pellet:prey ratios. Improved understanding of variation in pellet:prey ratios will enable more accurate estimation of this input parameter for bioenergetics models, and therefore more reliable estimates of prey consumption in future studies.

# 4 A quiet corner of the playground? Drivers of the broad-scale marine distribution of European Storm-petrels breeding on Mousa, Shetland

## 4.1 Abstract

Knowledge of how seabirds use the marine environment is key to understanding their ecology and conservation, given that they spend large proportions of their lives at sea. Due to their small size, which makes them difficult to observe at sea, our knowledge of how storm-petrels use the marine environment has been limited, but the ongoing miniaturisation of tracking devices is changing this. I used GPS tracking data to investigate the relative importance of prey availability, intraspecific competition and predation risk on the marine distribution of European Storm-petrels breeding on Mousa, Shetland. I used a total of 43 foraging trips made by 28 birds tracked during incubation, brooding and the post-brood stage in 2015–2018. Trip durations were similar across all breeding stages and years, but birds tracked in 2018 remained closer to the colony than those tracked in other years. Results from a pseudo-absence analysis, in which I compared GPS locations with random but accessible locations, suggest that intraspecific competition and predation risk are important drivers of marine distribution for birds breeding on Mousa. The tracked birds also displayed higher usage of areas with greater seabed ruggedness and lower sea surface temperatures, which may be associated with increased food availability. Tracking from additional colonies will be crucial for understanding whether these drivers are similar for European Storm-petrels breeding elsewhere, and for other species of storm-petrel.

## 4.2 Introduction

Seabirds spend a large proportion of their lives at sea, so knowledge of their marine distributions and habitat requirements is essential for a comprehensive understanding of their ecology. Understanding how seabirds use the marine environment is also crucial for marine spatial planning and conservation management, which are becoming increasingly important as the oceans face rapid and accelerating anthropogenic change. Studying seabirds at sea is challenging, especially for the highly pelagic and wide-ranging Procellariiformes, but the remote-sensing and tracking revolution is transforming our understanding of the behaviour and ecology of seabirds away from their breeding colonies (Croxall et al., 2005; Costa et al., 2012; Pollet et al., 2019b).

Tracking devices have only recently become sufficiently miniaturised to deploy on the smallest taxon of seabirds, the storm-petrels, and their marine distributions are not yet well understood. Since most storm-petrel colonies in the UK are located within presumed commuting range of the edge of the continental shelf, it was previously assumed that European Storm-petrels breeding in Britain foraged at the shelf edge, and this idea was supported by vessel-based surveys that have tended to find higher concentrations of storm-petrels in these areas (Waggitt et al., 2020). However, it is not possible to determine the provenance or breeding status of birds observed on vessel-based surveys, and recent GPS tracking has shown that, rather than travelling to the shelf edge to the west of the colony, European Storm-petrels breeding on Mousa, Shetland, consistently use a restricted foraging area in the northern North Sea, to the southeast of the island (Bolton, 2020).

We do not yet understand what might be driving the restricted marine distribution of European Storm-petrels breeding on Mousa, but there are a number of possible influences. Firstly, use of different areas of the marine environment is related to accessibility. During the breeding season seabirds are central place foragers (Orians and Pearson, 1979): they depart from the colony to visit foraging areas but must return to the colony to continue nest defence, incubation, brooding or chick-provisioning. This constraint to regularly return to the colony means that accessibility decreases with distance from the colony, and there are time and energetic limits to the distance birds can travel to forage. For many seabirds, foraging trips made during the incubation stage are longer in duration than those made during chick-rearing, meaning that accessibility of marine areas can vary with breeding stage. However, Bolton (2021) found that, although foraging trips made by European Storm-petrels during incubation were longer in duration that those made during chick-rearing, they did not differ in foraging range or total distance travelled.

Secondly, seabird foraging trips are influenced by food availability. The diet of seabirds, and the distribution of their food resources, are often poorly understood, so remotely-sensed variables such as sea surface temperature (SST) and chlorophyll-*a* concentration, which influence productivity, are commonly used as proxies for food availability in models of seabird distribution (e.g. Grecian et al., 2016; Clay et al., 2017; Krüger et al., 2018; McDuie et al., 2018). Many seabird species have been found to target static oceanographic features such as shelf edges and fronts, where upwelling and water mixing processes result in increased productivity and a concentration of food resources (Scott et al., 2013; Dean et al., 2015). The level of mixing of the water column is influenced by variables such as bathymetry and seabed topography (Cox et al., 2018). Weather conditions such as wind speed may further affect the ability of storm-petrels to successfully locate and retrieve food from the sea surface.

Thirdly, since individuals of the same species have a much higher niche overlap than those of different species, competition between conspecifics tends to be greater than interspecific competition (Chesson, 2000). Several seabird species display spatial segregation of foraging areas between neighbouring colonies (parapatric conspecifics), although key areas of high resource abundance may be shared (Lewis et al., 2001; Grémillet et al., 2004; Paiva et al., 2010; Wakefield et al., 2013; Dean et al., 2015; Bolton et al., 2018).

In addition, although many seabirds are apex predators, the small size of storm-petrels means they have a high predation risk. On St Kilda, there is evidence of intense, unsustainable predation of Leach's Storm-petrels by Great Skuas (Votier et al., 2006; see Chapters 2 and 3), which have rapidly increased in number in Scotland over recent decades. Predation risk has a strong influence on the nesting location and breeding behaviour of storm-petrels; they almost always breed in burrows on islands free from non-native mammalian predators and movement to and from the nest site occurs only under darkness (Warham, 1990; De León et al., 2006; Miles, 2010).

Although there are reports of storm-petrels being predated on at sea by larger seabirds (Beck and Brown, 1972; Furness, 1987), the extent to which this predation risk affects their at-sea distribution and behaviour is not known.

In this chapter I use GPS tracking data from Bolton (2021), plus data from an additional breeding season, to examine the broad-scale marine distribution of European Storm-petrels breeding on Mousa, Shetland. I first calculate basic trip metrics to identify differences between trips made in different breeding stages (as calculated by Bolton, 2020) and years. I then use a generalised additive mixed model (GAMM) fitted to all at-sea locations to model broad-scale spatial usage in relation to environmental variables, intraspecific competition and predator density. I test the hypothesis that the use of a restricted area to the southeast of the colony is driven not only by oceanographic conditions relating to prey availability, but also by intraspecific competition and predation risk. I predicted that usage would be higher in areas with lower densities of predators and of conspecifics breeding elsewhere.

## 4.3 Methods

### 4.3.1 Fieldwork

Fieldwork was carried out on Mousa between mid-July and late August in 2014–2018. I collected data in collaboration with Mark Bolton in 2018 and data from 2014–2017 were made available from Bolton (2021). In the 1990s, approximately 100 nest boxes were installed in natural habitat and in stone walls across the island (Bolton, 1996), with up to 50 nest boxes being occupied by breeding pairs each year. The nest boxes enable breeding birds to be monitored, marked and captured with minimum disturbance.

We inspected nest boxes each day during daylight hours prior to tag deployment but, due to their sensitivity to disturbance, adults were handled only for the deployment and retrieval of GPS devices. To assess which birds to tag and the best day to deploy the tags, we individually marked adult birds in each nest box with coloured, non-toxic paint, which we applied to their tertial feathers while they remained on the nest.

Marking enabled us to monitor nest attendance and deploy tags on adults that were due to depart on a foraging trip, thereby reducing battery depletion while birds remained on the nest.

In 2014, Biotrack PinPoint 8 tags were used, which were able to store a total of eight locations (GPS “fixes”). In 2015–2018, we used PathTrack NanoFix® GEO mini tags, with a specified capacity of 80 fixes. Tags weighed < 1 g (typically 0.93 g), which was 3–4% of adult body mass. We deployed GPS tags less than an hour before nightfall so that if handling caused a tagged bird to depart the nest early (not observed in this study), the risks to both the adult (from predation) and egg or chick (from exposure) were minimised, as the time that the egg or chick was unattended before the non-tagged partner returned was reduced. We caught birds by hand on the nest and weighed the adult and chick to 0.1 g. We attached a tag to four or six central tail feathers using three 3 mm wide strips of waterproof Tesa® tape and returned the tagged bird to its nest, covering the exit until the bird had settled. We continued to inspect nests daily following tag deployment. Adult European Storm-petrels return to and depart from the nest only at night so, for incubating and brooding birds, which remained at the nest during the day, we removed tags just before nightfall on the evening following the bird’s return. For post-brooding birds, which make only short nocturnal visits to the nest for chick-provisioning, we checked nests repeatedly through the night, and retrapped tagged birds when they were first encountered. We weighed birds upon tag removal which, for incubating and brooding birds, was at a similar time in their nest attendance cycle to the body mass recorded at tag deployment, allowing us to compare pre- and post-deployment body mass as an indication of negative effects of tagging. For any tagged birds that were not recaptured, the tag would fall off after several days once the tape deteriorated.

We programmed tags to record bird locations every 15 to 60 minutes, with the fix interval chosen based on the capacity and battery life of the tag and the predicted length of the upcoming foraging trip, based on our pre-deployment monitoring of nest attendance.

### 4.3.2 Tag effects

Importantly, tagging was not found to negatively impact birds tracked in 2014–2017, based on a comparison of pre- and post-deployment body mass and a comparison of daily nest failure rates between nests where birds were tagged and control nests where no tagging took place (Bolton, 2020). Unfortunately, the number of active nests in the 2018 tagging period did not allow us to monitor a sufficient number of control nests to investigate differences in daily nest failure rates, but I used a paired t-test to compare the change in body mass between tagged birds at deployment and retrieval in 2018.

### 4.3.3 Data processing and trip metrics

I visualised GPS data in QGIS (version 3.8) and manually split tracks into separate trips based on the bird's departure from and return to the colony. Although I wanted to maximise the data available for the habitat use analysis, retaining partial trips may result in biases, for example if tags are more likely to fail on longer trips or under particular conditions. So, following Bolton (2021), I removed trips for which the GPS tag failed before the bird returned to the colony or where large overnight gaps in recorded locations meant it was unclear whether or not the bird returned to the colony. I classified trips according to the breeding stage during which they took place, using three categories: incubation, brooding, and post-brooding. Following Bolton (2021), trip stage was classed as post-brooding if a bird did not remain in the nest during the day upon return from the trip, even if it had been brooding a chick when the tag was deployed and/or its partner was brooding the chick while the tagged bird was on the tracked foraging trip.

The data included multiple trips for some birds, so to check for independence between trips by the same individual I compared the overlap of 50% utilisation distributions (probability density that a bird is present at any given point) within and between birds using the 'indEffectTest' function of the track2KBA package (version 0.0.0.900; Beal et al., 2021), selecting the 'scaleARS' smoothing parameter and home range method. I used the same package to calculate trip duration, maximum distance from the colony, total distance travelled and trip direction, and tested for differences in trip metrics between years and breeding stages using generalised linear mixed-effects models (GLMMs). I built the GLMMs with the ‘glmer’ function of the lme4 package (version 1.1–26; Bates et al., 2015), with individual ID as a random term to account for the repeated measurement of some individuals. These models used the gamma error family and link functions selected to minimise AIC (log-link for trip duration, total distance, and direction, and identity link for maximum distance). Due to the temporal resolution of the GPS data, the first and last locations for some trips were at sea. While this is accounted for in the trip distance calculations as the distance to the colony from the first and last locations is added, it can mean that trip durations are underestimated. To account for this, I added a location at the colony one time-step before the first location for trips where that was at sea. I did not add a final location at the colony if the last GPS fix for a trip was at sea, as adding two new time stamps to a single trip would likely have resulted in overestimates of trip duration.

### 4.3.4 Presence vs pseudo-absence analysis

To compare the locations used by storm-petrels with all potentially accessible locations I conducted a pseudo-absence analysis (Pearce and Boyce, 2006). Visual assessment of the raw tracking data suggested that some birds may make several attempts to return to their nest, but may be put off by predators or the presence of researchers, and this can result in several fixes in the vicinity of the colony. I therefore removed GPS locations within 1 km of Mousa, to exclude birds at the colony and those performing colony-related behaviours from the analysis. Then, for each of the remaining observed locations (presences) I created five ‘absence’ points that were matched to the presence point by time, date and distance from the colony. There are many different methods for selecting pseudo-absence locations, but the selection of random points has been found to perform better than simulated tracks in which the start and end point of a track are retained but the intervening step lengths are randomised (O’Toole et al., 2021). Since storm-petrels are constrained to depart from and return to the colony during darkness, matching by time, date and colony distance ensured that all pseudo-absence locations were theoretically accessible for birds from Mousa at a given date and time. I used five pseudo-absence points for every presence, as a compromise between maximising the number of pseudo-absences and remaining within computational limits (Barbet-Massin et al., 2012). I weighted pseudo-absences as 0.2 and presences as 1 in the model, to ensure the weighted sum of the presences equalled the weighted sum of the pseudo-absences (Barbet-Massin et al., 2012). To control for colony distance, I used the 'gridDistance' function from the raster package (version 3.4–5; Hijmans, 2020) to calculate the distance from Mousa to each 0.01° x 0.01° cell of a raster of the surrounding area and randomly selected points that matched the distance (rounded to the nearest kilometre) from Mousa of the presence points. As storm-petrels tend not to travel over land other than to cross the colony to return to their nest site, I calculated distances avoiding land, to ensure they were more biologically accurate (Matthiopoulos, 2003; Wakefield et al., 2011). The resolution of the distance raster was limited by computational power and some pseudo-absence points were located on land. I discarded any pseudo-absences located on land and resampled them.

I built GAMM models with a binary response variable of presence (1) or absence (0) using the 'gam' function of the mgcv package (version 1.8-33), since the 'gamm' function is unsuitable for binomial data (Wood, 2011).

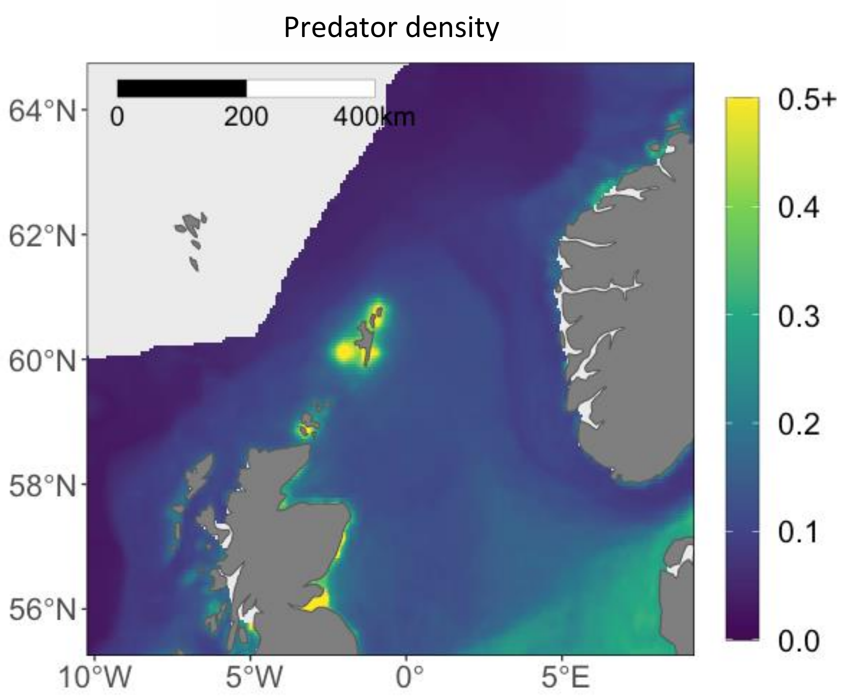
### 4.3.5 Explanatory covariates

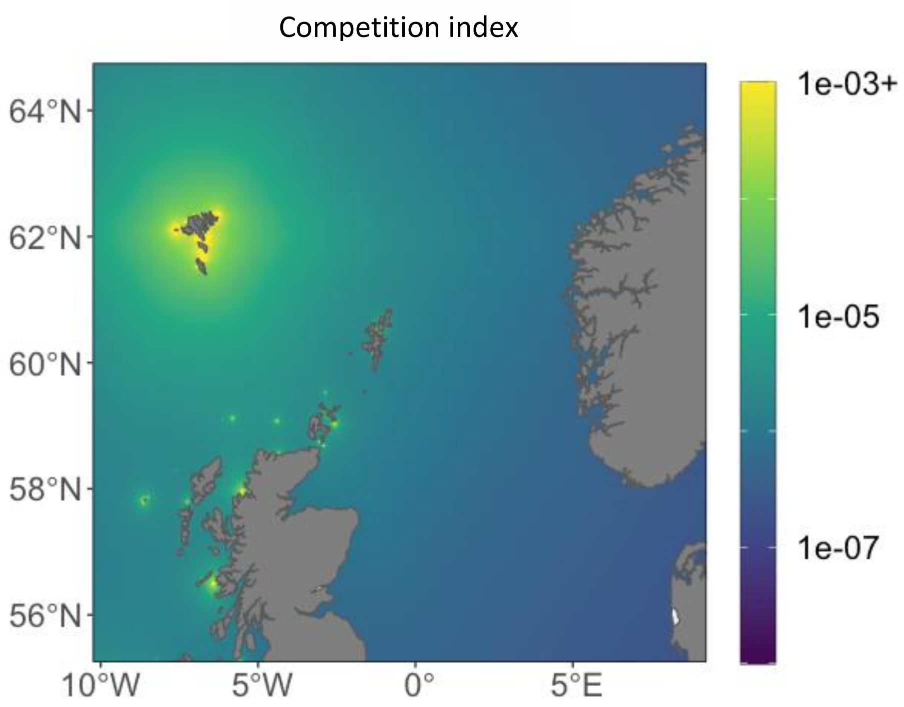
Example maps of the explanatory covariate data are shown in Figure 4.1. Since the diet of storm-petrels breeding on Mousa is not known in detail, the distribution of their prey is uncertain. Therefore, I used a series of environmental covariates known to influence marine productivity across a broad range of taxa. I used Movebank's Env-DATA system (Dodge et al., 2013) to annotate each location with the following environmental variables: (1) chlorophyll-*a* concentration, (2) sea surface temperature (both of these variables had an 8 day, 4 km resolution; MODIS Ocean/Aqua Mapped OceanColor, https://oceandata.sci.gsfc.nasa.gov), (3) wind u (east-west or zonal) and v (north-south or meridional) components at 10 m above sea level (with a resolution of 6 h and 0.75°; ECMWF Global Atmospheric Reanalysis, http://apps.ecmwf.int/datasets/data/interim_full_daily/?levtype=sfc), and (4) distance to the nearest coast (0.04° resolution; NASA, https://oceancolor.gsfc.nasa.gov/docs/distfromcoast/). Gaps in chlorophyll-*a* concentration and sea surface temperature were interpolated using an inverse-distance-weighted method, and all other variables were interpolated using bilinear (two-dimensional) interpolation (Dodge et al., 2013). I calculated wind speed from the wind u and v components using the formula: wind speed = $\sqrt{u^2 + v^2}$. I extracted seabed depth and slope from the GEBCO elevation raster (15 arc-second resolution; GEBCO Compilation Group, 2021) using the raster package (version 3.4-5; Hijmans, 2020), and calculated the terrain ruggedness index (TRI) using the spatialEco package (version 1.3-7; Evans, 2021). TRI is a measure of difference in elevation between adjacent cells of an elevation raster, and was calculated as the mean of the elevation differences between a given cell and its eight surrounding cells (Riley et al., 1999; Evans, 2021).

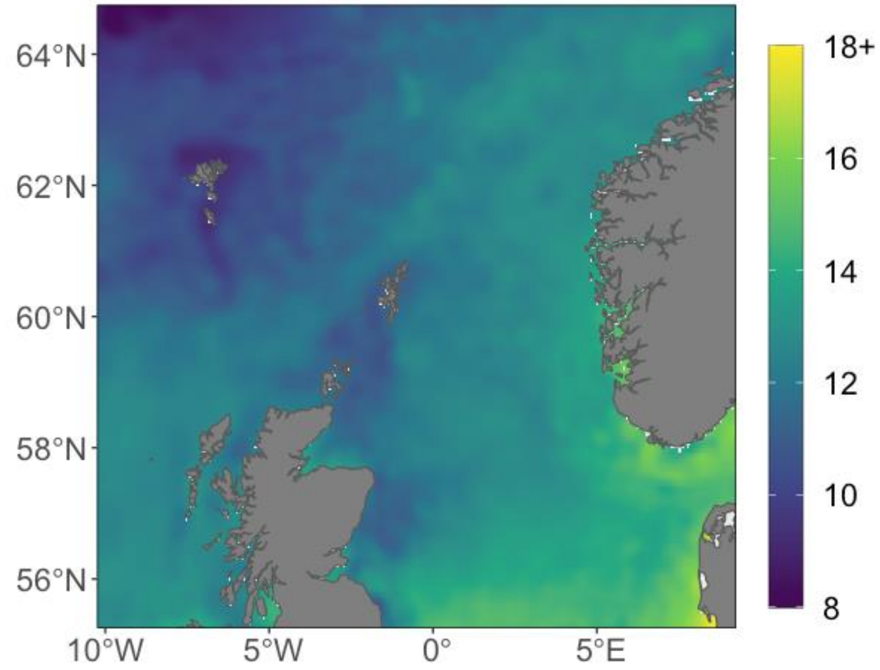
To investigate the influence of intraspecific competition, I created a 'competition' raster based on the distance and size of European Storm-petrel colonies other than Mousa. I used colony locations and population estimates from the Seabird 2000 census for the UK and Ireland (Mitchell et al., 2004), from the BirdLife International Data Zone (BirdLife International 2018) for the Faroe Islands, from the SEAPOP database (https://seapop.no/) for Norway and from Hey et al. (2019) for Iceland. For each colony, I calculated the distance to each cell of a 0.01 x 0.01° raster. Again, distances were calculated avoiding land in order for them to be biologically relevant. For the raster for each colony I divided the population size of the colony by distance$^2$ for each cell of the raster. I then summed across rasters for all colonies, to give a single raster where the value of each cell represented:

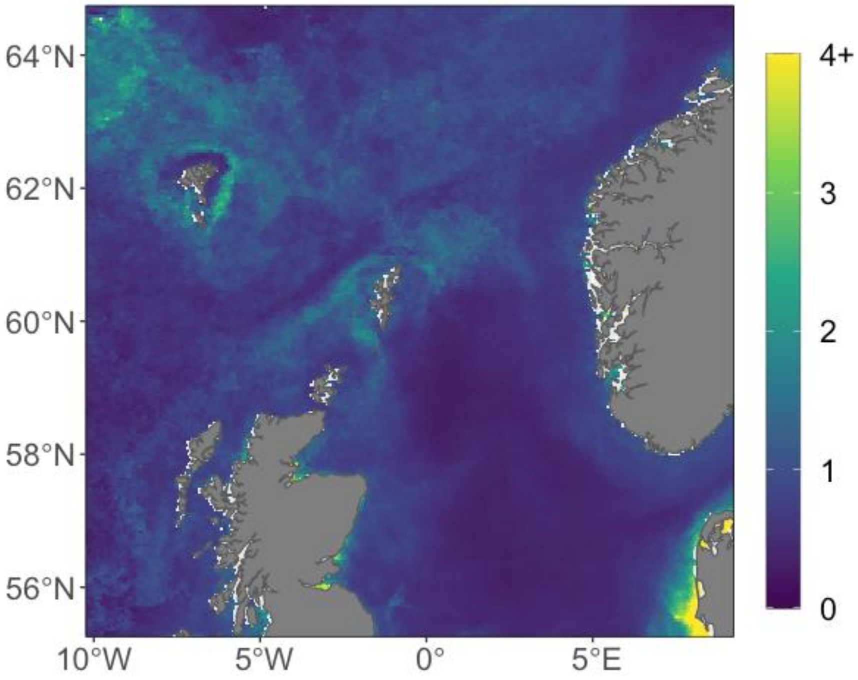
$$\sum\left(\frac{n_i}{d_i^2}\right),$$

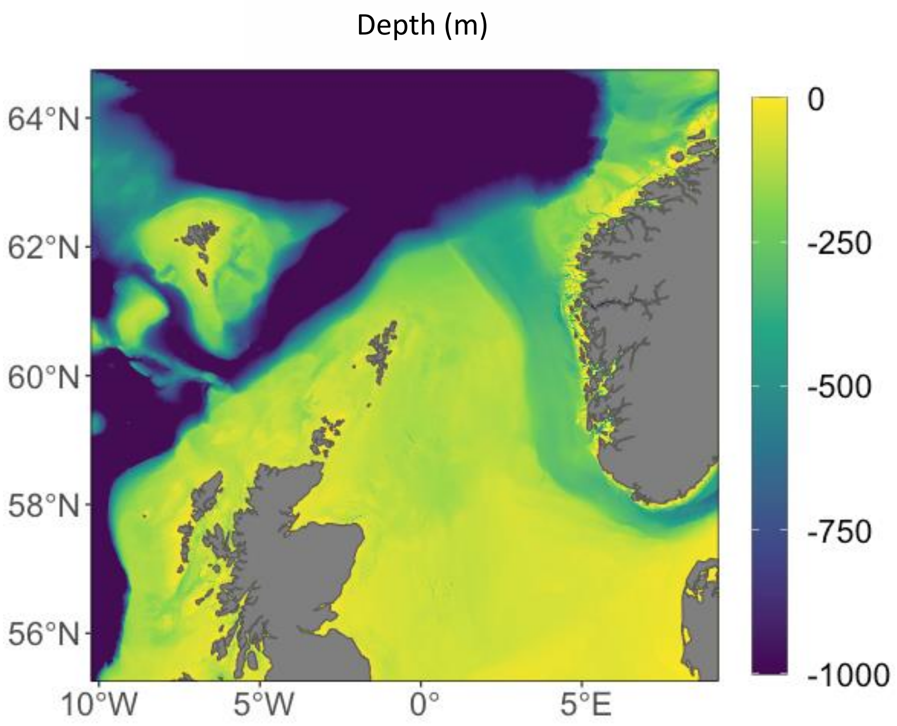
where $n_i$ is the population size (in pairs) of the $i$th colony and $d_i$ is the distance (in metres) to the $i$th colony, avoiding land (Wakefield et al., 2011). I then extracted the competition value from this raster for each presence and pseudo-absence point, using bilinear interpolation.

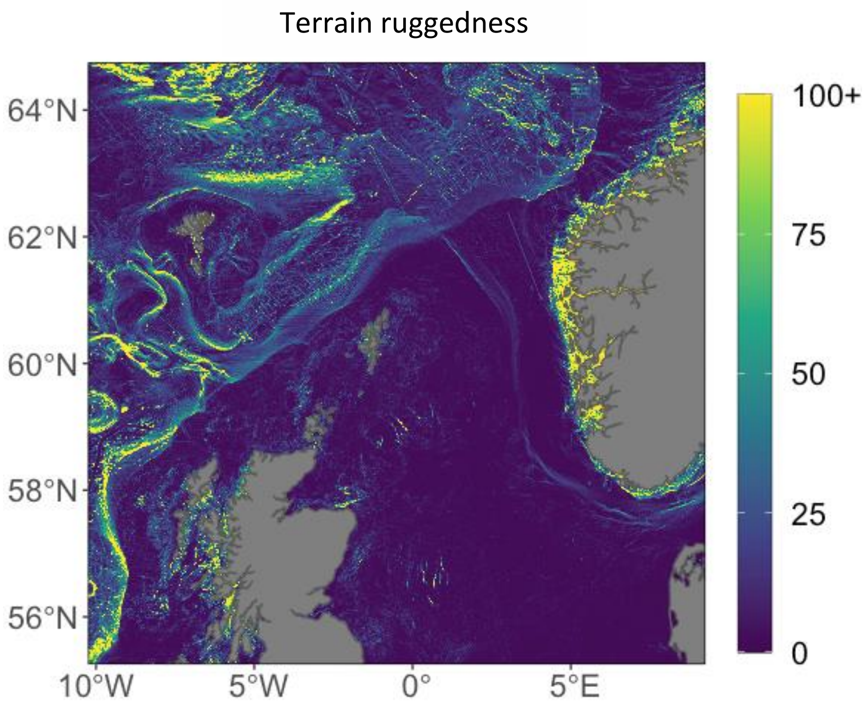

Predator density


Competition index


Sea surface temperature (°C)


Chlorophyll-*a* (mg/m$^3$)


Depth (m)


Terrain ruggedness

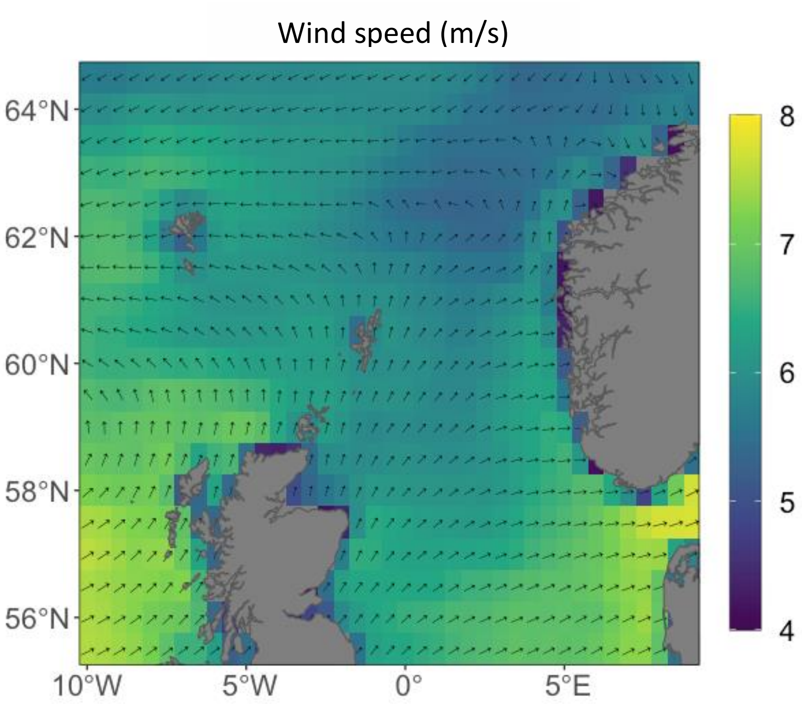


Figure 4.1. (Above and previous three pages.) Environmental variables used as explanatory variables in the model of European Storm-petrel habitat usage during foraging trips from Mousa, Shetland. For dynamic variables (sea surface temperature, chlorophyll-α concentration, wind speed), the mean values from across the study periods in all years are shown. Areas with missing data are shown in light grey.

To investigate the influence of predators on storm-petrel marine distributions, I used the sum of estimated Great Skua, Lesser Black-backed Gull and Herring Gull densities for the relevant month (July or August) from Waggitt et al. (2020) as a 'predators' variable. Since predation risk is more likely to influence storm-petrels during daylight, I created a binary daylight variable (day/night) using dawn and dusk times for each location from the suncalc package (version 0.5.0; Thieurmel and Elmarhraoui, 2019) and included the two-way interactions of predators x daylight in the initial model.

To reduce the skewness of the independent variables, I log-transformed predator density, competition, depth, TRI and chlorophyll-*a* concentration, square-root transformed distance to the coast and double square-root transformed slope. I checked for correlation between all transformed numerical covariates using the 'cor' function of the stats package (version 4.0.3; R Core Team, 2019) and checked for concurvity between the smoothed terms in the model (Wood, 2011).

All pseudo-absence locations were matched with presences by trip ID. To account for potential differences between years and trips, I included random effects of year and trip ID in the GAMM by specifying the splines as ‘bs = “re”’. To avoid overfitting, I modelled each smooth using cubic regression splines with shrinkage, and enabled terms to be penalised out of the model completely (Wood, 2006). I set the maximum number of knots to five to prevent overfitting, but examined higher values where model checks suggested the number of knots may be too low.

The predator density data from Waggitt et al. (2020) were not available for the entire pseudo-absence area (Figure 4.1), meaning that 25 pseudo-absence points did not have predator density data associated. Since the GAMMs only included complete cases, I ran the final model with and without the predator density variable, to ensure that the other environmental variables for the area without predator density could contribute to the model.

Pseudo-absences were matched to presences by date, time and distance from the colony, meaning that both presences and pseudo-absences were mostly close to the colony during darkness and further away during daylight, since tracked birds departed from and returned to the colony at night. To check the assumption that storm-petrels avoid inshore areas during daylight I randomised the binary daylight variable for the pseudo-absence locations so that they were no longer matched with presences and re-ran the GAMM with the predator x daylight interaction.

## 4.4 Results

### 4.4.1 Tag deployments, retrievals and potential negative effects in 2018

Tag deployment and retrieval rates for 2015-2018 are given in Table 4.1. Details of deployments and retrievals and an analysis of potential negative effects of tagging in 2014-2017 are presented in Bolton (2021), so here I focus on the tagging carried out in 2018.

Table 4.1. Summary of the tags deployed and retrieved from European Storm-petrels breeding on Mousa, and the number of complete trips included in the trip metrics and pseudo-absence analysis. Note that an additional trip from a post-brooding bird in 2015 has been excluded as I did not consider it to be representative of normal at-sea movement. Some birds were tracked in multiple years or breeding stages, so the total number of birds differs from the sum of birds tracked in each year/breeding stage. The number of trips recorded for each bird is given in brackets where this differs from one trip per bird.

| Year | Breeding stage | No. tags deployed | No. tags retrieved (%) | No. tags with complete trips | No. trips | No. locations |
|---|---|---|---|---|---|---|
| 2015 | Incubation | 10 | 8 (80%) | 5 | 5 | 213 |
| | Brooding | 3 | 3 (100%) | 2 | 2 | 90 |
| | Post-brooding | 6 | 5 (83%) | 4 | 4 | 268 |
| 2016 | Incubation | 2 | 1 (50%) | 1 | 1 | 28 |
| | Brooding | 2 | 2 (100%) | 2 | 2 | 97 |
| | Post-brooding | 6 | 4 (67%) | 4 | 8 (1,1,2,4) | 267 |
| 2017 | Incubation | 2 | 1 (50%) | 1 | 2 (2) | 120 |
| | Brooding | 3 | 3 (100%) | 3 | 3 | 132 |
| | Post-brooding | 5 | 2 (40%) | 2 | 2 | 188 |
| 2018 | Brooding | 7 | 7 (100%) | 7 | 9 (1,1,1,1,1,2,2) | 560 |
| | Post-brooding | 3 | 2 (67%) | 2 | 4 (2,2) | 317 |
| Overall totals | | 49 | 38 (78%) | 27 | 42 | 2,280 |

Table 4.2. Trip metrics by breeding stage and year for European Storm-petrels GPS tracked from Mousa, Shetland. N = number of trips. Breeding stage codes refer to incubation (I), brooding (B) and the post-brood stage (P).

| Year | Breeding stage | N | Mean duration (hours) | Mean maximum distance from colony (km) | Mean total distance travelled (km) | Mean direction (degrees) |
|---|---|---|---|---|---|---|
| 2015 | I | 5 | 53.52 ± 21.90<br>(21.50–74.15) | 232.02 ± 83.54<br>(102.90–303.04) | 630.77 ± 263.09<br>(222.26–919.58) | 158.26 ± 9.68<br>(146.49–171.14) |
| | B | 2 | 24.78 ± 0.01<br>(24.77–24.78) | 154.90 ± 21.90<br>(21.50–74.15) | 423.09 ± 139.76<br>(324.26–521.91) | 160.97 ± 5.19<br>(157.30–164.64) |
| | P | 4 | 35.80 ± 13.60<br>(23.47–50.42) | 190.97 ± 42.97<br>(157.66–253.67) | 534.19 ± 132.73<br>(376.40–672.85) | 157.72 ± 17.09<br>(135.02–175.14) |
| 2016 | I | 1 | 30.00 | 153.66 | 402.83 | 135.14 |
| | B | 2 | 26.00 ± 0.00<br>(26.00–26.00) | 119.43 ± 4.06<br>(116.55–122.30) | 341.60 ± 8.98<br>(335.25–347.95) | 157.27 ± 0.72<br>(156.76–157.78) |
| | P | 8 | 26.64 ± 8.76<br>(21.50–47.95) | 137.04 ± 39.55<br>(81.71–206.17) | 364.67 ± 101.91<br>(214.17–581.75) | 163.56 ± 16.53<br>(137.06–194.31) |
| 2017 | I | 2 | 36.50 ± 14.14<br>(26.50–46.50) | 137.42 ± 44.56<br>(105.91–168.92) | 398.71 ± 174.18<br>(275.55–521.88) | 153.71 ± 1.76<br>(152.47–154.96) |
| | B | 3 | 24.94 ± 1.43<br>(23.32–26.00) | 127.03 ± 16.13<br>(112.87–144.59) | 355.84 ± 41.48<br>(308.00–381.68) | 166.46 ± 30.93<br>(139.56–200.25) |
| | P | 2 | 48.34 ± 1.87<br>(47.02–49.67) | 217.80 ± 86.20<br>(156.84–278.75) | 624.57 ± 109.22<br>(547.34–701.80) | 155.05 ± 0.61<br>(154.62–155.48) |
| 2018 | B | 9 | 22.67 ± 1.49<br>(20.00–24.50) | 82.63 ± 31.82<br>(44.63–141.39) | 250.47 ± 63.00<br>(145.16–332.97) | 159.23 ± 23.83<br>(119.37–190.31) |
| | P | 4 | 21.50 ± 2.34<br>(19.00–24.25) | 96.14 ± 60.73<br>(45.18–175.26) | 258.54 ± 103.42<br>(172.40–388.33) | 158.15 ± 15.42<br>(138.18–173.41) |

We deployed ten GPS tags on chick-rearing storm-petrels in 2018. Of these, we retrieved nine tags. The non-retrieved tag was the only one to be deployed on a bird breeding in a natural nest site rather than a nest box, and this made retrieval more challenging. Despite the tagged adult not being recaptured, it appeared to be visiting the nest for chick provisioning as large mass gains by the chick on some nights were consistent with feeding by both parents (cf. Bolton, 1995).

There was no statistically significant difference in the body mass of birds at deployment and retrieval for birds tagged in 2018 (mean difference = -0.67 g, confidence interval -2.38–1.05 g, t = -0.897, df = 8, p = 0.396), though this is not necessarily informative as meal size may vary between foraging trips and, for post-brooding birds, the second body mass measurement was taken later in the night than the first measurement, and may have been taken before or after feeding the chick. During the fieldwork period there were no nest failures at nests where adults were tagged and all the chicks of tagged birds continued to gain body mass. However, fledging success is unknown since accessing Mousa late in the breeding season was not possible.

### 4.4.2 Number of trips obtained and trip metrics

Due to the limitations of the tags (maximum of 8 GPS fixes per deployment), data for trips made in 2014 were very limited and I excluded them from the analysis. A total of 43 complete trips were obtained for 28 birds between 2015 and 2018, with birds tracked in the incubation, brooding and post-brood breeding stages in 2015 to 2017, and the brooding and post-brood stages in 2018 (Table 4.1). I removed one trip from a post-brooding bird in 2015 from the analysis as the bird was apparently storm-driven to the coast of Norway (Bolton, 2020), with large gaps in its trajectory, and I did not consider this trip to be representative of normal at-sea movement. There was no evidence of higher 50% utilisation distribution overlap for trips by the same individual compared to between individuals, either within years (two-sample Kolmogorov-Smirnov test implemented within the track2KBA package (Beal et al., 2021) D = 0.323, P = 0.091) or across years (D = 0.213, p = 0.238), so I included all trips for each individual in the pseudo-absence analysis. The final data included one bird with five trips, three birds with three trips each, five birds with two trips each, and 18 birds with a single trip each. Four birds were tracked in more than one year. Figure 4.2 shows the location of all presence and pseudo-absence points.

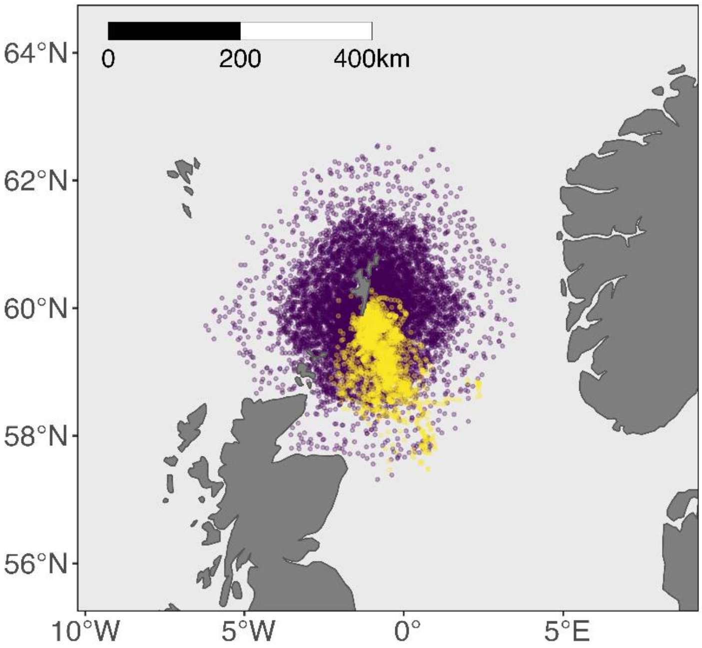


Figure 4.2. Presence (yellow) and pseudo-absence (purple) points for European Storm-petrels tracked from Mousa, Shetland. For every presence point (from GPS tracking data), five pseudo-absence points are randomly selected but match presences in distance from the colony.

Trip metrics and summary statistics for all trips are provided in Appendix 2 (Tables A2.1–A2.3). Across all trips, the mean duration was 31 ± 14 (SD) hours (range: 19–74 hours). Although there was a tendency for incubation trips to be longer than trips made during chick-rearing (Table 4.2), overall the difference in trip duration between breeding stages was not statistically significant when year was controlled for (GLMM to explain trip duration, $\mathcal{X}_2^2$= 5.07, p = 0.08). The difference in trip duration between years was also not statistically significant ($\mathcal{X}_3^2$= 5.97, p = 0.11).

The mean maximum distance from the colony was 141 ± 66 km (range 45–303 km). Maximum distance from the colony did not differ between breeding stages (GLMM to explain maximum distance from the colony, $\mathcal{X}_2^2$= 0.70, p = 0.71) but did differ between years ($\mathcal{X}_3^2$ = 36.78, p < 0.001), with birds remaining closer to the colony in 2018 (Table 4.2).

The mean total distance travelled on a trip was 393 ± 175 km (range 145–920 km). There was no difference in total trip distance between breeding stages (GLMM to explain trip duration, $\mathcal{X}_2^2$= 0.10, p = 0.95), but this metric did differ between years ($\mathcal{X}_3^2$= 26.20, p < 0.001), with birds in 2018 travelling shorter distances overall (Table 4.2).

The mean trip direction (the angle between the colony and the furthest location from the colony) was 159 ± 17 degrees (range 119–200 degrees), and this did not differ between breeding stages (GLMM to explain trip direction, $\mathcal{X}_2^2$= 0.33, p = 0.85), or years ($\mathcal{X}_3^2$= 1.31, p = 0.73, Table 4.2).

### 4.4.3 Presence vs pseudo-absence analysis

Distance to the coast was strongly correlated with predator density (Spearman’s rho = -0.84) so I excluded it from the GAMM models to avoid concurvity. I also excluded seabed slope since it was highly correlated with the Terrain Ruggedness Index (TRI; Spearman’s rho = 0.91) and did not have a statistically significant effect in the GAMM. The interaction between predator density and daylight was statistically unstable so I removed it from the final model.

The random effects of year and trip ID were not statistically significant (p = 0.936 and p = 1.000, respectively) but all remaining smoothed terms were statistically significant and retained in the final model (Table 4.3). The probability of presence peaked at a predator density of around 0.2 individuals per km$^2$ and declined at densities lower or higher than this. Presence decreased sharply with increasing parapatric intraspecific competition. There was a negative association between presence and SST. Presence peaked at a chlorophyll-*a* concentration of approximately 1 mg per $mg^3$ and a seabed depth of around 100 m. Overall there was a positive association between presence and TRI and probability of presence peaked slightly at intermediate wind speeds. Repeating the analysis without the predator variable did not result in any substantial changes to the observed relationships between presence and the other independent variables (see Appendix 2, Table A2.4 and Figure A2.1).

Table 4.3. Results of GAMM to explain European Storm-petrel marine distribution using presence vs pseudo-absence analysis.

| Parameter | Estimate | Standard Error | Z value | p-value |
|---|---|---|---|---|
| Intercept | -1.160 | 0.093 | -12.47 | < 0.001 |
| Smooth terms | edf | Ref. df | $X^2$ value | p-value |
| log(predators) | 1.988 | 4 | 25.430 | < 0.001 |
| log(competition) | 2.937 | 4 | 262.911 | < 0.001 |
| log(depth) | 1.330 | 4 | 7.098 | 0.005 |
| log(TRI) | 2.336 | 4 | 9.535 | 0.007 |
| log(chlorophyll-*a*) | 3.232 | 4 | 30.605 | < 0.001 |
| SST | 3.587 | 4 | 47.811 | < 0.001 |
| Wind speed | 1.720 | 4 | 7.350 | 0.010 |
| Year (random effect) | 0.003 | 3 | < 0.0001 | 0.936 |
| Trip ID (random effect) | 0.0005 | 41 | < 0.0001 | 1.000 |

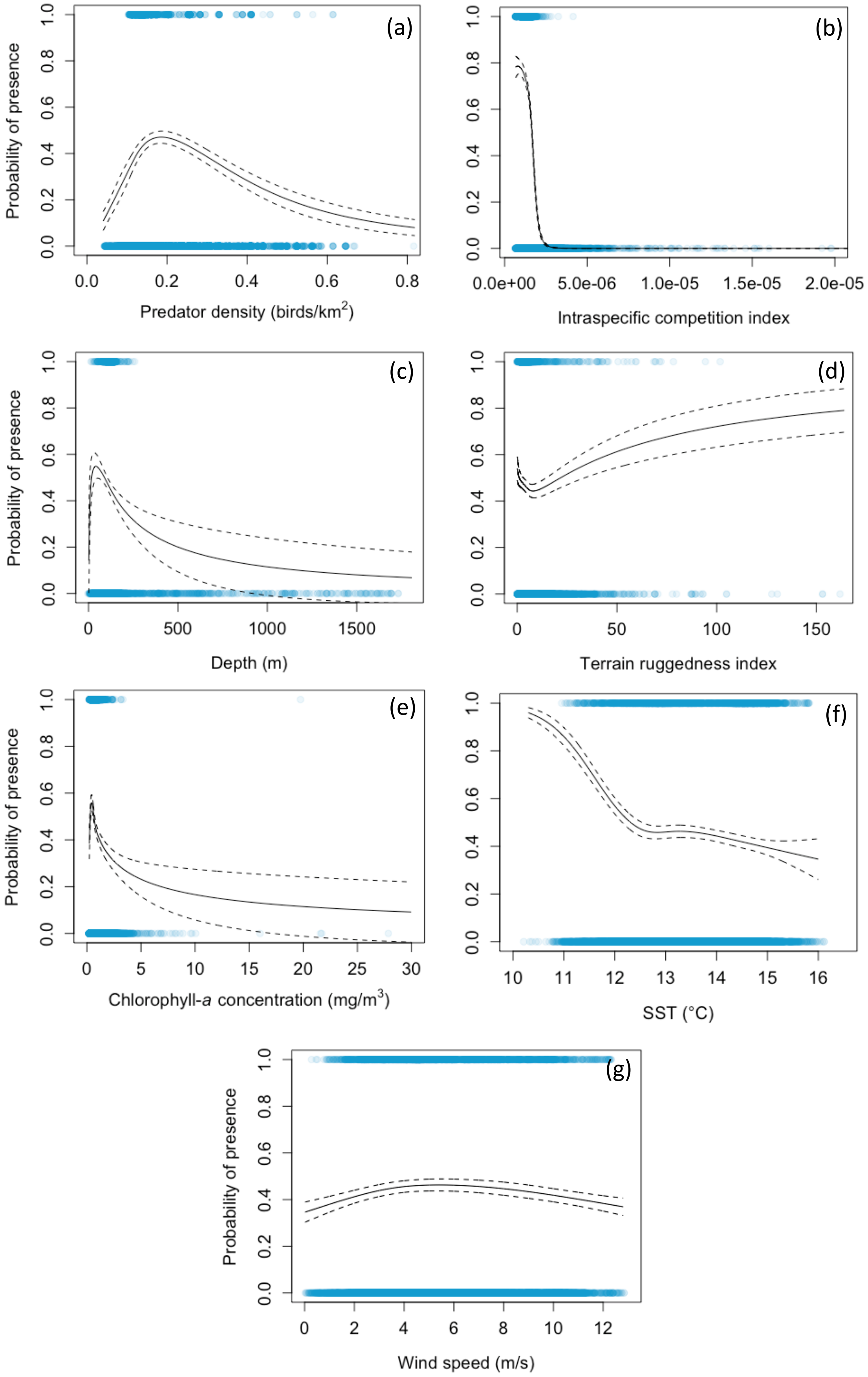


Figure 4.3. Probability of European Storm-petrel presence across a range of environmental variables, as predicted by a presence vs pseudo-absence GAMM.

Re-running the GAMM with the predator x daylight interaction and randomised daylight variable for pseudo-absences (i.e. pseudo-absences matched to presences by distance to the colony but not time of day) produced almost identical model estimates for the other parameters (Appendix 2, Table A2.5 and Figure A2.2), but showed clearly the increased usage of higher predator density (i.e. inshore) areas at night compared with during the day (Figure 4.4).

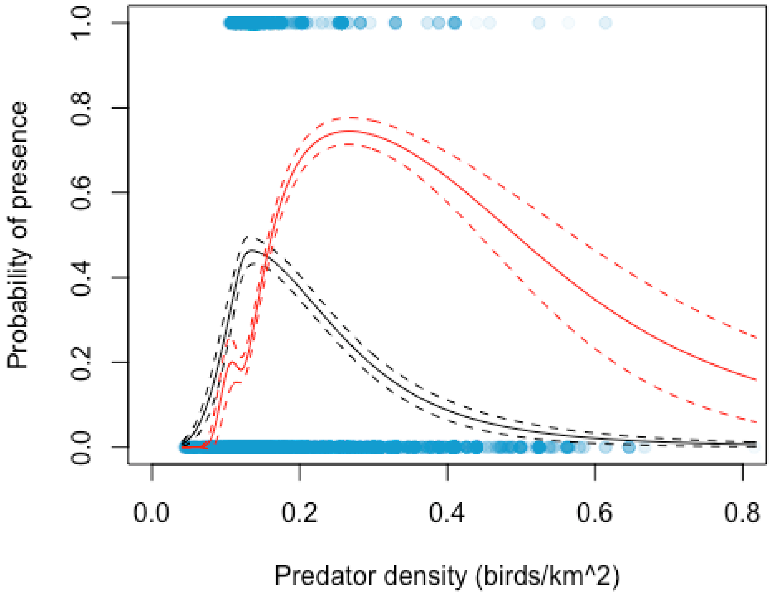


Figure 4.4. Probability of presence of European Storm-petrels at differing predator densities during daylight (black line) and night time (red line), based on a pseudo-absence analysis in which pseudo-absences were matched to presences by distance to the colony but not time of day.

## 4.5 Discussion

This is one of the first studies to investigate the environmental influences on marine habitat use of European Storm-petrels during the breeding season using tracking data (De Pascalis et al., 2021; Rotger et al., 2021; Wilkinson, 2021). The small size of European Storm-petrels (the smallest of the Atlantic seabirds) makes them an extreme case study of the influence of oceanography, weather, competition and predators on seabird marine distributions. The storm-petrels tracked from Mousa in this study used a restricted area of the shallow waters of the continental shelf, apparently avoiding areas with high parapatric intraspecific competition and predator densities.

### 4.5.1 Trip metrics

Breeding European Storm-petrels tracked from Mousa travelled to the south of the colony on trips of similar duration in all years and breeding stages. Foraging range and total distance travelled were similar in 2015–2017, but in 2018 birds remained closer to the colony and travelled shorter distances overall than in other years (Table 4.2).

Trip durations (Table 4.2; Appendix 2, Tables A2.1–A2.3) were similar to those of incubating and chick-rearing Mediterranean Storm-petrels tracked in Sardinia, Italy, (50.8 ± 11.1 and 24.4 ± 12.3 hours, respectively) although the mean foraging range and total distance travelled was greater for Mediterranean birds during incubation (297.6 ± 82.3 and 737.0 ± 217.3 km, respectively; De Pascalis et al., 2021). Incubating Mediterranean Storm-petrels tracked from Benidorm Island, Spain, completed trips of longer duration (72.72 ± 21.6 hours) and greater total distance (992.47 ± 305.55 km), and reached a greater maximum distance from the colony (358.80 ± 104.81 km; Rotger et al., 2021).

### 4.5.2 Presence vs pseudo-absence analysis

The results of the pseudo-absence analyses suggest that European Storm-petrels breeding on Mousa avoid competition with conspecifics from neighbouring colonies and avoid areas with high densities of predators, especially during daylight. Although gulls and skuas can predate on storm-petrels at night (Votier et al., 2006; Miles, 2010; pers. obs.), they are visual hunters and the risk to storm-petrels from these predators is presumably much higher during daylight.

The tracked birds remained over relatively shallow waters (compared to the pseudo-absence locations). Usage increased with increasing TRI, although the ruggedness of the seabed within the study area is generally low, with the maximum TRI values associated with presences and pseudo-absences corresponding to the ‘slightly rugged’ category of Riley et al. (1999). Bathymetric features that increase sea bed roughness can increase the vertical mixing of the water column, particularly in shallow waters (Cox et al., 2018), meaning an increase in the availability of prey for surface-feeding storm-petrels. European Storm-petrels have previously been found to preferentially and repeatedly target the relatively shallow waters over an underwater bank rather than the deeper waters of a nearby flat site, again suggesting that prey availability is enhanced in such areas, and may be a more predictable food source (Scott et al., 2013). However, the bank site studied by Scott et al. (2013) was also associated with increased chlorophyll-*a* concentration (although actual values are not given), whereas the areas used by storm-petrels in this study were characterised by lower chlorophyll concentrations than the available area in general (represented by the distribution of pseudo-absence locations). Storm-petrels from Mousa also tended to use areas with lower SST, which is associated with increased productivity. Presence was highest at intermediate wind speeds, although the effect of wind speed was small. It may be that storm-petrel flight is most energy efficient at intermediate wind speeds or that very high or very low wind speeds make it difficult for birds to forage on the sea surface using their unique sea-anchor soaring flight (Withers, 1979; Sugimoto, 1998; Alexander, 2002).

### 4.5.3 Further considerations

While the European Storm-petrels breeding on Mousa may avoid the shelf edge due to intraspecific competition from birds breeding at the much larger Faroese colonies, the marine environment is complex and the variables I used to model habitat usage will not have captured all of the environmental variation. In particular, the prevailing wind direction may mean that some areas are more accessible than others (Alerstam et al., 2019; Ventura et al., 2020), and further consideration of wind, including wind direction, could be informative (unpublished data).

The temporal and spatial resolution of the explanatory variables will also affect how representative they are of the environment experienced by the tracked birds, and therefore how accurately the model describes the relationship between storm-petrel habitat use and the environmental variables. For example, the mean monthly predator density variable I used in the models was based on observations from daytime boat-based surveys over several decades (Waggitt et al., 2020), but the actual distribution of predators likely varies at different times of day and may have changed over time.

Since the diet of storm-petrels breeding on Mousa is not currently well understood, it is unclear whether variables such as SST and chlorophyll-*a* concentration are good proxies for food availability (Grémillet et al., 2008). Molecular analysis of regurgitates and faecal samples from European Storm-petrels on Mousa in 2010 and 2014–16 identified Norway Pout *Trisopterus esmarkii* and Whiting *Merlangius merlangus* as the most common prey items in each year (F. Wood, unpublished data). Both Norway Pout and Whiting are widespread in the North Sea and have spawning grounds to the southeast and southwest of Shetland, respectively (Nash et al., 2012; González-Irusta and Wright, 2017). Molecular analysis of diet cannot determine the life stage of the prey consumed but it is assumed that storm-petrels forage on the eggs and larvae of these fish species, which appear to be abundant within the area used by breeding birds. While these spawning grounds appear to provide an abundant food source for storm-petrels breeding on Mousa, the birds may well be feeding opportunistically on the most abundant prey within a foraging area that is determined largely by other drivers, such as the density of predators and conspecifics.

It is not necessarily possible to draw general conclusions about European Storm-petrel habitat requirements from a single-colony study, and tracking from additional Atlantic colonies is crucial for improving our understanding of how the species as a whole uses the marine environment. The breeding status and provenance of the storm-petrels observed at the continental shelf edge to the west of Shetland remains unknown and tracking birds from colonies closer to the shelf edge would be very informative.

In this chapter I investigated the broad-scale marine distribution of GPS-tracked storm-petrels by modelling all observed locations in relation to a set of randomly generated ‘pseudo-absences’. These locations will include a variety of behaviours, including transit, foraging and resting on the water, and we would expect food availability to have a greater influence on foraging locations than on the overall marine distribution of storm-petrels. I examine finer scale habitat use and the drivers of foraging distributions in Chapter 5.

# 5 Spatial and temporal variation in behaviours of breeding European Storm-petrels at sea

## 5.1 Abstract

Knowledge of the spatio-temporal dynamics of the behaviour of seabirds at sea can improve our understanding of the threats that they may face in the marine environment. Advances in tracking technologies and statistical methods have enabled behaviours to be determined from seabird locational data, even for the smallest of seabirds. I applied hidden Markov models (HMMs) to GPS tracking data from European Storm-petrels breeding on Mousa, Shetland, to provide an insight into their at-sea behaviour during the chick-rearing period. The HMMs identified two distinct behavioural states, which I interpret to represent foraging and transit behaviour. Foraging behaviour occurred mainly during the day, and transit peaked around dusk and dawn as birds departed from and returned to the colony. There was limited overlap in core foraging areas between years, suggesting that storm-petrels are not reliant on particular static environmental features to bring food items to the sea surface. A binary generalised additive mixed model (GAMM) of foraging *versus* transit behaviour identified conspecific competition (but not predator density or proxies of prey availability) as a key driver of foraging distribution. It is clear from this study that even the relatively low temporal resolution data provided by tracking devices currently available for birds as small as European Storm-petrels can provide important insights into their at-sea behaviour and habitat use. Tracking of European Storm-petrels from additional colonies in the northeast Atlantic will enable us to draw more general conclusions about the habitat requirements of this species.

## 5.2 Introduction

Information on the broad-scale movements and habitat use of seabirds at sea (as examined in Chapter 4) is useful for identifying important marine areas for different species, and understanding how changes to the marine environment may impact seabirds, but this understanding can be greatly enhanced by knowledge of a species' behaviour at sea. Understanding the spatio-temporal dynamics of seabird behaviour, such as where and when they are foraging, can help us better assess the risks posed by pressures such as climate change, fisheries, pollution and offshore energy extraction (Camphuysen et al., 2012; Granadeiro et al., 2018; Cleasby et al., 2022; De Pascalis et al., 2022).

The combination of advances in both tracking technologies and statistical modelling techniques has enabled some categories of seabird behaviour to be inferred from locational data (Wakefield et al., 2009; Dean et al., 2013). Data from additional devices such as time-depth recorders and accelerometers can provide further information for identifying behaviour (Dean et al., 2013; Sánchez et al., 2018), but these are not yet small enough to be deployed on very small seabirds such as storm-petrels. However, basic two-dimensional movement trajectories, such as those acquired by GPS tracking, can be sufficient for identifying different categories of seabird behaviours such as foraging, transit and resting, leading to advances in our understanding of at-sea behaviour for even the smallest of seabirds (Zhang et al., 2019; De Pascalis et al., 2021; Collins et al., 2022).

GPS tracking devices provide a time series of location data from which several metrics of animal movement can be derived. Apparent movement speed is the Euclidean distance between location fixes divided by the time between fixes. This is rarely a bird's actual movement speed, however, as a) it assumes that travel between the fixes is in a straight line, and b) the period between fixes may include periods when the bird is not moving at all (e.g. resting on the sea surface). Turning angle is the difference in compass bearing between the straight-line movement before a location fix (i.e. from $t_{-1}$ to $t_0$) and the straight-line movement after that fix (i.e. from $t_0$ to $t_{+1}$). Turning angle concentration represents the consistency in turning angle. Thus, a bird flying consistently in a straight line will have a low turning angle and a high turning angle concentration, but a bird following a tortuous path will have a high turning angle and a low turning angle concentration. The apparent movement speed and turning angle will depend on the temporal scale of location sampling, because a lower fix rate averages speed and turning angle across a longer period.

Various classification methods are available to infer categories of behaviour from these primary metrics (see Bennison et al., 2018). First passage time analysis uses an estimate of the time taken for an animal to cross a circle of a given radius as a measure of the time spent in an area (Fauchald and Tveraa, 2003). Expectation-Maximisation Binary Clustering (EMbC) is an unsupervised multivariate state-space framework that clusters fixes into four categories based on binary discretisation of input parameters (Garriga et al., 2016). Hidden Markov models (HMMs) are time-series models that assume observations (i.e. animal relocations) are determined by a series of unobservable discrete states (i.e. behaviours), and can be used to determine the most likely sequence of these hidden states (Langrock et al., 2012). HMMs have been shown to perform particularly well at identifying seabird foraging behaviour (Bennison et al., 2018).

All of these methods tend to classify seabird at-sea behaviour into two or more states. **Transit or commuting behaviour** is characterised by high movement speeds and low turning angles (i.e. fast, direct movement). **Resting on the water** tends to be represented by low movement speeds and low or intermediate turning angles, as birds drift on the current. **Foraging behaviour** is generally characterised by slower, more tortuous movements (i.e. low speeds and high turning angles) as birds engage in area-restricted search (ARS), spending more time in areas where they are likely to encounter prey. ARS behaviour can occur at different spatial scales as, for example, seabirds may first search over a large area for a suitable prey patch, and then remain within this smaller prey patch while actively feeding.

The poor detectability of storm-petrels at sea, due to their small size and nocturnal activity, means that we know relatively little about their at-sea behaviour and foraging habitat. Much of our knowledge of European Storm-petrel foraging behaviour comes from a small number of studies of their diet, based on the identification of prey in the regurgitates of birds caught at colonies or on migration (e.g. D’Elbée and Hémery, 1998; Thomas et al., 2006; Albores-Barajas et al., 2011) but here, I use the GPS tracking data collected from birds on Mousa, Shetland, to improve our understanding of the at-sea behaviour of this species.

Specifically, I aimed to identify (1) the temporal distribution of at-sea behaviours, (2) the spatial distribution of these behaviours, (3) the biotic and abiotic environmental drivers of foraging distributions, and (4) between-year variation in the spatial/temporal distributions of foraging behaviour. As in Chapter 4, I hypothesized that the foraging locations of European Storm-petrels would be influenced by predator density as well as by conspecific competition and prey availability, which have been shown to be drivers of foraging distributions in several seabird species. However, we might expect foraging locations to be driven by prey availability to a greater degree than the locations of all behaviours combined (i.e. the locations used in the analysis in Chapter 4).

## 5.3 Methods

### 5.3.1 Behaviour classification

I used the complete trips identified in Chapter 4 with fix rates of 30 minutes (n = 20 trips) and 15 minutes (n = 8 trips) for the behaviour analysis. I excluded trips with a 60-minute fix rate (n = 10 trips) because their lower resolution reduces the ability to categorise behaviours, which we might expect to last for much shorter periods than the 60-minute resolution. Behavioural classification using HMMs requires movement trajectories to have a regular time interval between fixes, meaning that tracking data must be regularised and interpolated or subset. Adjusting tracks with a 20-minute fix rate to fit a 30-minute interval would have resulted in the majority of locations being estimated, rather than positions actually recorded by the tag. For this reason, I also excluded trips with a 20-minute fix rate (n = 4 trips) from the behaviour analysis. This left only two trips at the incubation stage, from only one bird, so I retained only trips made by chick-rearing birds.

Occasionally GPS data have missing locations, where the tag has failed to record a fix. Where more than one missing location occurred in a row, I split the track into segments to avoid interpolating over extended periods. I then interpolated and regularised data within each segment to 30-minute intervals using a correlated random walk, performed by the 'crawlWrap' function of the momentuHMM package (version 1.5.2; McClintock and Michelot, 2018). This meant that tracks with a 15-minute fix rate were thinned to include only the fixes at 30-minute intervals. While this thinning resulted in the removal of some data and a reduction in the resolution of trips with a 15-minute fix rate, it allowed me to include data for all trips in the same HMM, thereby increasing the amount of data that the classification was based on.

I then used the 'fitHMM' function of the momentuHMM package to fit HMMs to the regularised data. HMMs used the step length (modelled with a gamma distribution) and turning angle (modelled with a wrapped Cauchy distribution) between successive locations to estimate the distributions of step length and turning angle for different behavioural states. The most likely sequence of behavioural states was then estimated using the Viterbi algorithm (Zucchini et al., 2016). To avoid circularity with the subsequent GAMM analysis of environmental influences on behaviour, I did not include any additional covariates in the HMMs. To select the most appropriate starting parameter values for the models, I compared the log-likelihood of a series of 100 models that each used starting values drawn from a realistic range.

To decide on the most suitable number of behavioural states for the final model, I fitted a series of HMMs with between one and four states, all of which could be considered a biologically reasonable number of at-sea movement behaviours for European Storm-petrels (e.g. commuting, large-scale ARS, fine-scale ARS or feeding, and resting). The log-likelihood increased for every additional state, but to avoid over-fitting I selected the model that resulted in the greatest increase in log-likelihood, following Pohle et al. (2017).

### 5.3.2 Temporal distribution of behaviours

To examine short-term (diel) variation in behaviour, I calculated the proportion of relocations classified as each behavioural state that occurred during each hour of the 24-hour cycle. To examine longer-term variations in behaviour, I tested for differences in the proportion of relocations classified as foraging between years and breeding stages using a generalised linear mixed-effects model (GLMM) built with the ‘glmer’ function of the lme4 package (version 1.1-26; Bates et al., 2015), with year and breeding stage (brooding *versus* post-brooding) as additive fixed effects, and individual ID as a random effect to control for differences between individuals.

### 5.3.3 Spatial distribution of behaviours

I pooled the data for all trips and used the ‘kernelUD’ function of the adehabitatHR package (version 0.4.19; Calenge, 2006) to estimate the 50% and 95% utilisation distributions (UDs) for all locations together, and individually for each of the resulting behavioural categories. I specified a 1 x 1 km cell size and used the *ad hoc* method, as described by Kie (2013), to choose a smoothing parameter (h-value) that avoided over-smoothing, while retaining a largely contiguous 95% UD. Note that this method is different from the ‘href’ method of selecting a smoothing parameter, which is sometimes also referred to as the ‘*ad hoc’* method (see Appendix 3, Figure A3.1). I also estimated UDs for foraging relocations pooled within years and calculated Bhattacharya’s affinity (BA) using the ‘kerneloverlaphr’ function of the adehabitatHR package (Calenge, 2006) to estimate the overlap in foraging UDs between years (Fieberg and Kochanny, 2005).

### 5.3.4 Drivers of foraging distribution

To investigate the drivers of foraging habitat selection I built binomial GAMMs using a binary response variable of foraging (1) or transit (0), based on the HMM classification for each relocation. Since the ‘gamm’ function of the mgcv package is unsuitable for binomial data I used the ‘gam’ function and specified random effects using the ‘bs = “re”’ argument (Wood, 2011). I used Movebank’s Env-DATA system (Dodge et al., 2013) to annotate each location with the following environmental variables: (1) chlorophyll-*a* concentration, (2) sea surface temperature (both of these variables had an 8 day, 4 km resolution; MODIS Ocean/Aqua Mapped OceanColor, https://oceandata.sci.gsfc.nasa.gov), (3) wind u (east-west or zonal) and v (north-south or meridional) components at 10 m above sea level (with a resolution of 6 h and 0.75°; ECMWF Global Atmospheric Reanalysis, http://apps.ecmwf.int/datasets/data/interim_full_daily/?levtype=sfc), and (4) distance to the coast (0.04° resolution; NASA, https://oceancolor.gsfc.nasa.gov/docs/distfromcoast/). Gaps in chlorophyll-*a* concentration and sea surface temperature were interpolated using an inverse-distance-weighted method, and all other variables were interpolated using bilinear interpolation (Dodge et al., 2013). I calculated wind speed from the wind u and v components using the formula: wind speed = $\sqrt{u^2 + v^2}$. I extracted seabed depth and slope from the GEBCO elevation raster (15 arc-second resolution; GEBCO Compilation Group, 2021) using the raster package (version 3.4-5; Hijmans, 2020), and calculated the terrain ruggedness index (TRI) using the spatialEco package (version 1.3-7; Evans, 2021). The initial model also included distance to the colony and time of day (as decimal hour).

To investigate the influence of predators on foraging locations I used the sum of estimated Great Skua, Lesser Black-backed Gull and Herring Gull densities (individuals per km$^2$) for the relevant month (July or August) from Waggitt et al. (2020) as a ‘predators’ variable. Since predation risk is more likely to influence storm-petrels during daylight, I created a binary daylight variable (day/night) using dawn and dusk times for each location, calculated using the suncalc package (version 0.5.0; Thieurmel and Elmarhraoui, 2019) and included the two-way interactions of predator density x daylight in the initial model. I used the same intraspecific competition data as in Chapter 4.

To improve the spread of the environmental data to facilitate modelling their effects as independent variables, I log transformed chlorophyll-*a* concentration, predator density and competition, square root transformed distance to the coast and distance to the colony, and double square root transformed slope and TRI.

I checked for correlation between covariates using the ‘cor’ function of the stats package (R Core Team, 2019) and checked for concurvity between the smoothed terms in the GAMMs using the ‘concurvity’ function of mgcv (Wood, 2011).

I fitted all covariates as smooth terms. To avoid overfitting, I modelled most smoothers using cubic regression splines with shrinkage, and enabled terms to be penalised out of the model completely (Wood, 2011). Based on the nature of the hypothesised relationships I set the maximum number of knots to five to prevent overfitting and tried increasing this where model checks suggested it may be too low. I used a cubic cyclic spline for the decimal hour covariate, and allowed the model estimator to choose the appropriate number of knots for this smoother by cross-validation. To account for spatial autocorrelation I also included a two-dimensional spatial smoother of the coordinates for each point using thin plate regression splines, and allowed the number of knots to be selected by cross-validation (Cleasby et al., 2015). For this “isotropic” spatial smoother, I used coordinates in the Universal Transverse Mercator (UTM) projection rather than latitude and longitude, to avoid distortion of the distances between points.

I built a full model and used backwards stepwise selection to remove terms that had excessive concurvity values (‘worst concurvity’ > 0.8). I used K-fold cross-validation to select the most appropriate terms to remove from the model and assess model performance (Aarts et al., 2008; Clay et al., 2017; Dehnhard et al., 2020). To do this I randomly allocated data points into five ‘folds’ and trained the model on five datasets, each with one fold withheld, before testing the model on the withheld fold. I used the area under the receiver operator characteristic curve (AUC) to assess model performance and checked for significant differences between model AUCs using the pROC package (version 1.18.0; Robin *et al.*, 2011). Cross-validation is a conservative method of model selection but is often used with tracking datasets that tend to have high levels of temporal and spatial autocorrelation, as it is less prone to over-parametising models than information criterion approaches such as AIC (Aarts et al., 2008).

## 5.4 Results

I used a total of 26 trips (15 during the nestling brooding stage and 11 during the post-brood stage) and 1,219 relocations in the analysis. Of these 1,219 relocations, 318 (26%) were regularised or interpolated in some way, with the majority of these being minor adjustments due to inconsistency in the timing of the fix (i.e. the GPS tag recorded a fix slightly later than scheduled).

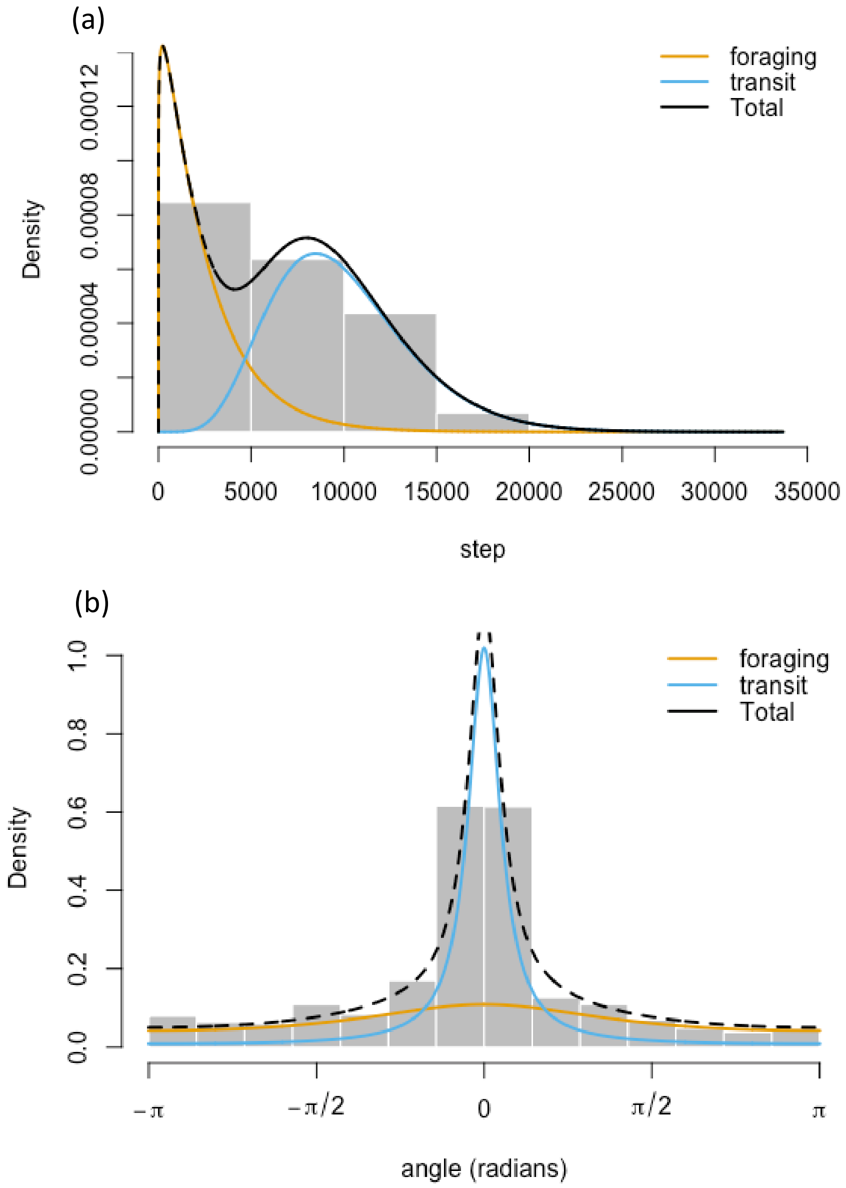


Figure 5.1. Probability distributions of (a) step length and (b) turning angle for the 'foraging' and 'transit' behavioural states, estimated by a two-state hidden Markov model (HMM) based on GPS data from 26 trips by chick-rearing European Storm-petrels breeding on Mousa, Shetland.

### 5.4.1 Behavioural classification

The greatest increase in log-likelihood was between the one and two state HMMs, so I used the two-state model for behaviour classification. State 1 was characterised by slow movement speeds (1.38 ± 1.32 (SD) m/s) and a low turning angle concentration (rho = 0.23, i.e. low consistency of direction) and I interpreted this behavioural state as predominantly containing foraging behaviour, although it also likely includes periods when birds were resting on the water (Figure 5.1). State 2 was characterised by faster speeds (5.49 ± 2.07 m/s) and a higher turning angle concentration (rho = 0.83; i.e. more directed movement), which I interpreted as primarily transiting/commuting behaviour (Figure 5.1). The mean trip speed was 3.65 ± 1.24 m/s. The maximum speed between any two locations was 18.84 m/s, and the mean maximum speed per trip was 9.42 ± 2.80 m/s. Table 5.1 gives a summary of mean and maximum speeds per trip for each breeding stage and year.

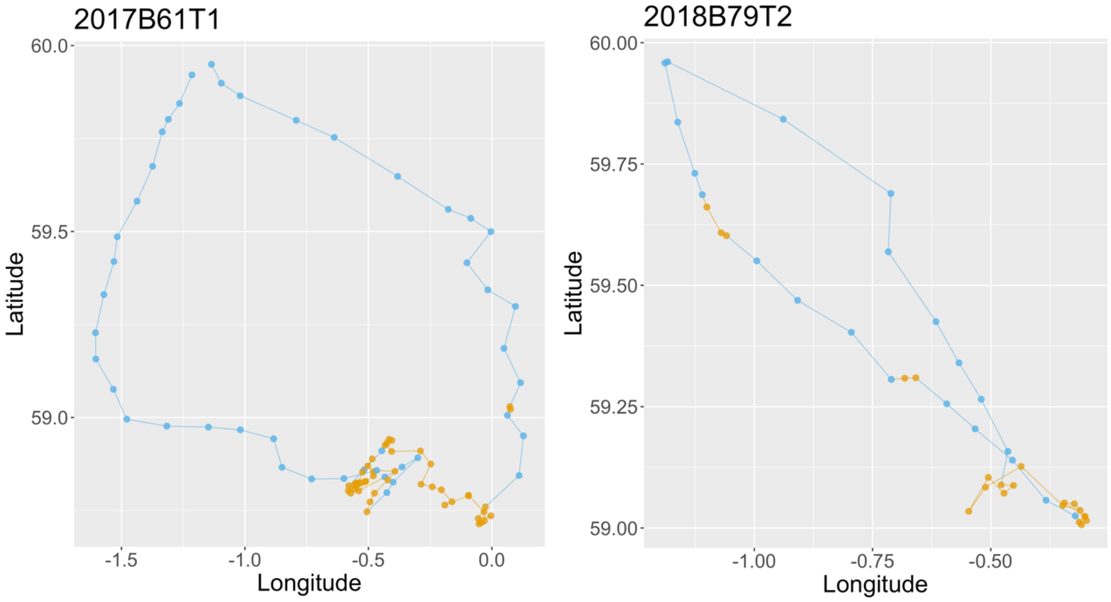


Figure 5.2. Examples of behavioural classification of European Storm-petrel foraging tracks. Blue indicates State 1 (‘transit’) and orange indicates State 2 (‘foraging’).

Figure 5.2 shows two examples of tracks with locations classified by behavioural state, and plots of all tracks are in Appendix 3 (Figure A3.2). The proportion of locations classified as State 2 (foraging-type behaviour) for trips in each breeding stage in each year is given in Table 5.1. The mean proportion of relocations per trip that were classified as foraging was 0.43 ± 0.19 (SD), and the GLMM to explain behavioural state, with breeding stage and year as independent variables, suggested that the proportion of relocations classified as foraging did not differ significantly between the brooding (0.47 ± 0.19) and post-brooding (0.37 ± 0.19) stages ($\mathcal{X}_1^2$ = 0.38, p = 0.539). The same GLMM identified a significant difference in the proportion of foraging relocations per trip between years ($\mathcal{X}_3^2$ = 44.54, p < 0.001), with birds in 2015 apparently spending less time foraging (0.14 ± 0.07) and birds tracked in 2018 apparently spending more time foraging (0.53 ± 0.16) than birds in 2016 (0.40 ± 0.15) or 2017 (0.36 ± 0.17).

Table 5.1. Number of trips and locations for each year and breeding stage used to classify behaviour in a hidden Markov model of European Storm-petrel movements at sea. The proportion of relocations per trip classified as State 2 (‘foraging’) and the mean and maximum speed per trip are also given.

| Year | Breeding stage | No. of trips | No. of relocations | Proportion foraging ± SD | Mean speed ± SD (m/s) | Max speed ± SD (m/s) |
|---|---|---|---|---|---|---|
| 2015 | Brooding | 1 | 44 | 0.11 | 6.48 | 10.70 |
| | Post-brooding | 2 | 109 | 0.15 ± 0.10 | 4.55 ± 0.94 | 8.79 ± 1.10 |
| 2016 | Brooding | 2 | 100 | 0.45 ± 0.09 | 2.31 ± 1.54 | 4.66 ± 3.72 |
| | Post-brooding | 4 | 181 | 0.37 ± 0.17 | 4.64 ± 0.50 | 12.60 ± 4.54 |
| 2017 | Brooding | 3 | 133 | 0.32 ± 0.18 | 4.03 ± 0.97 | 8.70 ± 0.56 |
| | Post-brooding | 1 | 90 | 0.50 | 3.23 | 10.87 |
| 2018 | Brooding | 9 | 397 | 0.57 ± 0.13 | 3.09 ± 0.90 | 9.05 ± 1.63 |
| | Post-brooding | 4 | 165 | 0.44 ± 0.21 | 3.30 ± 1.29 | 9.64 ± 1.23 |

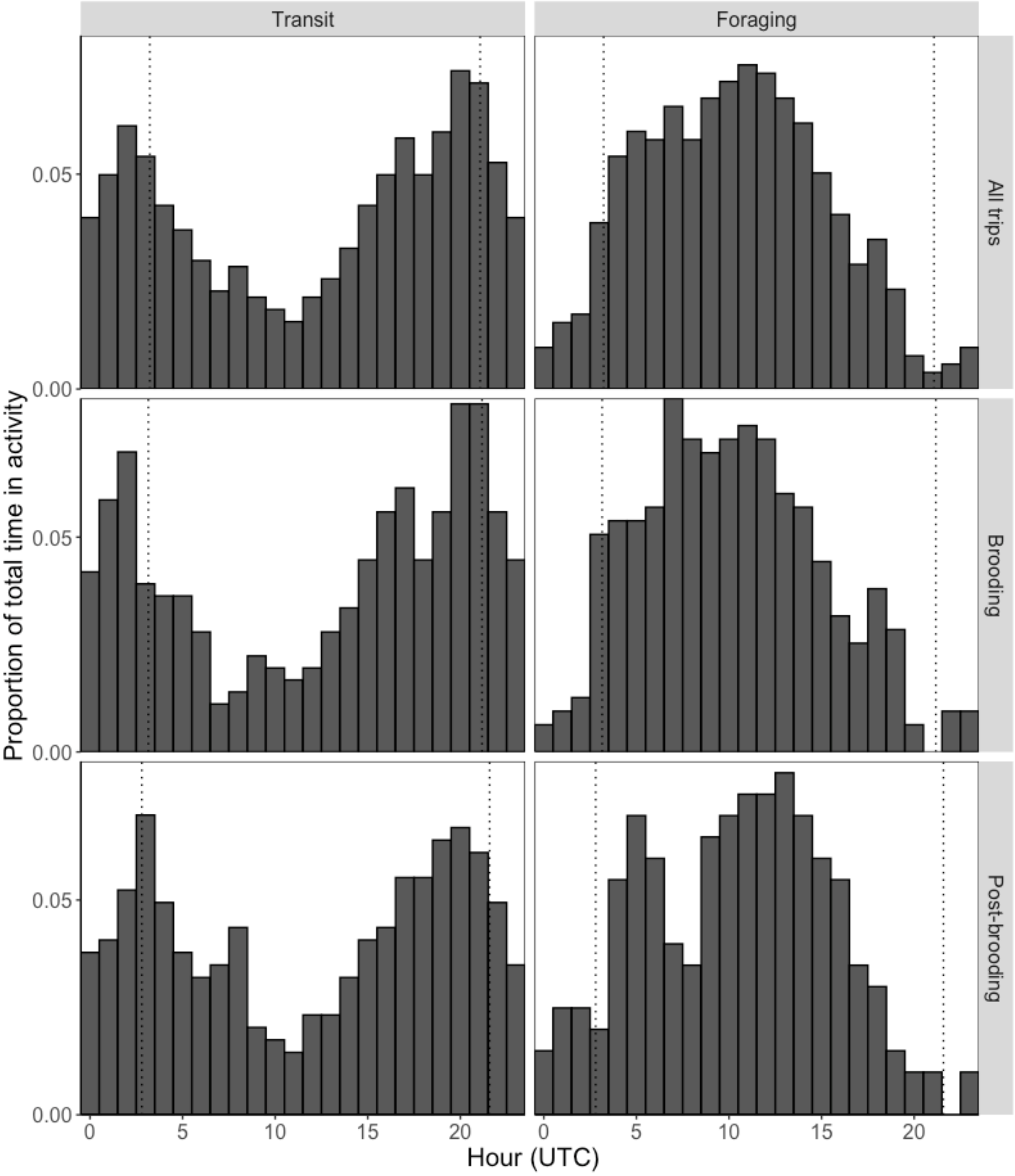


Figure 5.3. Proportion of all transit and foraging behavioural states occurring in each hourly period of the 24-hr cycle for all trips combined, and for trips split by breeding stage. Behavioural states were estimated by a two-state hidden Markov model based on GPS data for 15 trips by brooding and 11 trips by post-brooding European Storm-petrels breeding on Mousa, Shetland. Dotted vertical lines show the mean time of dawn and dusk for locations in each breeding stage.

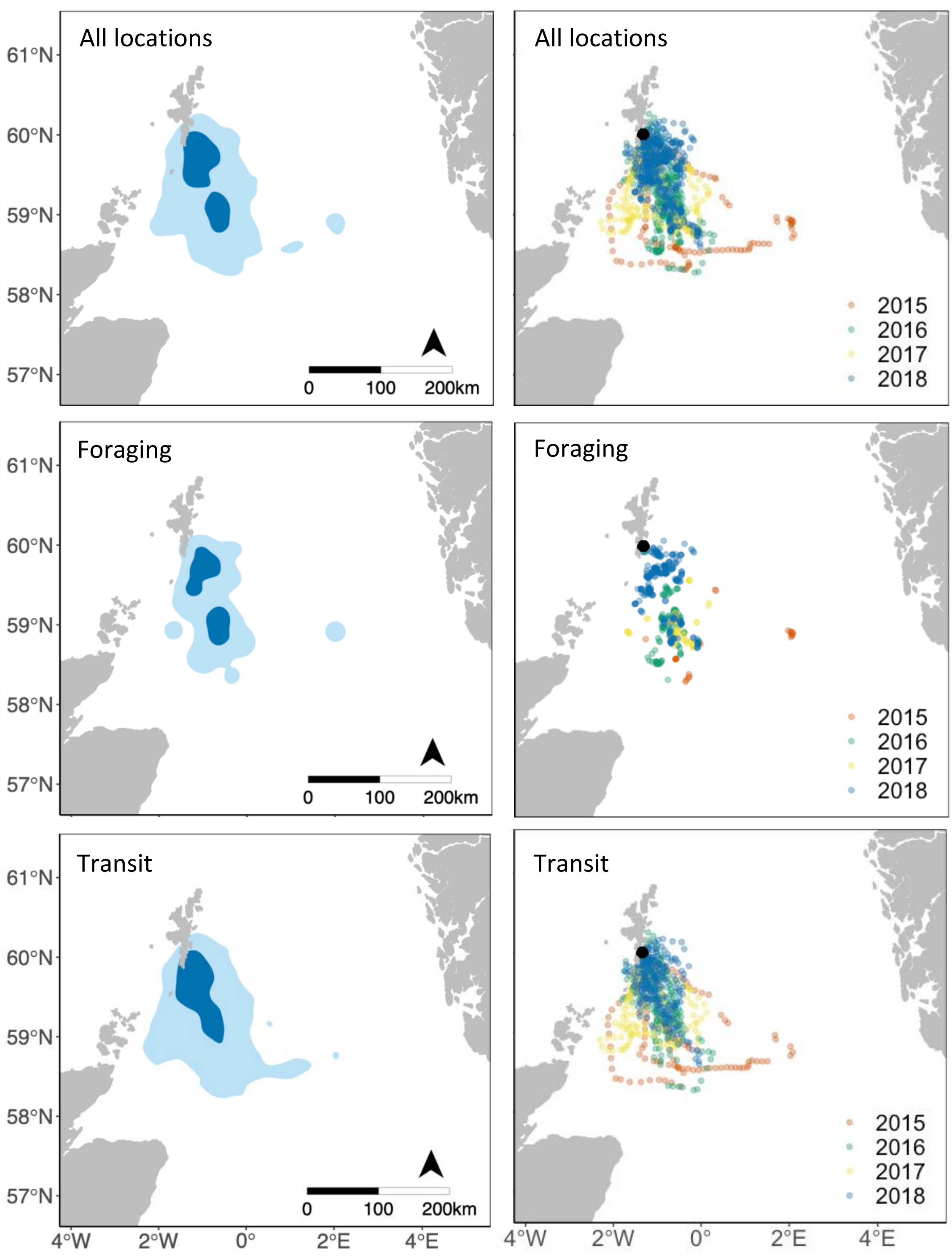


Figure 5.4. 50% (dark blue) and 95% (light blue) utilisation distributions (left) and data points coloured by year (right) for all locations and separate foraging and transit behaviours for European Storm-petrels tracked from Mousa, Shetland (black dot). Behavioural states were estimated by a two-state hidden Markov model based on GPS tracking data.

### 5.4.2 Temporal distribution of behaviours

Peaks in locations classed as State 1 (transiting behaviour) occurred around dawn and dusk, when birds depart from and return to the colony. State 2 (foraging) occurred throughout the daylight hours but less during the night. This pattern was seen across all chick-rearing birds, as well as in the individual brooding and post-brooding stages (Figure 5.3).

### 5.4.3 Spatial distribution of behaviours

I selected an h-value of 9.4 km as the best compromise between over- and under-smoothing UDs, based on the *ad hoc* method (see Methods section). Graphical outputs from the various h-values tested using the *ad hoc* method are in Appendix 3 (Figure A3.1). The 50% kernel density contour for all trips combined identified two core foraging areas – one near the colony and one further to the southeast (Figure 5.4). The separate kernel density contours for each year show clearly that birds tracked in 2018 foraged closer to the colony than birds tracked in other years (Figure 5.5). There was limited overlap in foraging areas between years, and in 2015 and 2018 there was no overlap in the core foraging areas with any other year (BA estimate = 0.00; Table 5.2).

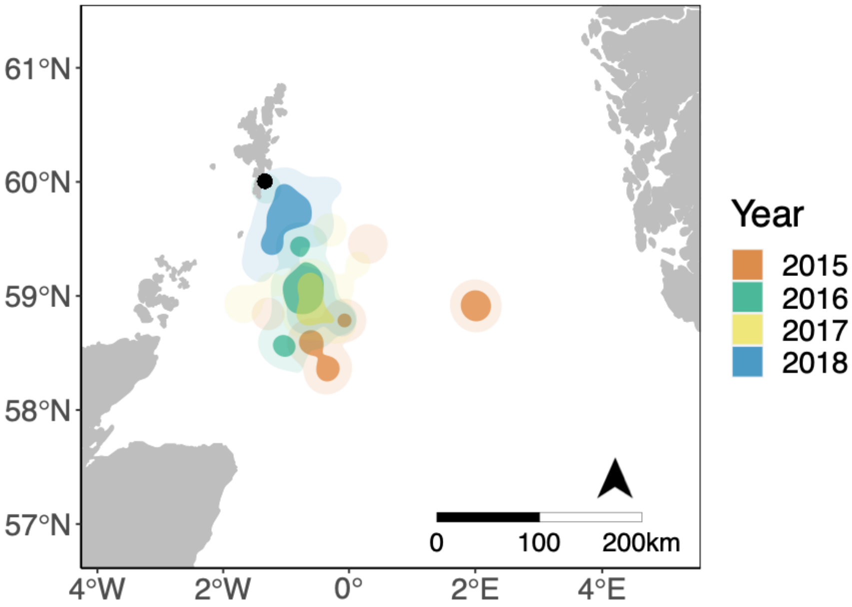


Figure 5.5. 50% (dark) and 95% (light) foraging utilisation distributions for chick-rearing European Storm-petrels tracked from Mousa, Shetland (black dot) in 2015–2018.

Table 5.2. Bhattacharya's affinity (BA) estimates of utilisation distribution (UD) overlap for core (50%) and general (95%) foraging areas for breeding European Storm-petrels tracked from Mousa, Shetland, in 2015–2018. BA can vary from 0 to 0.50 for 50% Uds and from 0 to 0.95 for 95% Uds.

| | **50%** | | | | **95%** | | | |
|---|---|---|---|---|---|---|---|---|
| **Year** | **2015** | **2016** | **2017** | **2018** | **2015** | **2016** | **2017** | **2018** |
| **2015** | 0.50 | 0.00 | 0.00 | 0.00 | 0.95 | 0.18 | 0.18 | 0.07 |
| **2016** | 0.00 | 0.50 | 0.27 | 0.00 | 0.18 | 0.95 | 0.66 | 0.39 |
| **2017** | 0.00 | 0.27 | 0.50 | 0.00 | 0.18 | 0.66 | 0.95 | 0.35 |
| **2018** | 0.00 | 0.00 | 0.00 | 0.50 | 0.07 | 0.39 | 0.35 | 0.95 |

### 5.4.4 Drivers of foraging distribution

Distance to the coast and distance to the colony had high concurvity with each other and with several of the environmental covariates, and so I removed them both from the model. Removing distance to the coast resulted in a marginally significant improvement to the model AUC (change in AUC = 0.0004, Z = 2.04, p-value = 0.041) and removing distance to the colony had a marginally non-significant effect on AUC (change in AUC = -0.001, Z = -1.941, p-value = 0.052). The inclusion of the spatial smoother allowed the model to still account for spatial variation in foraging behaviour (Figure 5.7). Slope and TRI had high concurvity with each other but both were automatically penalised out of the models during fitting, whether included individually or together. The binary daylight term and its interaction with predator density were not significant and so I removed them from the model to avoid overlap with the time of day term.

Depth, TRI, chlorophyll-*a* concentration and sea surface temperature were all penalised out of the final model during fitting. Predator density was retained in the model but was not a significant effect. The fixed effects of competition, wind speed and time of day were all significant. The spatial smoother and the random effects of year and trip ID were also significant and retained in the final model (Table 5.3). The final model had an AUC of 0.88, suggesting good predictive performance.

The probability of behaviour being classified as 'foraging' decreased with increasing inter-colony intraspecific competition and increased with increasing wind speed, within the range of wind speeds experienced by the tracked birds (Figure 5.6). The probability of foraging was also higher in the morning, with a peak at around 10:00 UTC (Figure 5.6), as also indicated in the raw data by the time of day plot (Figure 5.3).

Table 5.3. Parameter estimates for the final binomial GAMM to explain European Storm-petrel foraging locations vs non-foraging locations, based on data from Mousa, Shetland.

| **Parameter** | **Estimate** | **Standard Error** | **Z value** | **p-value** |
|---|---|---|---|---|
| Intercept | -1.542 | 1.187 | -1.3 | 0.194 |
| **Smooth terms** | **edf** | **Ref. df** | **$\mathcal{X}^2$ value** | **p-value** |
| Predator density | 4.720e-01 | 4 | 1.891 | 0.141 |
| Competition | 1.598e+00 | 4 | 9.714 | < 0.001 |
| Depth | 5.690e-05 | 4 | 0.000 | 0.803 |
| TRI | 1.072e-04 | 4 | 0.000 | 0.469 |
| Chlorophyll-*a* | 8.048e-05 | 4 | 0.000 | 0.519 |
| SST | 5.772e-05 | 4 | 0.000 | 0.693 |
| Wind speed | 3.493e+00 | 4 | 795.524 | < 0.001 |
| Time of day | 5.291e+00 | 8 | 168.282 | < 0.001 |
| Spatial smoother | 1.595e+01 | 29 | 359.218 | < 0.001 |
| Year (random effect) | 2.658e+00 | 3 | 487.091 | 0.003 |
| Trip ID (random effect) | 2.024e+01 | 25 | 182.946 | < 0.001 |

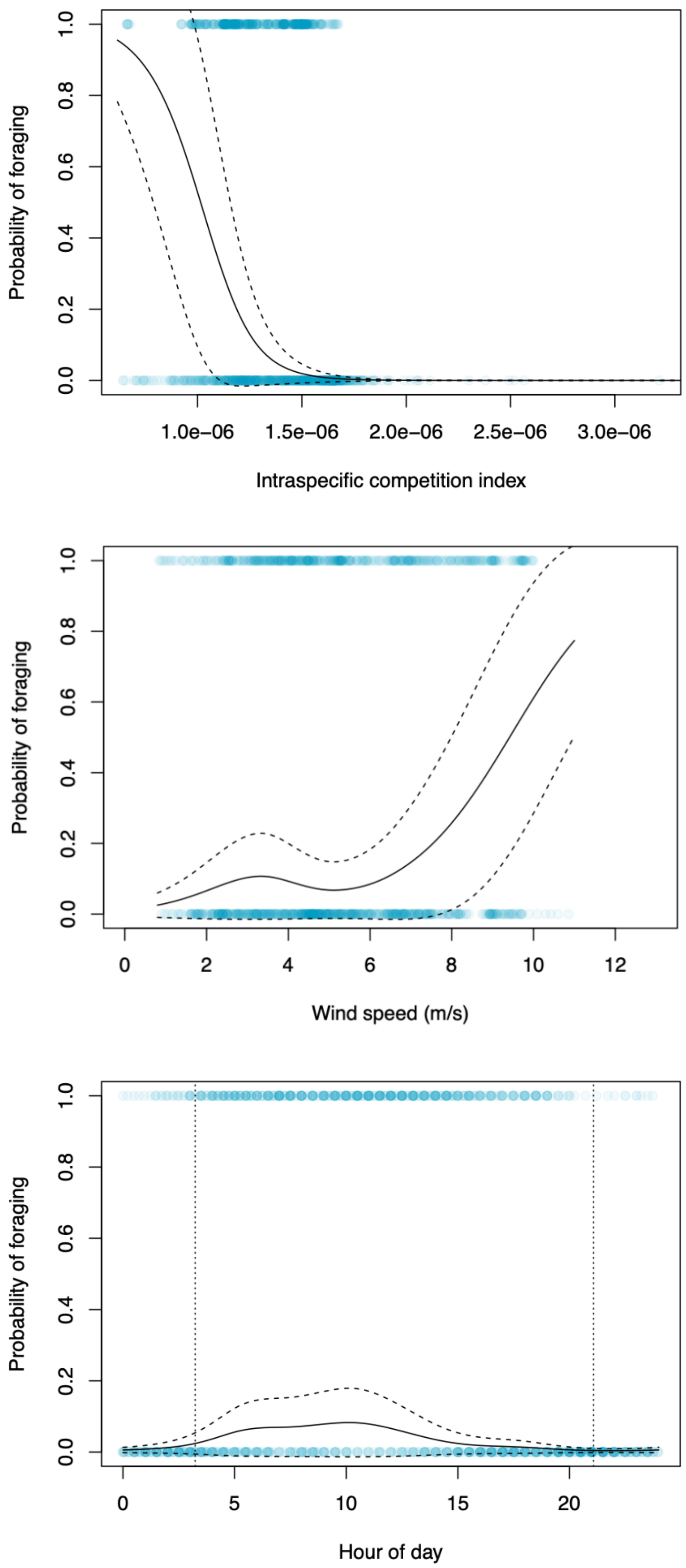


Figure 5.6. Prediction plots for significant fixed effects from the final GAMM of foraging behaviour for European Storm-petrels tracked from Mousa, Shetland. The vertical dotted lines in the hour of day plot show the mean times of dawn and dusk for all locations.

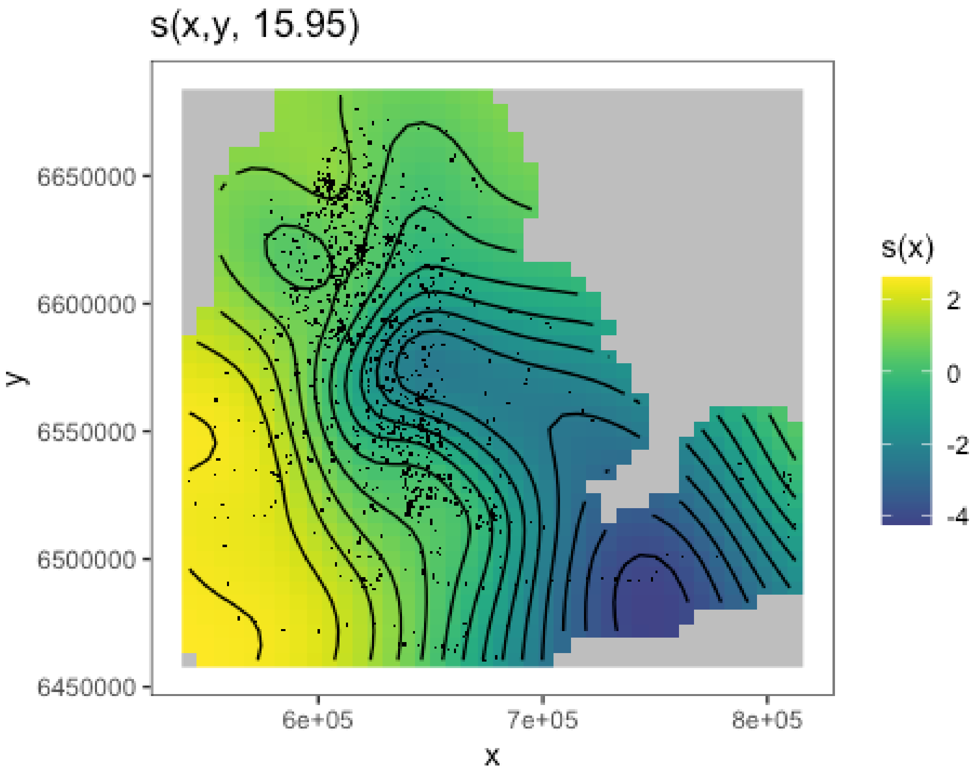


Figure 5.7. Two-dimensional spatial smoother from the final GAMM for foraging behaviour for European Storm-petrels tracked from Mousa, Shetland. Coordinates are projected in the Universal Transverse Mercator projection to avoid distortion of the distances between points. Plotted using the mgcViz package (version 0.1.9; Fasiolo et al., 2018).

## 5.5 Discussion

Tracking devices that are small enough for European Storm-petrels to carry are still relatively new, and this study includes some of the first GPS tracking data for the species (Bolton, 2020; De Pascalis et al., 2021; Rotger et al., 2021; Wilkinson, 2021). Despite the relatively coarse temporal resolution of the GPS tags compared to those available for larger birds, this analysis has shown that the resulting data can still reveal useful and previously unknown information about the movement and behaviour of these tiny seabirds at sea.

### 5.5.1 Behavioural classification

Although the two-state HMM was most appropriate for the data, it is important to acknowledge that the at-sea behaviour of storm-petrels is unlikely to be cleanly divided into two distinct states, and the states identified by the HMM are unlikely to represent transit and foraging behaviours exactly. Storm-petrels spend some of their time at sea resting on the water (Ricklefs et al., 1986; Aguado-Giménez et al., 2016). Resting on the water and drifting with the current will result in short step lengths and low or intermediate turning angles (e.g. Dean et al., 2013), so this behaviour will likely have been included in State 2 (which I termed 'foraging') by the HMM. Visual assessment of the tracking data, particularly for those trips recorded at a higher resolution (i.e. with a 15-minute fix-rate), reveals some curvilinear series of points that appear to indicate birds resting on the water (see Appendix 3, Figure A3.2). These series tend to occur during daylight within sections of the tracks that are likely to represent foraging behaviour (intermediate step lengths and high turning angles), so the inclusion of resting behaviour in State 2 is unlikely to have substantially altered the foraging Uds or the characterisation of foraging areas in the GAMM.

It is also important to note that the relatively coarse resolution of the tracking data may limit the ability of the HMM to identify all behaviours or all bouts of behaviours, which may last for very brief periods, far shorter in duration than the 30-minute interval between the GPS location fixes. In addition, the HMM required that data were interpolated and regularised, and this could bias the locations or trajectories that are used in the model, resulting in inaccurate behavioural classifications. To minimise this effect, I split trips into segments so that no more than one missing point was interpolated in a row. As a further model check I also carried out behavioural classification using the EmbC package (Garriga et al., 2019), which performs binary clustering of step length and turning angle distributions without requiring data to be interpolated or regularised (Garriga et al., 2016). The EmbC analysis (not shown) resulted in a very similar output to the HMM, suggesting that interpolation of the data did not meaningfully affect the behavioural classification. Although EmbC does not require interpolation, it can only split movement parameters in a binary manner and always results in four different behavioural clusters. I opted for the HMM as the primary analysis because it gave me the ability to test for the most appropriate number of behaviours given the data, and has been shown to work well for identifying seabird foraging behaviour (Bennison et al., 2018).

In addition, while the HMM results in relocations being classified as distinct states, that does not mean that the state (or behaviour) occurred at the exact location of the GPS fix, but that it likely occurred at some time during the subsequent fix interval (i.e. within the following 30-minute period, in this case).

The apparent movement speeds of the storm-petrels in this study (mean = 3.65 ± 1.24 (SD) m/s; Table 5.1) were similar to those recorded from colonies in Ireland, where the mean speed was 4.05 m/s (Wilkinson, 2021). The mean speed of Mediterranean Storm-petrels tracked from Sardinia and Benidorm during incubation was also similar, at 4.0 m/s and 4.18 m/s, respectively (De Pascalis et al., 2021; Rotger et al., 2021), but those tracked from Sardinia during chick-rearing had a slightly lower mean speed (2.63 m/s; De Pascalis et al., 2021). The maximum speeds reached by storm-petrels in this study (mean = 9.42 ± 2.80 (SD) m/s; Table 5.1) were also similar to those recorded by Wilkinson (2021) and De Pascalis et al. (2021), which were 11.18 m/s and 12.5 m/s, respectively. These maximum speeds are almost certainly wind-assisted.

### 5.5.2 Temporal distribution of behaviours

Although European Storm-petrels are known to forage nocturnally in some contexts (e.g. D’Elbée and Hémery, 1998; Thomas et al., 2006), in this study almost all behaviour identified as foraging occurred during daylight. The apparent lack of nocturnal foraging in the tracked birds may be a result of their need to depart from and return to the colony under darkness, which lasts for only a short period during the breeding season in Shetland. Given that many foraging trips during chick-rearing last around 24 hours (see Chapter 4), this leaves little opportunity for birds to forage at night, unless they do so just after leaving or just before returning to the colony. Although storm-petrels do sometimes forage inshore at night (D’Elbée and Hémery, 1998; Thomas et al., 2006; Albores-Barajas et al., 2011) or even sometimes during the day (Poot, 2008), this may be more likely to occur in areas or times of lower predator density. The presence of Great Skuas on Mousa, and more widely across Shetland, may prevent storm-petrels from foraging near the coast at any time, since this species is known to predate storm-petrels nocturnally as well as diurnally (Votier et al., 2006). Birds may engage in more nocturnal foraging during incubation, when foraging trips last multiple days, allowing them to remain in foraging areas overnight. Nocturnal foraging may also be more common in non-breeders or outside the breeding season (e.g. Thomas et al., 2006), when birds are not constrained by having to return to the colony regularly.

Overall, 42% of relocations were classified as low speed, high turning angle, which I inferred to represent foraging. This is lower than for birds tracked from Illauntannig and High Island, Ireland, for which 61% and 59% of relocations were classed as foraging, respectively (Wilkinson, 2018) and for Mediterranean Storm-petrels tracked from Sardinia during chick-rearing in 2019 and incubation in 2020, for which 76% and 60% of relocations were classed as foraging, respectively (De Pascalis et al., 2021). However, in the present study a higher proportion of the trip was classed as foraging than in incubating Mediterranean Storm-petrels tracked from Benidorm, for which 32% of relocations were classified as ARS behaviour (Rotger et al., 2021). The reasons for such variation in the proportion of time spent foraging are unclear, but may be related to differences in trip duration and distance (e.g. with birds foraging closer to the colony or undertaking trips of more than one day having additional time available for foraging), variation in prey availability or quality, or differences in energy requirements. Differences in analytical techniques may also lead to differences in the proportion of a trip that is interpreted as 'foraging'.

### 5.5.3 Spatial distribution of behaviours

Although the 95% UD for all relocations classified as foraging covered much of the overall area used by storm-petrels, the 50% UD identified two core foraging areas (Figure 5.4). The core foraging areas of tracked birds differed between years, however (Figure 5.5; Table 5.2). In 2018, tracked birds tended to forage closer to the colony than in other years, and the birds tracked in 2015 tended to forage further from the colony, although the sample size for 2015 was small. Multi-year tracking data is therefore important for this species, particularly when used to assess the risks posed by new developments (e.g. offshore wind farms), to design protected areas for the species, or when aiming to draw generalisations from the data.

Birds foraged closest to the colony in 2018 and appeared to spend the highest proportion of their time foraging (i.e. a larger proportion of relocations were classified as foraging), while birds in 2015 foraged furthest from the colony and appeared to spend the lowest proportion of their time foraging. This suggests that it may be more profitable to remain closer to the colony if possible, as transit times will be lower the closer a bird forages to the colony, which increases the time available for foraging. Alternatively, it is possible that prey is more readily available or more profitable further from the colony, reducing the time a bird needs to spend foraging after a longer transit.

### 5.5.4 Drivers of foraging distribution

The GAMM for foraging behaviour did not identify any of the proxies of prey distributions as drivers of storm-petrel foraging locations. However, as discussed in Chapter 4, variables such as sea surface temperature and chlorophyll-*a* concentration may not be good indicators of prey availability, since there may be spatial or temporal mismatch between primary productivity and organisms at higher trophic levels (Grémillet et al., 2008). These variables were measured at an eight-day resolution and this may also have limited their ability to accurately reflect prey availability, which may be more dynamic. Storm-petrels may also be responding to fine-scale cues or small prey patches beyond the spatial resolution of the environmental variables used as a proxy for prey distribution. For example, Mediterranean Storm-petrels have been found to forage in shallow areas with strong currents that may bring prey to the surface (De Pascalis et al., 2021). Although previous studies have found that storm-petrels aggregate over underwater features, such as banks, that cause upwellings (Scott et al., 2013), depth and terrain roughness did not appear to influence the foraging distribution of storm-petrels tracked from Mousa. The fact that the core foraging areas differed substantially between years further suggests that the birds are not dependent on specific static topographic features to bring prey to the sea surface. Instead, inter-annual variation in other oceanographic variables, such as currents, may lead to spatial differences in prey availability between years. Being generalists, the birds may also be foraging on different prey in different years, taking advantage of the relative availability of different prey types. Molecular analysis of diet samples from storm-petrels breeding on Mousa between 2010 and 2016 suggests diet composition does not vary significantly between years and that Norway Pout and Whiting are an important dietary component (F. Wood, unpublished data). It is likely that storm-petrels are feeding on the larval or juvenile stages of these fish species and it may be that the distribution of spawning grounds or the movement of young varies between years. A better understanding of storm-petrel diet is key to determining how their at-sea movements are influenced by prey distributions.

Although predator density was correlated with broad-scale marine distribution (Chapter 4), it does not appear to influence the distribution of foraging-type movement behaviour, but again, the predator density data were based on surveys across many years, so are not an exact measure of predator distributions at the times the storm-petrels were tracked. In contrast, conspecific competition appears to be a key driver of both the broad-scale at-sea distribution (Chapter 4) and specific foraging locations of storm-petrels tracked from Mousa. Segregation of foraging areas for conspecifics from different colonies has been identified in many multi-colony tracking studies of a wide range of seabird species (Bolton et al., 2018), including Leach's Storm-petrels (Hedd et al., 2018), and tracking of storm-petrels from additional colonies in the northeast Atlantic would be very useful for determining the extent of inter-colony foraging area overlap in this species.

Wind speed was also identified as having a significant effect on storm-petrel foraging behaviour, with birds more likely to forage in locations with higher wind speeds. It is possible that wind speed affects the flight speed (i.e. step length) and tortuosity (i.e. turning angle) of storm-petrels and that this in turn leads to a difference in behaviour classification by the HMM. If storm-petrels fly more slowly and less directly in stronger winds then the HMM may have included the behaviour in State 2, which I have considered to represent foraging behaviour. The effects of wind on storm-petrel at-sea behaviour deserve further investigation.

This is one of the first studies to look at the fine-scale movements of European Storm-petrels in the Atlantic, where the species has been tracked from very few colonies. Drawing firm conclusions about the habitat requirements of the species from a single-colony study would be unwise, but further tracking of European Storm-petrels at additional colonies is underway and should greatly improve our understanding of the at-sea behaviour and habitat use of this species.

# 6 General Discussion

## 6.1 Overview

The work presented in this thesis encompasses several interlinking themes, providing insights into storm-petrel populations and predation rates (Chapters 2 and 3), habitat use on land (Chapter 2) and at sea (Chapters 4 and 5).

In Chapter 2 I applied a novel method to the census of storm-petrels to improve precision and explicitly account for multiple sources of variation in response rates and nest site density, as well as improving survey efficiency. The survey of Leach's Storm-petrels on the St Kilda archipelago confirmed an ongoing population decline, likely driven by high rates of predation by Great Skuas (Chapter 3). Based on these results, the Leach's Storm-petrel was up-listed to 'Red' on the Birds of Conservation Concern List following the fifth review of the conservation status of birds in the UK, Channel Islands and Isle of Man (Stanbury et al., 2021). I also established that the previous population estimate for Leach's Storm-petrels on Elliðaey was likely to be an overestimate but, nevertheless, the population is likely to have declined significantly prior to the survey in 2018. Given the recent up-listing of Leach's Storm-petrel to 'Vulnerable' on the IUCN Red List (BirdLife International, 2020), there is a need to continue monitoring the species' population trajectory and incorporate new information (such as population estimates) into its conservation status as it becomes available.

The analysis of Great Skua pellet composition described in Chapter 3 indicates that generic estimates of pellet:prey ratios may be unreliable as the number of pellets produced per storm-petrel consumed can differ between sites and species. My finding that pellet:prey ratios on St Kilda were lower than previously estimated suggests that Great Skuas in the archipelago may be consuming even more Leach's Storm-petrels than previously estimated. Given the number of birds consumed at St Kilda in relation to the local breeding population, it appears highly likely that Great Skuas are predating non-breeding Leach's Storm-petrels that visit the archipelago, perhaps from colonies as far afield as Iceland and the western Atlantic.

The behaviour of storm-petrels at sea has remained particularly hard to study due to the species' small size limiting vessel- and aerial-based observations and the use of tracking devices. Only in the last 10 years has tracking of storm-petrels become possible, as tracking devices have become increasingly miniaturised. The analyses presented in Chapters 4 and 5 use data collected by GPS-tracking to provide novel insights into the marine habitat use of European Storm-petrels in the northeast Atlantic. I found that the broad-scale marine distribution of European Storm-petrels breeding on Mousa is likely driven by a combination of factors, including the avoidance of predation and intraspecific competition (Chapter 4). The areas used for foraging differ between years and, while foraging areas tend to have reduced intraspecific competition, predator avoidance appears to be a less important factor (Chapter 5). The results in Chapter 4 confirm the assumption that the scheduling of storm-petrel foraging trips to depart from and arrive at the colony at night is driven by a need to avoid predators and, unlike several other studies (D'Elbée and Hémery, 1998; Thomas et al., 2006; Poot, 2008), in Chapter 5 I found no evidence of near-shore foraging by European Storm-petrels either during the day or at night.

## 6.2 Predation

Despite being highly vulnerable to predation, storm-petrels as a group are globally widespread and highly successful (Brooke, 2004). However, extreme increases in predation pressure, as has occurred on St Kilda, can lead to population declines (Stenhouse et al., 2000; Newson et al., 2008; Miles, 2010; Fife et al., 2015). Bioenergetics models suggested that Great Skuas consumed 15,000 Leach's Storm-petrels on St Kilda in 1996 (Phillips et al., 1999b) and 21,000 a year in 2007–2009 (Miles, 2010), but the lower pellet:prey ratio I found in Chapter 3 suggests that these predation figures may have been even higher. Given that the breeding population of Leach's Storm-petrel on St Kilda was estimated to be 45,433 pairs in 1999/2000, these predation rates are equivalent to around 17–25% of breeding adults. It is likely, however, that many of the storm-petrels consumed by Great Skuas are non-breeders, which disperse widely during their pre-breeding years (Bicknell et al., 2012). For example, ringing studies show that birds may even end up breeding at colonies thousands of miles from their natal site (Bicknell et al., 2012). Leach's Storm-petrels do not appear to be subjected to severe predation pressure on Elliðaey (Hey et al., 2019), but non-breeding birds from Elliðaey, and even from colonies in the western Atlantic, may visit St Kilda. This could result in predation on St Kilda acting as a sink that impacts on multiple Leach's Storm-petrel populations across the North Atlantic (Bicknell et al., 2014).

I have shown that predation risk not only affects behaviour on land (enforcing exclusively nocturnal attendance at the nest), but also influences the movements of storm-petrels at sea (Chapter 4). Specifically, the model in Chapter 4 in which I used a randomised daylight term clearly supports the theory that storm-petrels come to land only at night in order to avoid predators (Watanuki, 1986) and, at a broad scale, the foraging trips of European Storm-petrels avoid areas with high predation risk (Chapter 4).

## 6.3 Foraging

As shown by Bolton (2021), European Storm-petrels consistently travel in a south-easterly direction from the colony at Mousa, but I have shown that the distance they travel varies between years (Chapter 5). This suggests that they are not targeting specific static oceanographic features and instead are foraging more dynamically or opportunistically. However, the continental shelf over which the birds are moving is relatively devoid of major features and it would be interesting to determine whether birds breeding at other colonies in the northeast Atlantic consistently travel to particular features across multiple years. For example, whether birds from Faroese colonies travel westwards to the relatively nearby continental shelf edge.

Despite evidence for nearshore foraging by European Storm-petrels elsewhere (D'Elbée and Hémery, 1998; Thomas et al., 2006; Poot, 2008), I found no evidence of this from birds breeding on Mousa. This lack of coastal foraging may be a result of the high density of predators around the Shetland coast, or it may be due to the temporal constraints on foraging trip length, which mean that birds tend to be commuting to or from the colony at night, rather than foraging. These are not mutually exclusive explanations for nocturnal colony attendance, so both of these mechanisms may apply.

## 6.4 Oceanography and climate change

The influence of oceanography on the marine distribution of European Storm-petrels is less clear, but the results from Chapter 4 suggest that the birds may be more likely to use sea areas over more rugged terrain and with lower sea surface temperature, while Chapter 5 suggests an increase in foraging at higher wind speeds (within the range of wind speeds encountered by the tracked birds). The shelf area over which birds from Mousa are travelling on foraging trips is relatively uniform, and their distribution at sea appears to be primarily driven by a need to avoid predation and competition (Chapter 4). However, there are many other environmental variables that may be influencing storm-petrels' movements at sea, and with increased computing power it would be possible to investigate additional potential drivers of marine habitat use such as transient, small-scale currents and fronts, which may result in increased prey availability (Bost et al., 2009; Cox et al., 2018). The prevailing wind direction may also influence the direction of foraging trips made by birds breeding on Mousa (Alerstam et al., 2019), since they generally fly with a crosswind (Spear and Ainley, 1997; unpublished data), and a more detailed investigation of the influence of wind could be revealing.

European Storm-petrels breeding on Mousa are currently using areas with lower sea surface temperatures, which are likely associated with higher productivity due to increased mixing of the water column (Simer et al., 2021). The North Sea is already showing a significant warming trend (Tinker and Howes, 2020), with associated changes in the zooplankton community as copepod assemblages shift northwards (Beaugrand et al., 2002). Copepods form part of the diet of storm-petrels (D'Elbée and Hémery, 1998), and changes in copepod assemblages and phenology may impact storm-petrels directly (Hipfner, 2008), as well as causing changes at other trophic levels, potentially reducing the abundance of fish prey available to storm-petrels foraging from Mousa (Beaugrand et al., 2002).

## 6.5 Conservation implications

The high rate of predation of Leach's Storm-petrels by Great Skuas on St Kilda presents a conservation conundrum. Although we do not know whether the decline in the Leach's Storm-petrel population is entirely due to predation by Great Skuas, the high predation pressure is likely to be a contributing factor. In the Mediterranean, targeted culling of individual Yellow-legged Gulls *Larus michahellis* that specialise in storm-petrel predation has been used to successfully reduce predation on storm-petrels (Sanz-Aguilar et al., 2009) but culling of individual 'problem' skuas is unlikely to be a viable management option on St Kilda (Miles, 2010). This is because the St Kilda archipelago is a Special Protection Area with both Great Skuas and Leach's Storm-petrels as designated features. Although the Leach's Storm-petrel is red-listed in the UK (Stanbury et al., 2021), it is abundant globally (6.7–8.3 million breeding pairs; BirdLife International, 2020), while the Great Skua is globally scarce, with just 16,000 breeding pairs, 60% of which breed in Scotland (Mitchell et al., 2004). Any decision regarding management of the Great Skua population to facilitate storm-petrel conservation would therefore be a difficult one, given the Great Skua's global conservation status and the importance of its UK colonies. Furthermore, the Great Skua population on St Kilda and throughout Scotland has suffered severe declines in 2021 and 2022 as a result of Highly Pathogenic Avian Influenza (HPAI; Banyard et al., 2022), and how this may affect the trajectory of Leach's Storm-petrel populations remains to be seen.

We are only just beginning to gain knowledge of storm-petrel movements at sea, and we do not yet fully understand the threats they may face in the marine environment. Although flares and lights from offshore oil and gas platforms are thought to be a potential threat to storm-petrels (Wiese et al., 2001; Ronconi et al., 2015), their impacts in the North Sea are unknown. Storm-petrels are known to interact with fishing vessels and fish farms (Aguado-Giménez et al., 2016) and may benefit from fisheries discards and waste. Fisheries bycatch does not appear to be a significant risk to these species, although it does sometimes occur (Bradbury et al., 2017; Costa et al., 2020).

Despite storm-petrels foraging over large distances (Hedd et al., 2018; Bolton, 2020) and having a wide prey base (D’Elbée and Hémery, 1998; Hedd and Montevecchi, 2006), predictions suggest that climate change could push both Leach’s Storm-petrel and European Storm-petrel to extinction in Scotland by end of the 21st Century (Russell et al., 2015), most likely as a result of bottom-up effects on their food resources (Daunt and Mitchell, 2013; Mitchell et al., 2020). Temperature has also been found to affect the breeding success of Leach’s Stor–petrels, with lower hatching success at Kent Island, New Brunswick, Canada in years with the highest annual global mean temperature (marine and terrestrial; Mauck et al., 2018). Climate change may also accelerate changes to breeding habitats (e.g. vegetation height and composition), which have been linked to population declines at some storm-petrel colonies (Mitchell et al., 2004; Cadiou et al., 2010; D’Entremont et al., 2020).

Leach’s Storm-petrels in the western Atlantic appear to have low adult survival (Fife et al., 2015; Pollet et al., 2019a) compared with those breeding in the Pacific (Rennie et al., 2020) and compared with Procellariiformes in general (Brooke, 2004). This low adult survival rate is thought to be driving the population declines at western Atlantic colonies, but survival data are lacking for Leach’s Storm-petrels in the eastern Atlantic.

Determining appropriate conservation interventions for storm-petrels can be challenging, but ensuring the biosecurity of islands with breeding colonies is key, given the apparent inability of both European and Leach’s Storm-petrels to coexist with rats (De León et al., 2006). Eradications of invasive non-native species on islands with suitable breeding habitat can result in rapid (re-)colonisation by storm-petrels, as has occurred on the Shiant Isles off the west coast of Scotland (First Storm-petrel chick for Shiant Isles (rspb.org.uk)), and these additional breeding colonies would help to buffer the species against local threats or habitat changes.

Long-term monitoring of demographic processes, including adult and immature survival and breeding success, is important for determining the causes of population change and can help to inform effective conservation actions to address current problems, as well as acting as an early warning system for potential future issues. The installation and maintenance of nest boxes at key breeding sites can greatly aid such monitoring (Bolton, 1996), given the inaccessibility of many natural nest sites. Potential differences between natural and artificial nest sites must obviously be considered, but there is no evidence for this on Mousa (Bolton, 1996).

## 6.6 Priorities for future work

Our understanding of the population trajectories and threats to storm-petrels in the northeast Atlantic would be greatly improved by a more frequent and rigorous programme of censusing and demographic monitoring (e.g. adult and immature survival, breeding productivity, timing and causes of breeding failure). The censuses of Leach's Storm-petrels described in Chapter 2 highlighted the need for clearly described methods to ensure population estimates are comparable.

Further tracking work was conducted in 2021 for European Storm-petrels breeding on Lunga, Treshnish Isles, Scotland, and for Leach's Storm-petrels breeding on St Kilda (RSPB unpublished data). Tracking in additional years and at further key colonies across the region will provide important information on how marine movements and habitat use vary between years, sites and species, and help to identify the threats that different populations may face at sea. This is particularly important given the current rapid expansion of the offshore renewable energy industry around Scotland and in the Faroes (Scottish Government, 2020; SEV, 2020). Tracking of European and Leach's Storm-petrels outside of their breeding season is also important, since both species undertake long-distance migrations (Pollet et al., 2014; M. Bolton unpublished data) and may encounter many additional threats away from the colonies. Geolocators are now small enough to deploy on European and Leach's Storm-petrels and were deployed on both species in Scotland in 2021, but their retrieval is currently being disrupted by the ongoing HPAI outbreak. The migrations of a small number of European Storm-petrels breeding on Mousa have also been successfully tracked (M. Bolton unpublished data).

Our knowledge of storm-petrels' foraging ecology would benefit greatly from studies of storm-petrel diet, in order to explain marine habitat use in terms of food availability and to predict how prey species and habitat use may be affected by future environmental change. While I collected diet samples from European Storm-petrels on Mousa and Leach's Storm-petrels on Elliðaey, unfortunately the Covid-19 lockdowns prevented me from analysing these samples within my PhD.

A better understandIng of populations, demographic rates, marine movements and diet would together provide crucial baseline data for an integrated understanding of the effects of climate change and anthropogenic activities on these species, and help to identify effective mitigation and conservation actions. For example, given the current HPAI outbreak, it has become important to understand the effects of this disease on adult survival, breeding behaviour, foraging efficiency, and the net impact on breeding productivity and recruitment. Provision of artificial nest boxes can facilitate this detailed monitoring of demographic change. Monitoring breeding attempts can provide information on the stage at which nests fail, and whether that might be due to predation, disease or food limitation (e.g. via poor chick growth). Once such impacts are identified, mitigation can be put in place. For storm-petrels, such mitigation can include enhanced biosecurity, nest box provision (where good quality breeding sites are limited; Bolton et al., 2004), predator management and the design and implementation of marine protected areas.

Compared to many seabirds, storm-petrels remain mysterious and challenging to study, but the work within my PhD has provided novel insights into the populations, behaviour and ecology of these tiny seabirds within the northeast Atlantic, and helped to highlight important knowledge gaps to be addressed in future to aid in their conservation.

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# Appendix 1

### ELLIÐAEY

## Covariate graphs for hierarchical distance sampling models

The figures below provide the effects graphs for top-performing hierarchical distance sampling models. Dashed lines represent 95% confidence intervals.

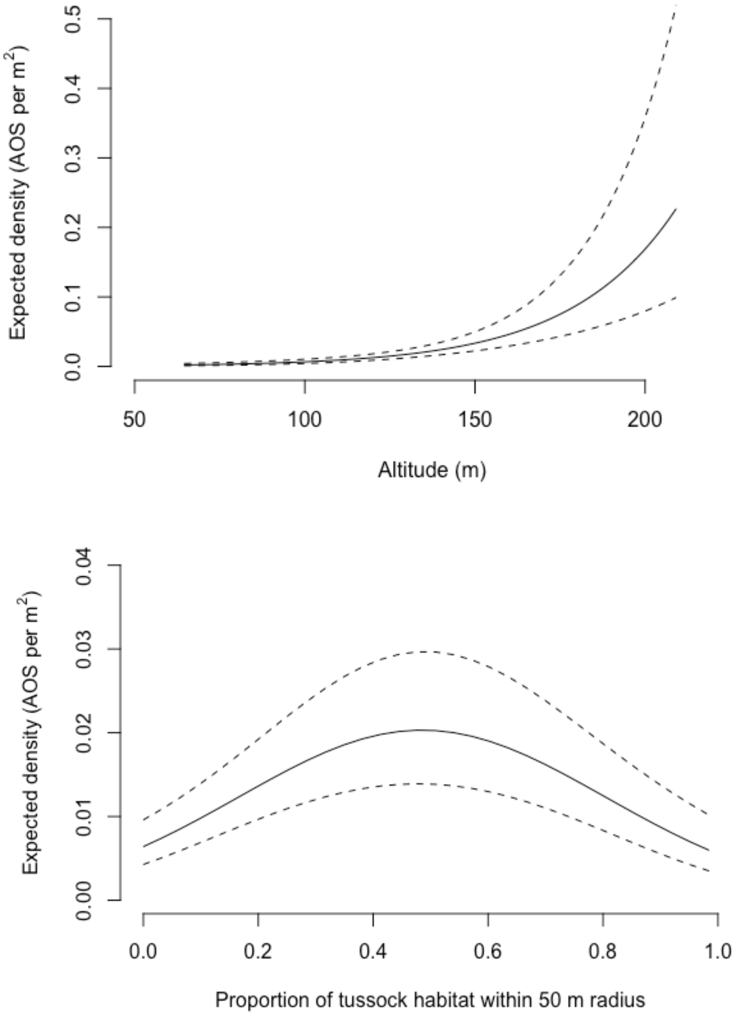


**Figure A1.1 Abundance covariates for Elliðaey model**

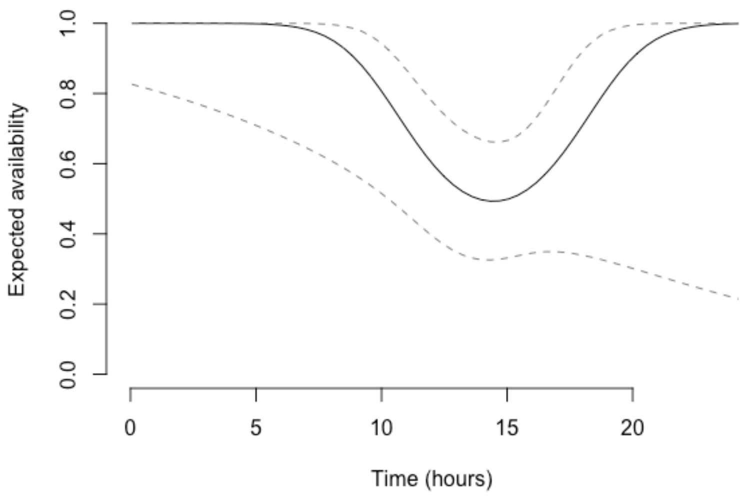


**Figure A1.2 Availability for Elliðaey model**

Note that because response rate likely varies with distance from the observer, availability should not be treated as response rate directly. Availability and detection probability are not completely disentangled in this scenario (see below).

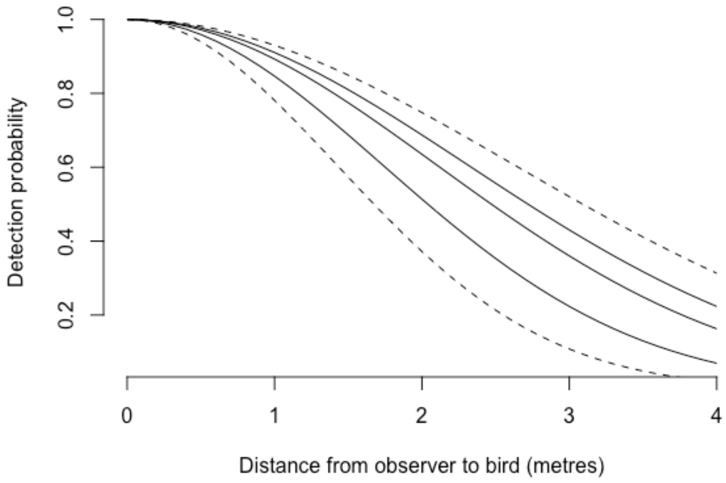


**Figure A1.3 Detection probability for Elliðaey model**

The bottom solid line represents the detection function on 24 June, the middle line 26 June and the top line 27 June. The dashed lines show the extremes of the confidence levels for all three dates (i.e. the upper confidence limit for 27 June and the lower confidence limit for 24 June. Note that availability and detection probability are not completely disentangled in this scenario (see below).

## ST KILDA

### Table A1.1 Summary of repeated playbacks per sector

Numbers in brackets represent data used in the HDS method, where that differed from the calibration plot method. We removed some survey points from the HDS analysis because inaccuracies in the recorded GPS locations meant that environmental covariate data would have been inaccurate. Table 3 in the main text gives a summary of playbacks and responses for each combined sector.

| **Island** | **Combined sector** | **Sector** | **No. of playbacks per survey point** | | | | | | | **Sites** | **Repeats** |
|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | **1** | **2** | **3** | **4** | **5** | **6** | **7** | | |
| **Boreray** | BOR1-2 | BOR1 | 125 | | 5 | 15 | | | | 145 | 200 |
| | | BOR2 | 14 | | | 10 | | 7 | 8 | 39 | 152 |
| | BOR3+ | BOR3 | 4 | | | | | | | 4 | 4 |
| | | BOR4 | 61 | | 4 | | | | | 65 | 73 |
| | | BOR5 | 20 | | 3 | | | | | 23 | 29 |
| | | BOR6 | 15 | | | | | | | 15 | 15 |
| | | BOR7 | 34 | | | | | 1 | | 35 | 40 |
| | | BOR8 | 32 | | | | | | | 32 | 32 |
| | | BOR10 | 28 | | | | | | | 28 | 28 |
| | | BOR10a | 39 | | | | | | | 39 | 39 |
| | | BOR11a | 32 | | | | | | | 32 | 32 |
| | | BOR11b | 32 | | | | | | | 32 | 32 |
| | Cleitean | Cleitean | 1 | 6 (5) | 9 (7) | 18 | 5 | 1 | | 40 (37) | 143 (135) |
| **Dun** | DUN B+C | DUNB | 56 (40) | 108 (101) | 1 (0) | 5 | 137 | 1 | | 308 (284) | 986 (953) |
| | | DUNC | 48 (30) | | | | | | | 48 (30) | 48 (30) |
| | DUN D | DUND | 51 | | | | 8 | | | 59 | 91 |
| **Hirta** | Other | H19 | 17 | | | | | | | 17 | 17 |
| | | H20 | 10 | | | | | | | 10 | 10 |
| | Carn Mòr | H21 | 171 | | | | | | | 171 | 171 |
| **Soay** | SOY | SOY3 | 17 | | | | | | | 17 | 17 |
| | | SOY6 | 7 | | | | | | | 7 | 7 |
| | | SOY8 | 2 | | | | | | | 2 | 2 |
| | | SOY9a | 8 | | | | | | | 8 | 8 |
| | | SOY9b | 8 | | | | | | | 8 | 8 |
| | | SOY10 | 13 | | | | | | | 13 | 13 |
| | | SOY12 | 17 | | | | | | | 17 | 17 |
| | SOY7 | SOY7 | 44 | | | | | | | 44 | 44 |

**Table A1.2 Calibration plot method population estimates and 95% confidence intervals using different survey radii.**

| | **4 m radius** | | **3.5 m radius** | | **3 m radius** | | **2 m radius** | |
|---|---|---|---|---|---|---|---|---|
| | **Population estimate (95% CI)** | **CI as % of mean** | **Population estimate (95% CI)** | **CI as % of mean** | **Population estimate (95% CI)** | **CI as % of mean** | **Population estimate (95% CI)** | **CI as % of mean** |
| **DUN B+C** | 5,805<br>(3,388–14,028) | 183% | 6,675<br>(3,974–14,203) | 153% | 7,948<br>(4,748–17,311) | 158% | 15,394<br>(6,857–76,350) | 451% |
| **DUN D** | 3,017<br>(1,306–8,022) | 222% | 3,777<br>(1,688–8,891) | 191% | 5,098<br>(2,261–12,494) | 201% | 9,665<br>(3,376–47,898) | 460% |

## Covariate graphs for hierarchical distance sampling models

The figures below provide the effects graphs for top-performing hierarchical distance sampling models. Dashed lines represent 95% confidence intervals.

### Dùn

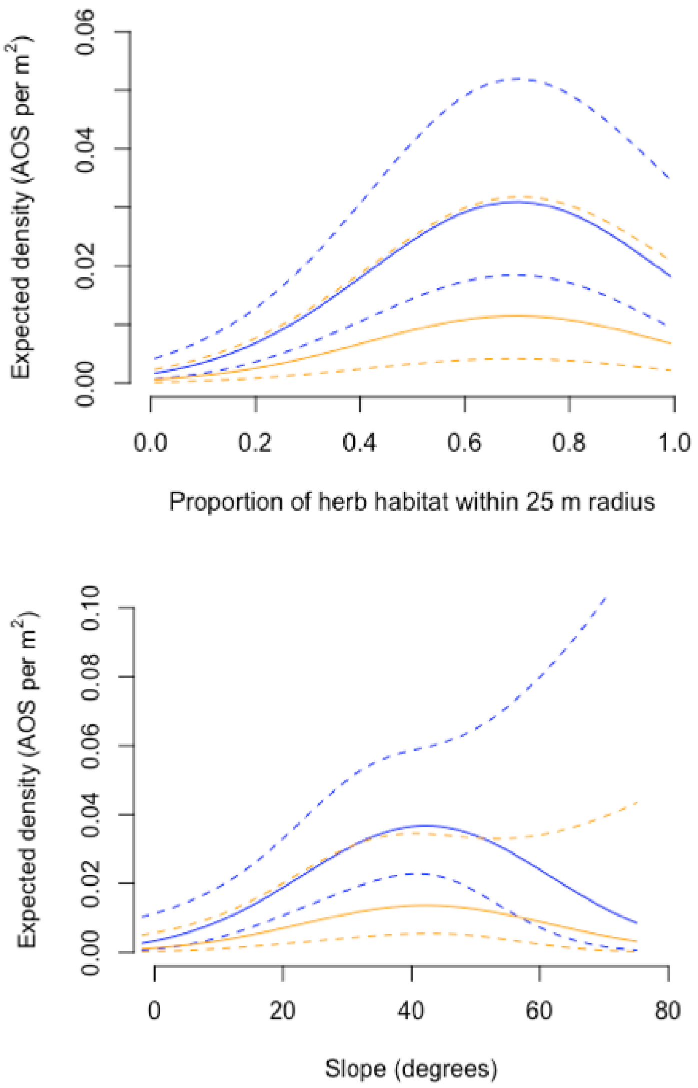


**Figure A1.4 Abundance covariates for Dùn-only model**

Blue lines represent the non-Puffin area (sectors B & C); orange lines represent the Puffin area (sector D).

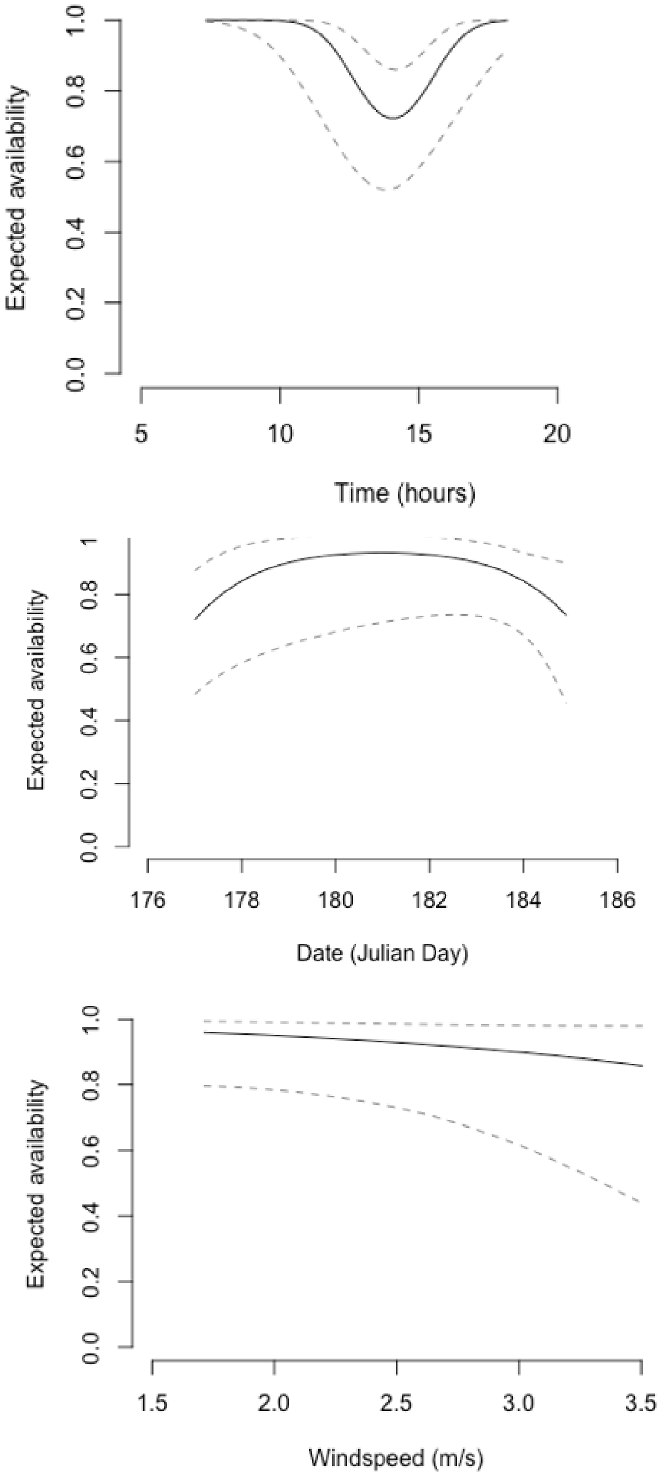


**Figure A1.5 Availability covariates for Dùn-only model**

Note that because response rate likely varies with distance from the observer, availability should not be treated as response rate directly. Availability and detection probability are not completely disentangled in this scenario (see below).

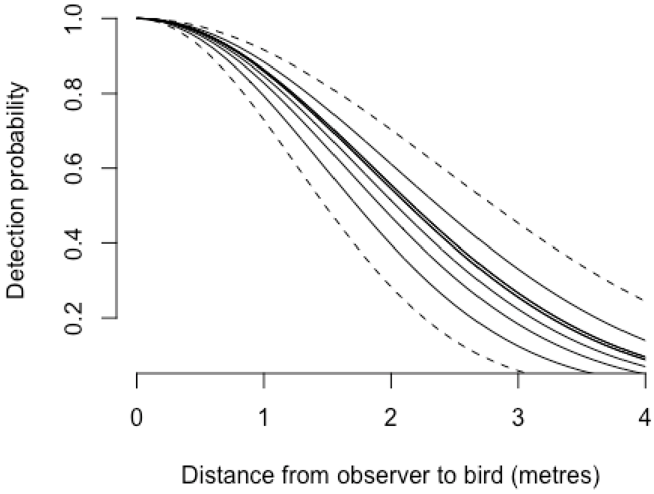


**Figure A1.6 Detection function for Dùn-only model**

Each solid line represents the detection function for a different observer. The dashed lines show the limits of the confidence intervals for all observers. Note that availability and detection probability are not completely disentangled in this scenario.

**All St Kilda**

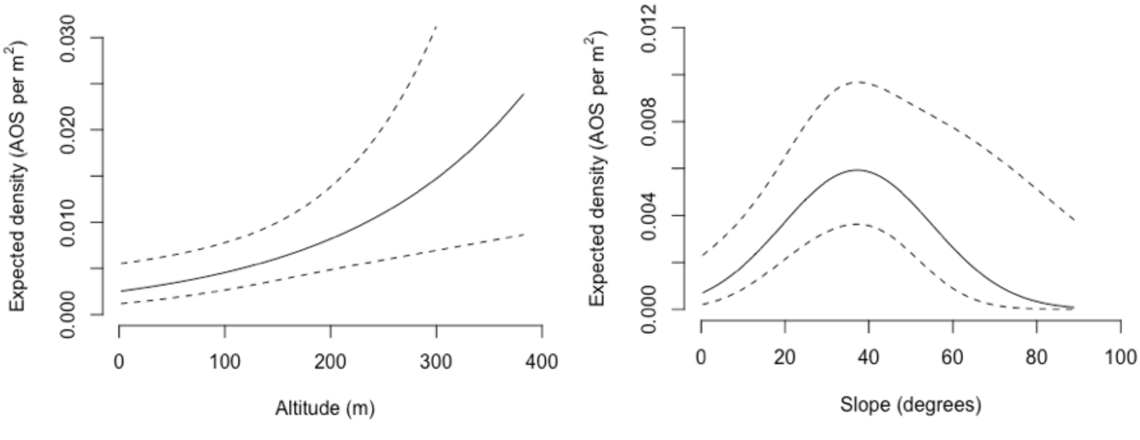


**Figure A1.7 Abundance covariates for 'all St Kilda' model**

There was also an effect of 'combined sector' on abundance. Abundance covariates are plotted for combined sector BOR1-2.

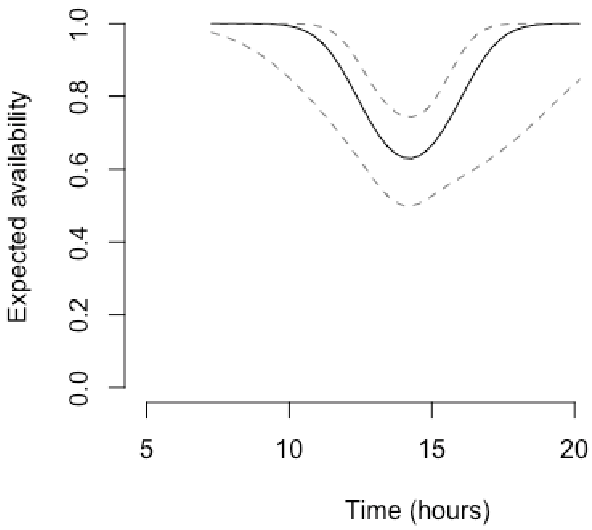


**Figure A1.8 Availability covariates for 'all St Kilda' model**

Note that because response rate likely varies with distance from the observer, availability should not be treated as response rate directly. Availability and detection probability are not completely disentangled in this scenario (see below).

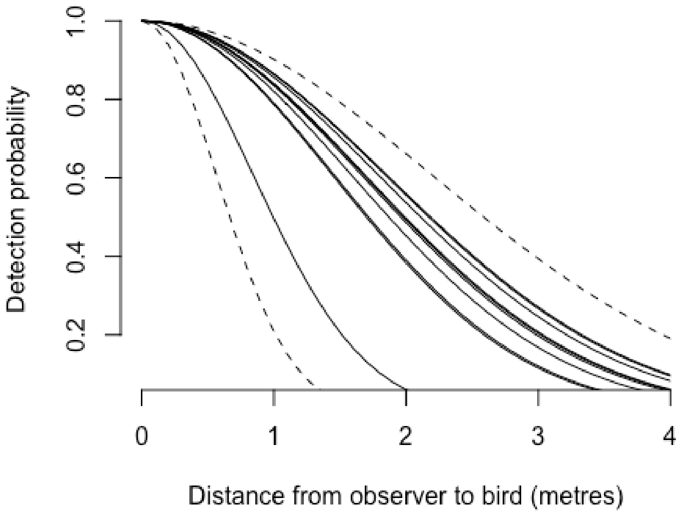


**Figure A1.9 Detection probability for 'all St Kilda' model**

Each solid line represents the detection function for a different observer. The dashed lines show the limits of the confidence intervals for all observers. Note that availability and detection probability are not completely disentangled in this scenario.

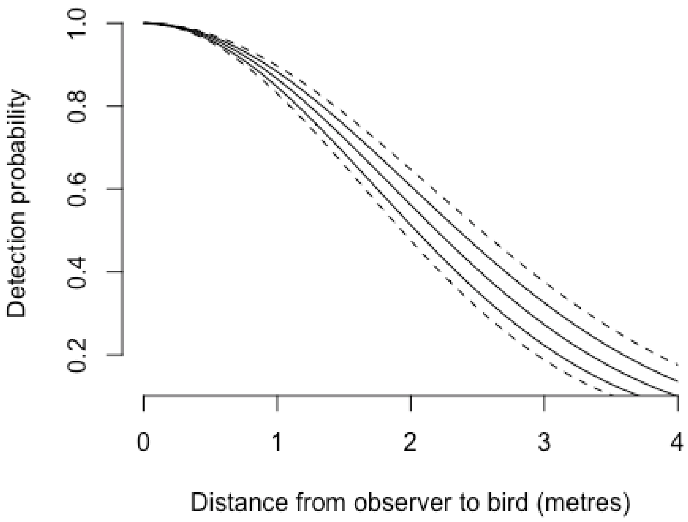


**Figure A1.10 Detection covariate for 'all St Kilda' model**

The top solid line represents the detection function at a wind speed of 2 m/s, the middle line a wind speed of 3 m/s and the bottom line a wind speed of 4 m/s. The dashed lines show the extremes of the confidence levels for all three wind speeds (i.e. the upper confidence limit for a wind speed of 2 m/s and the lower confidence limit for a wind speed of 4 m/s).

## Confounded availability and detection probability

For playback surveys, both the probability of a bird responding to playback (availability for detection) and the probability of an observer detecting a response (detection probability) are likely to decline with distance. Hierarchical distance sampling models do not explicitly account for a decline in availability with distance from the observer, so this has to be accounted for in the detection probability part of the model. Simulated data suggest that the models are able to do this effectively, with the product of availability and detection probability being identical for model outputs and the original simulated data (Figure A1.11). However, we must be aware that the outputs for availability and detection probability individually do not represent the real-world values for these parameters.

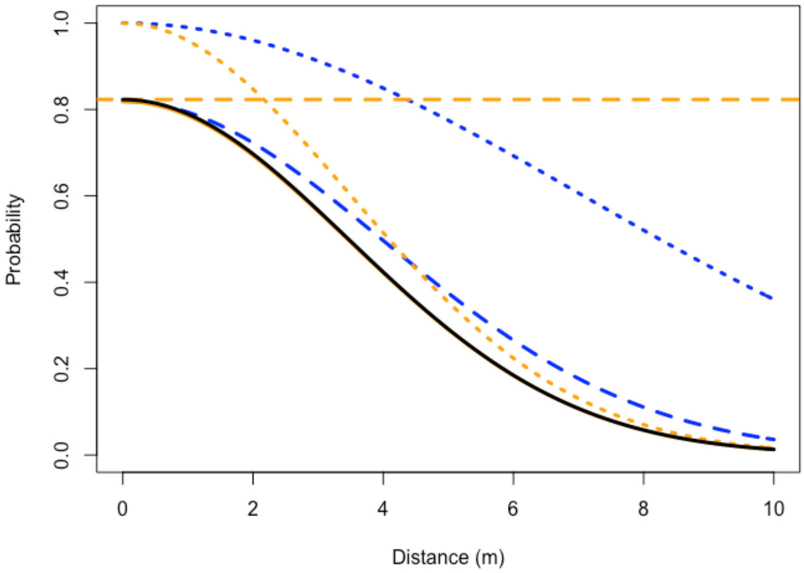


**Figure A1.11 Confounded availability and detection probability**

Simulated availability (blue dashed line) and detection probability (blue dotted line) and the model estimates for availability (orange dashed line) and detection probability (orange dotted line). Note that the availability estimate from the model is constant with distance from the observer, whereas in the simulated data availability declines with distance. The black line shows the product of availability and detection probability for both the simulated data and the model estimates, for which it is identical.

# Appendix 2

**Table A2.1** Trip metrics for all complete trips. Note that trip 2015B72T1 involved the bird apparently being storm-driven to the Norway coast and was excluded from the subsequent analysis.

| Bird ID | Trip ID | No. locations | Departure (UTC) | Return (UTC) | Duration | Total distance (km) | Maximum distance (km) | Direction (degrees) | Breeding stage |
|---|---|---|---|---|---|---|---|---|---|
| **2015B2** | 2015B2T1 | 65 | 17/07/2015 22:57 | 21/07/2015 01:06 | 74.15 | 919.58 | 303.04 | 157.38 | Incubation |
| **2015B232b** | 2015B232bT2 | 20 | 21/07/2015 02:02 | 21/07/2015 23:32 | 21.50 | 222.26 | 102.90 | 146.49 | Incubation |
| **2015B35** | 2015B35T1 | 32 | 20/07/2015 22:58 | 23/07/2015 00:58 | 50.00 | 618.71 | 285.61 | 171.14 | Incubation |
| **2015B50** | 2015B50T1 | 48 | 02/08/2015 00:00 | 03/08/2015 00:47 | 24.78 | 521.91 | 197.39 | 164.64 | Brooding |
| **2015B65Blue** | 2015B65BlueT1 | 80 | 31/07/2015 22:14 | 03/08/2015 00:39 | 50.42 | 672.85 | 253.67 | 135.02 | Post brooding |
| **2015B65Pink** | 2015B65PinkT1 | 71 | 17/07/2015 00:00 | 20/07/2015 02:06 | 74.10 | 780.25 | 275.02 | 152.24 | Incubation |

| Bird ID | Trip ID | No. locations | Departure (UTC) | Return (UTC) | Duration | Total distance (km) | Maximum distance (km) | Direction (degrees) | Breeding stage |
|---|---|---|---|---|---|---|---|---|---|
| **2015B72** | 2015B72T1 | 71 | 22/07/2015 23:00 | 25/07/2015 02:04 | 51.07 | 939.93 | 397.68 | 106.32 | Post brooding |
| **2015B73** | 2015B73T1 | 51 | 27/07/2015 22:57 | 28/07/2015 23:43 | 24.77 | 324.26 | 112.41 | 157.30 | Brooding |
|  | 2015B73T2 | 98 | 29/07/2015 02:16 | 30/07/2015 22:35 | 44.32 | 609.11 | 170.47 | 165.03 | Post brooding |
| **2015B76** | 2015B76T1 | 36 | 18/07/2015 23:00 | 20/07/2015 22:51 | 47.85 | 563.05 | 193.53 | 164.03 | Incubation |
| **2015B79** | 2015B79T1 | 42 | 31/07/2015 00:00 | 01/08/2015 01:00 | 25.00 | 376.40 | 157.66 | 155.70 | Post brooding |
| **2015N237** | 2015N237T1 | 65 | 21/07/2015 23:17 | 22/07/2015 22:45 | 23.47 | 478.39 | 182.08 | 175.14 | Post brooding |
| **2016B04** | 2016B04T1 | 51 | 14/08/2016 21:30 | 16/08/2016 21:27 | 47.95 | 581.75 | 206.17 | 159.58 | Post brooding |
| **2016B232** | 2016B232T1 | 48 | 15/08/2016 01:29 | 16/08/2016 02:33 | 25.07 | 376.29 | 166.03 | 173.62 | Post brooding |

| Bird ID | Trip ID | No. locations | Departure (UTC) | Return (UTC) | Duration | Total distance (km) | Maximum distance (km) | Direction (degrees) | Breeding stage |
|---|---|---|---|---|---|---|---|---|---|
| **2016B36** | 2016B36T1 | 25 | 22/08/2016 00:51 | 23/08/2016 01:56 | 25.08 | 340.63 | 134.55 | 194.31 | Post brooding |
| | 2016B36T2 | 23 | 23/08/2016 02:26 | 23/08/2016 23:56 | 21.50 | 382.78 | 99.53 | 165.20 | Post brooding |
| | 2016B36T3 | 24 | 23/08/2016 23:57 | 24/08/2016 23:57 | 24.00 | 331.35 | 121.88 | 151.57 | Post brooding |
| | 2016B36T4 | 22 | 25/08/2016 00:57 | 25/08/2016 22:57 | 22.00 | 214.17 | 81.71 | 137.06 | Post brooding |
| **2016B62** | 2016B62T1 | 52 | 20/08/2016 21:57 | 21/08/2016 23:57 | 26.00 | 347.95 | 122.30 | 156.76 | Brooding |
| | 2016B62T2 | 45 | 22/08/2016 02:27 | 23/08/2016 00:27 | 22.00 | 347.61 | 159.77 | 162.50 | Post brooding |
| | 2016B62T3 | 45 | 23/08/2016 01:27 | 24/08/2016 02:57 | 25.50 | 342.79 | 126.69 | 164.60 | Post brooding |
| **2016B88** | 2016B88T1 | 30 | 20/08/2016 20:59 | 22/08/2016 02:59 | 30.00 | 402.83 | 153.66 | 135.14 | Incubation |

| Bird ID | Trip ID | No. locations | Departure (UTC) | Return (UTC) | Duration | Total distance (km) | Maximum distance (km) | Direction (degrees) | Breeding stage |
|---|---|---|---|---|---|---|---|---|---|
| **2016N62** | 2016N62T1 | 49 | 20/08/2016 20:29 | 21/08/2016 22:29 | 26.00 | 335.25 | 116.55 | 157.78 | Brooding |
| **2017B36** | 2017B36T1 | 43 | 01/08/2017 22:16 | 02/08/2017 23:46 | 25.50 | 308.00 | 112.87 | 159.56 | Brooding |
| **2017B55** | 2017B55T1 | 46 | 02/08/2017 00:00 | 02/08/2017 23:19 | 23.32 | 381.68 | 144.59 | 200.25 | Brooding |
| **2017B61** | 2017B61T1 | 95 | 04/08/2017 01:43 | 06/08/2017 00:44 | 47.02 | 547.34 | 156.84 | 155.48 | Post brooding |
| **2017B67** | 2017B67T1 | 101 | 28/07/2017 22:20 | 31/07/2017 00:00 | 49.67 | 701.80 | 278.75 | 154.62 | Post brooding |
| **2017B73** | 2017B73T1 | 38 | 02/08/2017 21:30 | 04/08/2017 00:00 | 26.50 | 275.55 | 105.91 | 154.96 | Incubation |
|  | 2017B73T2 | 93 | 04/08/2017 00:30 | 05/08/2017 23:00 | 46.50 | 521.88 | 168.92 | 152.47 | Incubation |
| **2017N237** | 2017N237T1 | 52 | 03/08/2017 23:33 | 05/08/2017 01:33 | 26.00 | 377.86 | 123.63 | 139.56 | Brooding |

| Bird ID | Trip ID | No. locations | Departure (UTC) | Return (UTC) | Duration | Total distance (km) | Maximum distance (km) | Direction (degrees) | Breeding stage |
|---|---|---|---|---|---|---|---|---|---|
| **2018B01** | 2018B01T1 | 49 | 01/08/2018 22:00 | 02/08/2018 22:30 | 24.50 | 215.53 | 75.47 | 137.91 | Brooding |
| **2018B02** | 2018B02T1 | 44 | 05/08/2018 01:30 | 06/08/2018 00:00 | 22.50 | 170.08 | 51.00 | 119.37 | Brooding |
| **2018B10** | 2018B10T1 | 91 | 11/08/2018 21:30 | 12/08/2018 21:45 | 24.25 | 388.33 | 175.26 | 154.58 | Post brooding |
| | 2018B10T2 | 78 | 13/08/2018 02:00 | 13/08/2018 22:15 | 20.25 | 295.33 | 112.12 | 166.42 | Post brooding |
| **2018B19** | 2018B19T1 | 93 | 09/08/2018 23:00 | 10/08/2018 22:45 | 23.75 | 261.86 | 62.78 | 188.77 | Brooding |
| **2018B232b** | 2018B232bT1 | 42 | 04/08/2018 00:00 | 04/08/2018 23:00 | 23.00 | 145.16 | 44.63 | 140.37 | Brooding |
| **2018B26** | 2018B26T1 | 77 | 09/08/2018 01:30 | 09/08/2018 21:30 | 20.00 | 255.61 | 71.11 | 175.13 | Brooding |

| Bird ID | Trip ID | No. locations | Departure (UTC) | Return (UTC) | Duration | Total distance (km) | Maximum distance (km) | Direction (degrees) | Breeding stage |
|---|---|---|---|---|---|---|---|---|---|
| **2018B31** | 2018B31T1 | 94 | 09/08/2018 22:00 | 10/08/2018 22:00 | 24.00 | 267.08 | 81.40 | 190.31 | Brooding |
| | 2018B31T2 | 88 | 11/08/2018 01:45 | 11/08/2018 23:30 | 21.75 | 332.97 | 94.86 | 160.03 | Brooding |
| **2018B50** | 2018B50T1 | 87 | 11/08/2018 23:00 | 12/08/2018 21:30 | 22.50 | 172.40 | 45.18 | 138.18 | Post brooding |
| | 2018B50T2 | 72 | 13/08/2018 02:30 | 13/08/2018 21:30 | 19.00 | 178.12 | 51.97 | 173.41 | Post brooding |
| **2018B79** | 2018B79T1 | 47 | 02/08/2018 22:30 | 03/08/2018 22:00 | 23.50 | 313.52 | 141.39 | 165.50 | Brooding |
| | 2018B79T2 | 43 | 04/08/2018 01:00 | 04/08/2018 22:00 | 21.00 | 292.46 | 121.06 | 155.70 | Brooding |

**Table A2.2** Summary statistics for all trips combined. (Excluding the bird that was apparently storm-driven to the Norwegian coast.)

| Parameter | Mean | sd | Min | Max |
|---|---|---|---|---|
| **Duration (hours)** | 30.71 | 13.89 | 19 | 74.15 |
| **Max distance from colony (km)** | 141.49 | 66.49 | 44.63 | 303.04 |
| **Total distance travelled (km)** | 392.68 | 174.67 | 145.16 | 919.58 |
| **Direction** | 159.16 | 16.66 | 119.37 | 200.25 |

**Table A2.3** Trip metrics by breeding stage. (Excluding the bird that was apparently storm-driven to the Norwegian coast.)

| Breeding stage | Mean duration (hours) | Mean maximum distance from colony (km) | Mean total distance travelled (km) | Mean direction (degrees) |
|---|---|---|---|---|
| Incubation | 46.33 ± 20.13 (21.50–74.15) | 198.58 ± 80.17 (102.90–303.04) | 538.01 ± 238.61 (222.26–919.58) | 154.23 ± 10.85 (135.14–171.14) |
| Brooding | 23.77 ± 1.81 (20.00–26.00) | 104.59 ± 39.67 (44.63–197.39) | 303.20 ± 89.38 (145.16–521.91) | 160.56 ± 21.02 (119.37–200.25) |
| Post-brooding | 29.94 ± 11.63 (19.00–50.42) | 148.91 ± 61.27 (45.18–278.75) | 407.64 ± 159.30 (172.40–701.80) | 160.11 ± 14.73 (135.02–194.31) |

**Table A2.4** Model output for GAMM without ‘predator’ variable.

| Parameter | Estimate | Standard Error | Z value | p-value |
|---|---|---|---|---|
| Intercept | -1.171 | 0.096 | -12.15 | < 0.001 |
| Smooth terms | edf | Ref. df | $X^2$ value | p-value |
| log(competition) | 2.948 | 4 | 283.332 | < 0.001 |
| log(depth) | 1.799 | 4 | 9.727 | 0.003 |
| log(TRI) | 2.466 | 4 | 12.135 | 0.002 |
| log(chlorophyll-a) | 2.743 | 4 | 40.995 | < 0.001 |
| SST | 3.579 | 4 | 41.402 | < 0.001 |
| Wind speed | 1.900 | 4 | 9.705 | 0.004 |
| Year (random effect) | 0.002 | 3 | 0.000 | 0.860 |
| Trip ID (random effect) | 0.001 | 41 | 0.000 | 1.000 |

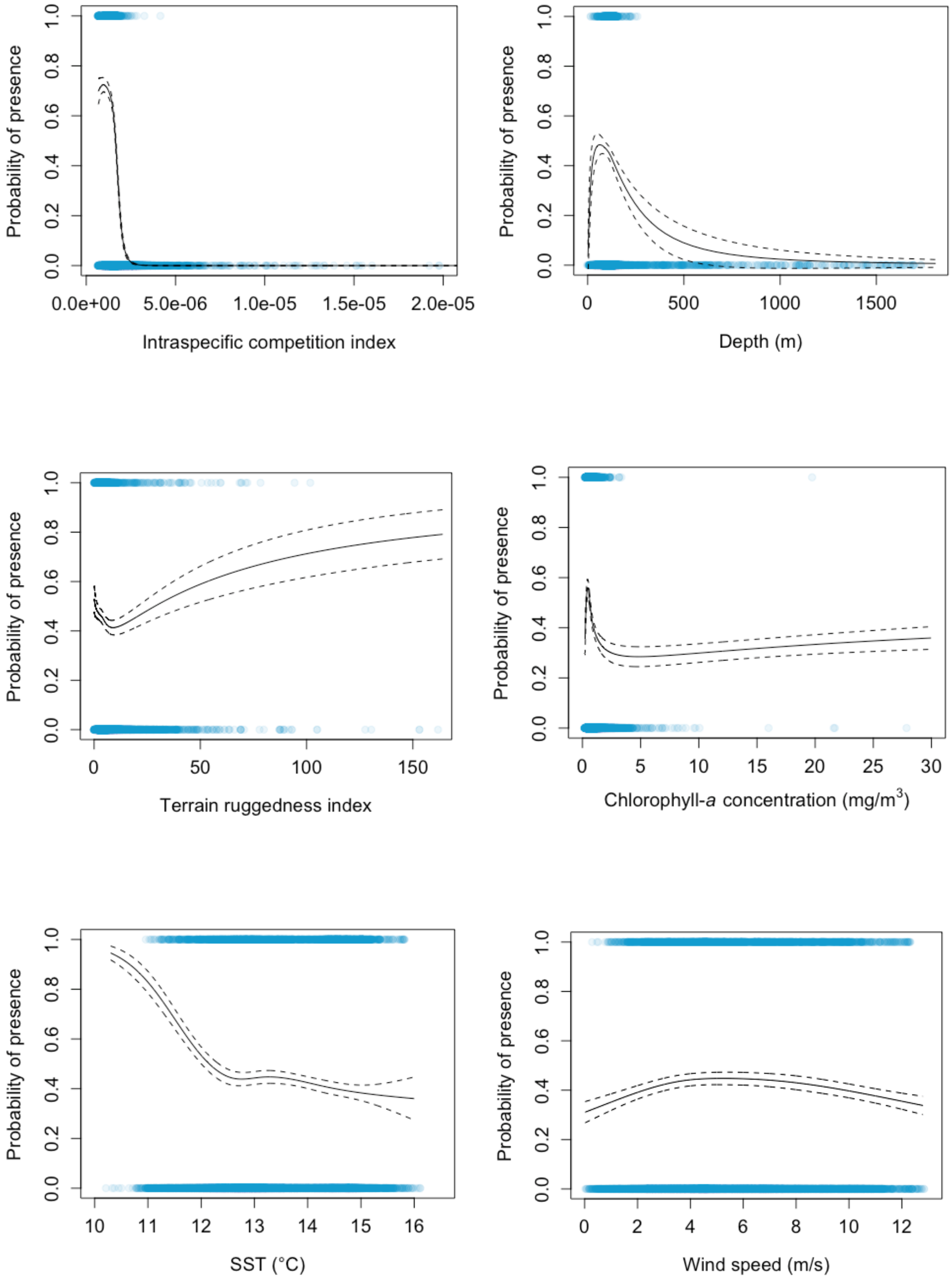


**Figure A2.1** Prediction plots for GAMM without the 'predator' variable.

**Table A2.5** Model output for GAMM with randomised daylight term (i.e. pseudo-absences not matched to presences by time of day).

| Parameter | Estimate | Standard Error | Z value | p-value |
|---|---|---|---|---|
| Intercept | -1.328 | 0.097 | -13.72 | < 0.001 |
| Smooth terms | edf | Ref. df | $X^2$ value | p-value |
| log(preds):night | 3.321 | 4 | 105.445 | < 0.001 |
| log(preds):day | 2.433 | 4 | 60.589 | < 0.001 |
| log(competition) | 2.931 | 4 | 243.873 | < 0.001 |
| log(depth) | 0.793 | 4 | 1.979 | 0.087 |
| log(TRI) | 1.862 | 4 | 4.544 | 0.071 |
| log(chlorophyll-*a*) | 3.304 | 4 | 35.109 | < 0.001 |
| SST | 3.645 | 4 | 54.740 | < 0.001 |
| Wind speed | 1.578 | 4 | 6.272 | 0.015 |
| Year (random effect) | < 0.001 | 3 | 0.000 | 0.847 |
| Trip ID (random effect) | < 0.001 | 41 | 0.000 | 0.998 |

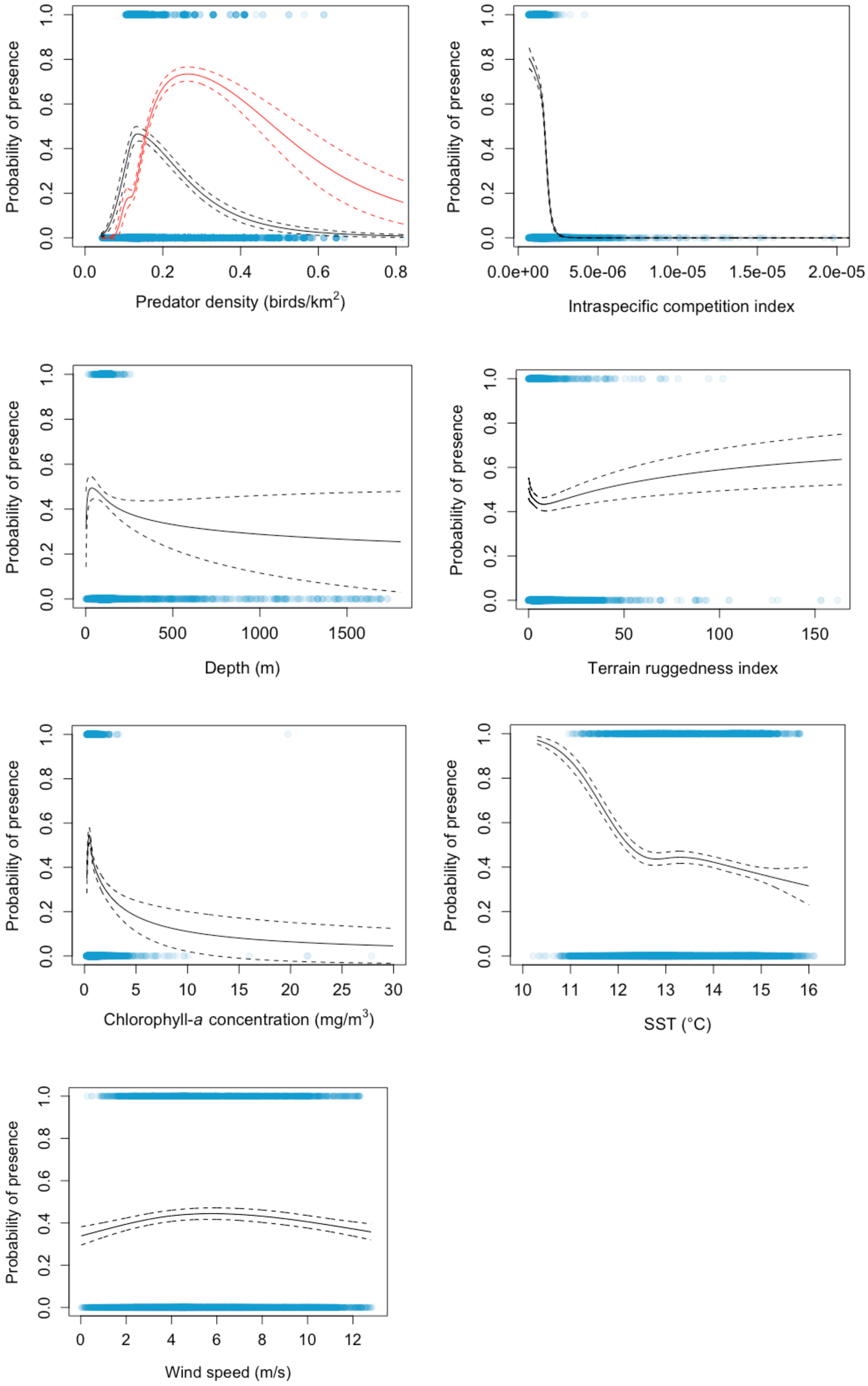


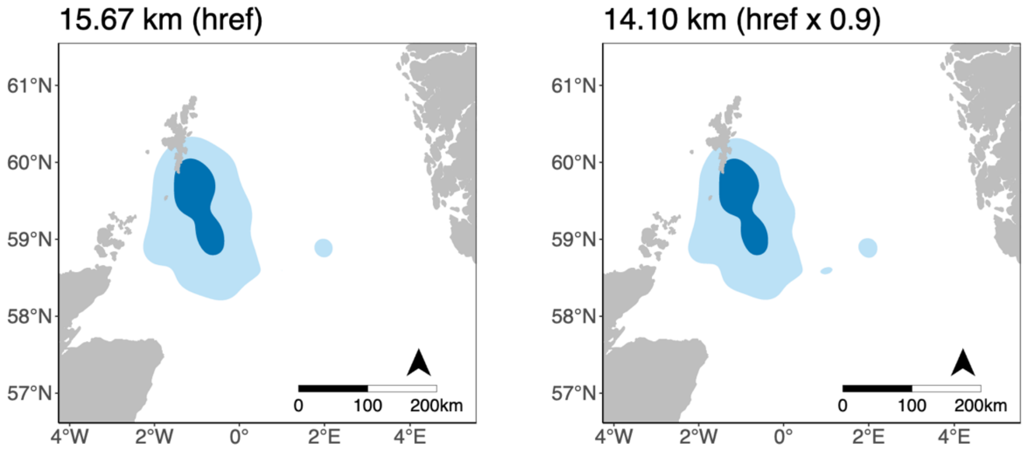
**Figure A2.2** Prediction plots for model with randomised daylight term.

# Appendix 3

## Choice of smoothing parameter for utilisation distributions

The default smoothing parameter (h-value) for the adehabitatHR package is href, but this is known to result in oversmoothing of utilisation distributions (Uds). I also tried the ‘scaleARS’ value (4.5 km) calculated by the track2KBA package (Beal et al., 2021), which uses first passage time analysis to estimate the scale of ARS of the tracked birds, but found that this resulted in under-smoothing of the kernels. As an alternative, Kie (2013) recommends testing a variety of smoothing values and choosing the lowest value at which the UD for all data remains largely contiguous and without any holes at the 95% contour level. As suggested by Kie (2013), I started with the href value of 15.67 km,stimateed by the track2KBA package, and reduced it incrementally by steps of 10% to find the most appropriate smoothing parameter.

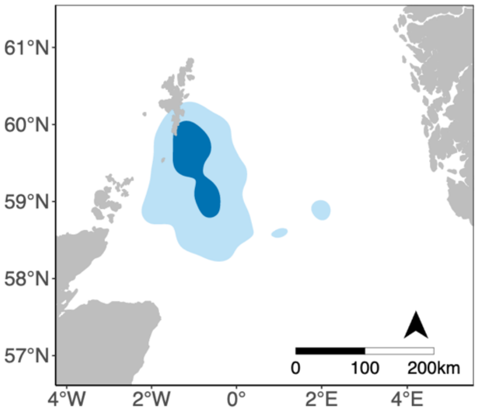
**Figure A3.1** (Below and overleaf.) Plots of 50% (dark blue) and 95% (light blue) utilisation distributions of chick-rearing European Storm-petrels GPS-tracked from Mousa, Shetland using different h-values.



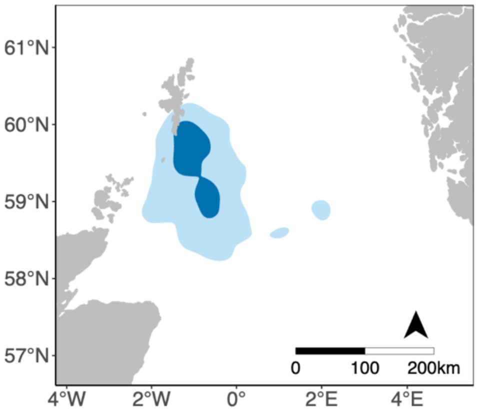
15.67 km (href)

14.10 km (href x 0.9)

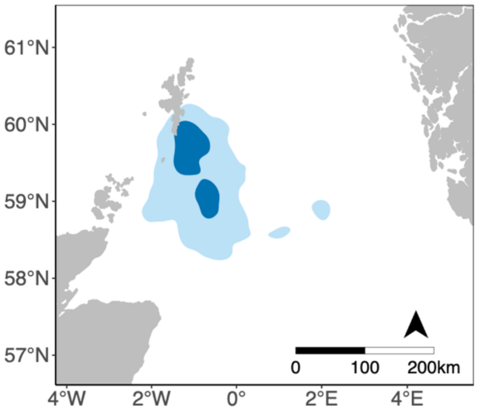
12.54 km (href x 0.8)



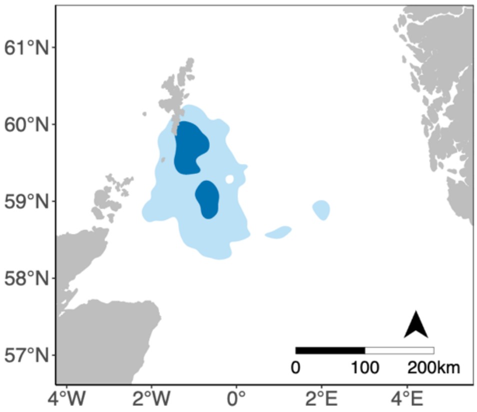
10.97 km (href x 0.7)



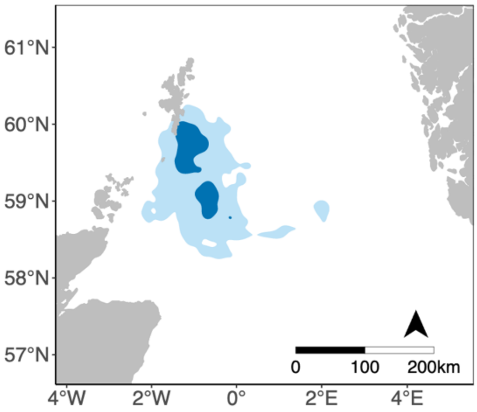
9.40 km (href x 0.6)



7.83 km (href x 0.5)



6.27 km (href x 0.4)



4.70 km (href x 0.3)

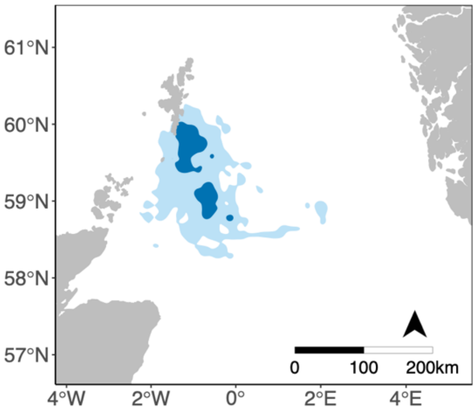
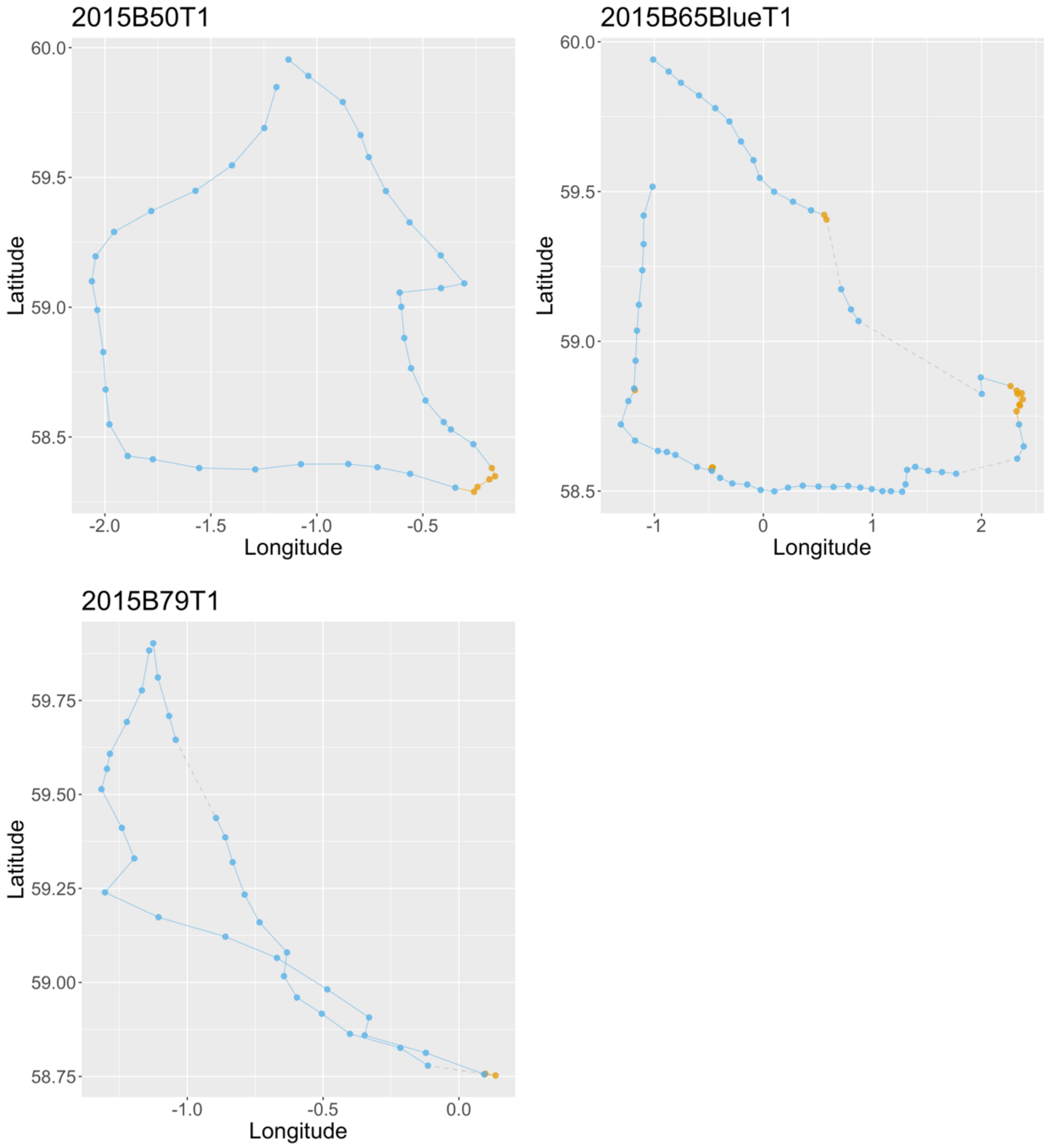
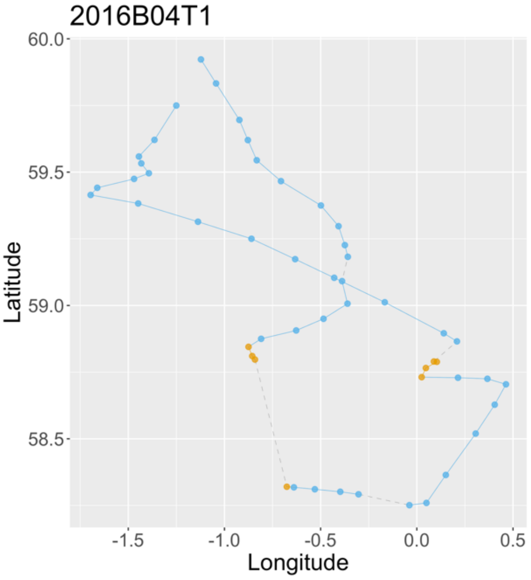


**Figure A3.2** (Across following five pages.) Plots of behavioural state allocation from hidden Markov model for all trips. Blue represents State 1 (transit) and orange represents State 2 (foraging). Dashed lines indicate sections of the track with more than one missing fix in a row which were not included in the modelling as I split the track in separate segments before and after the missing sections. Examples of possible ‘resting on the water’ behaviour are circled with a dark blue dashed line on trips 2018B50T2 and 2018B79T1.





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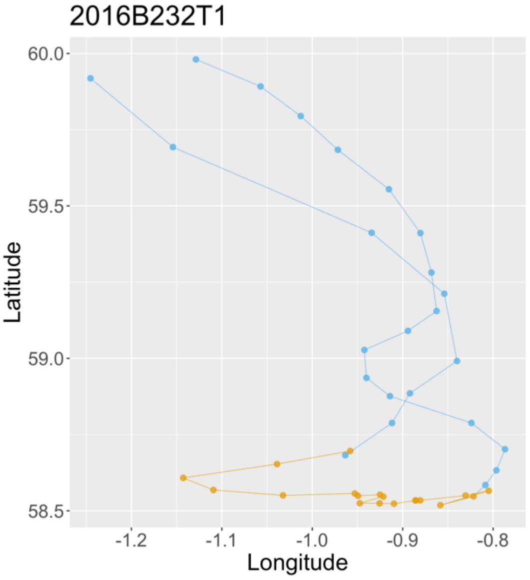

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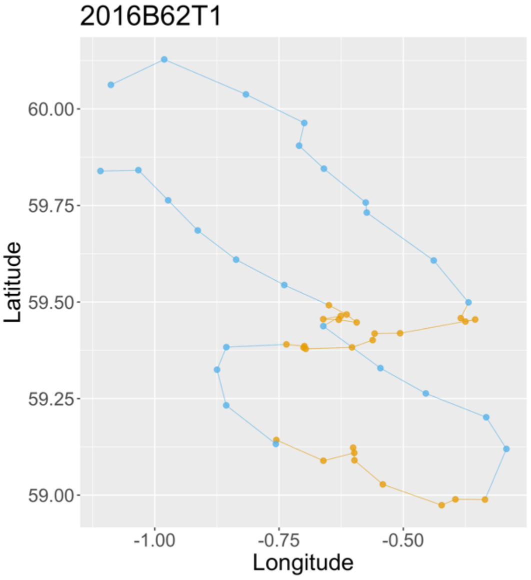

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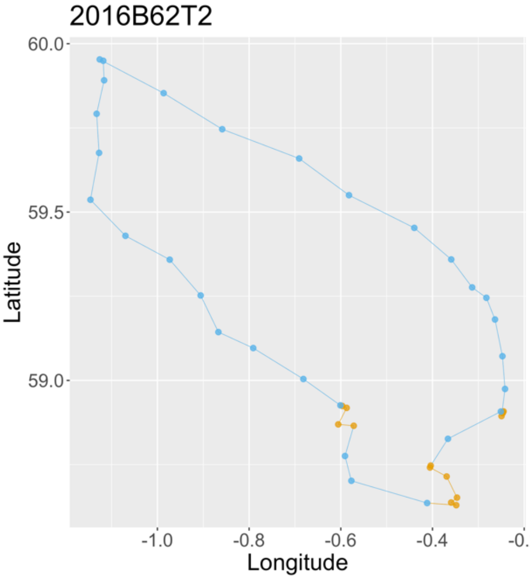

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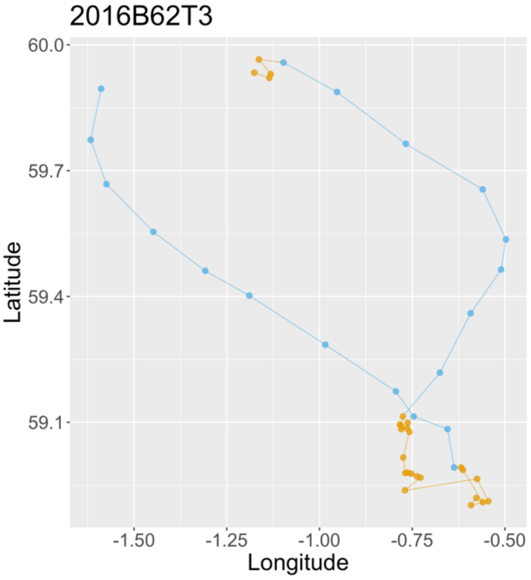

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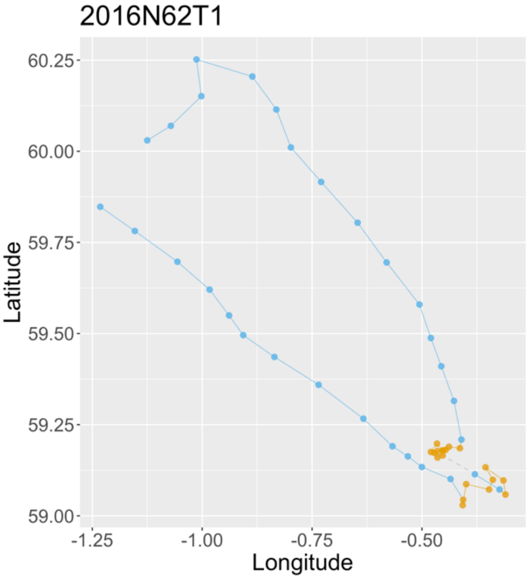
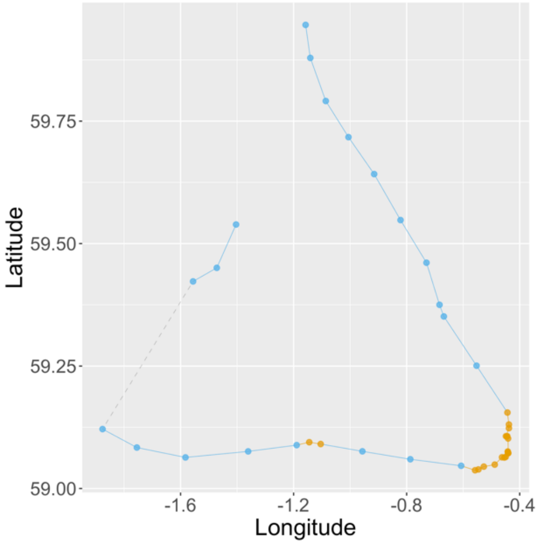


2016N62T1

2017B36T1



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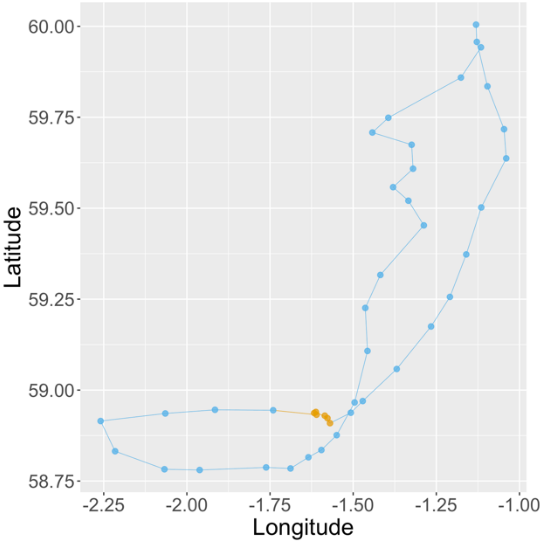

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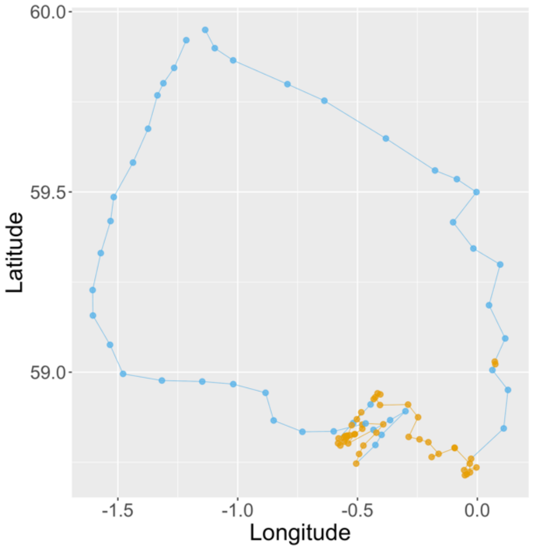

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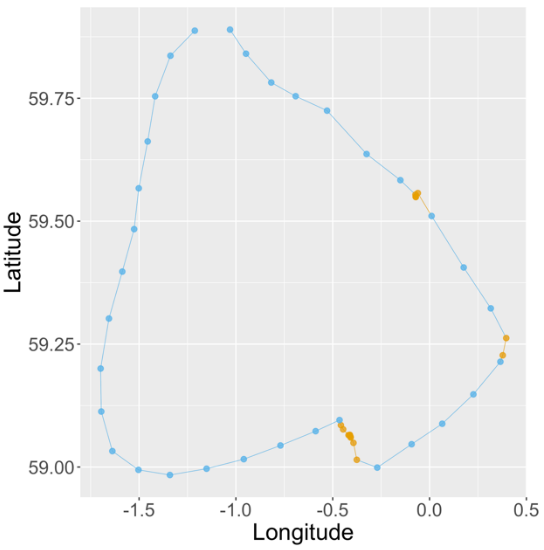

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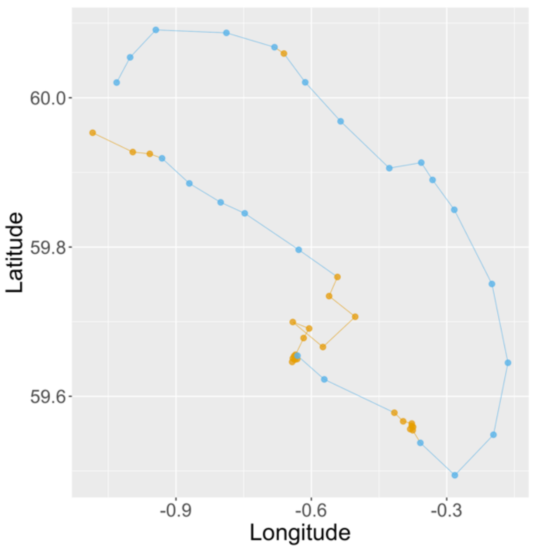

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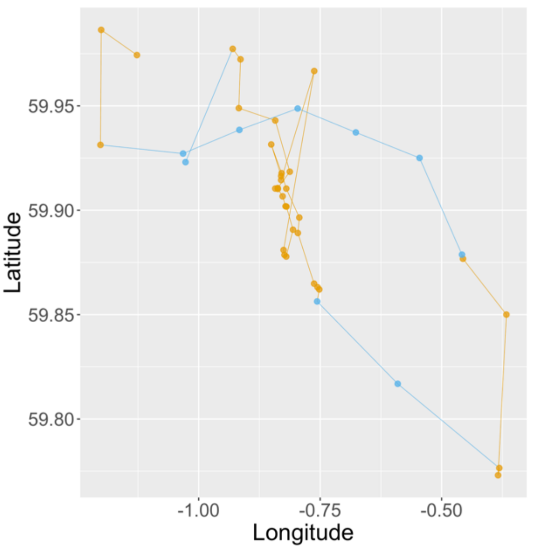

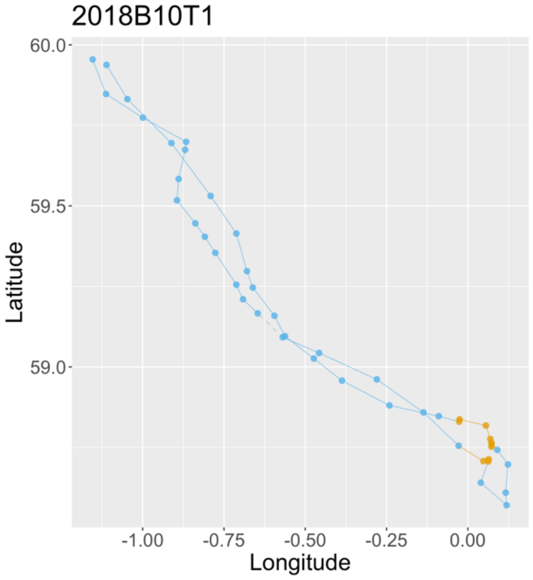
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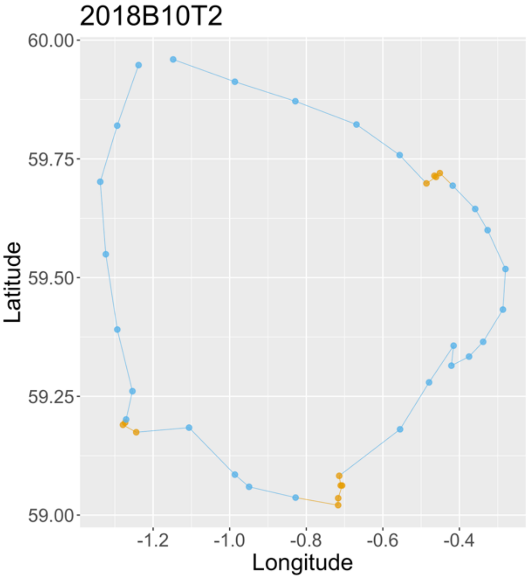
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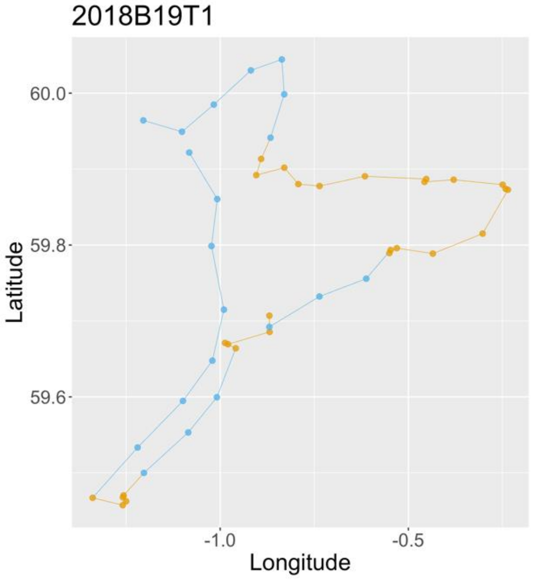
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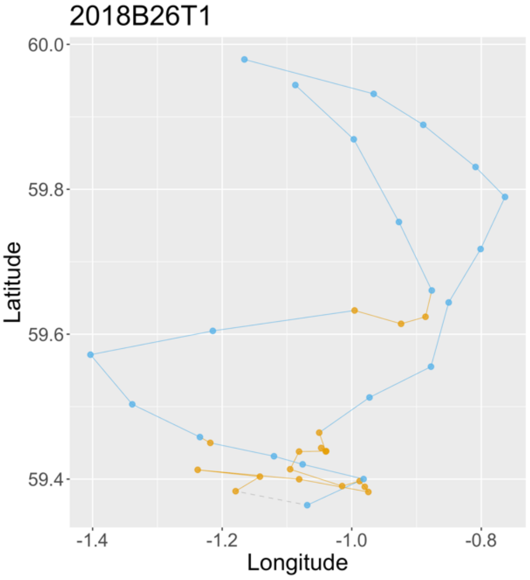
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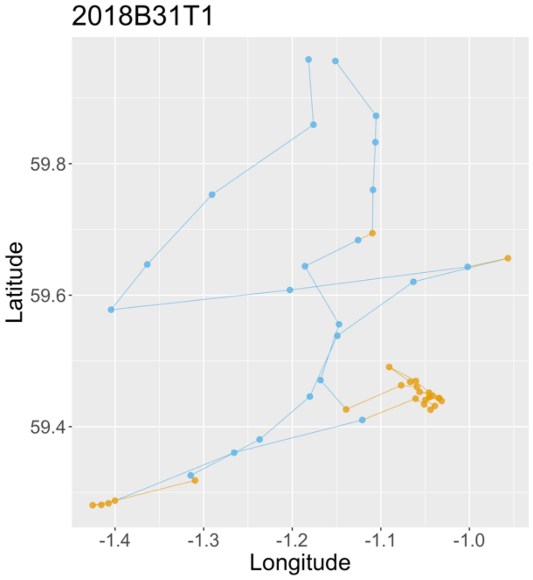
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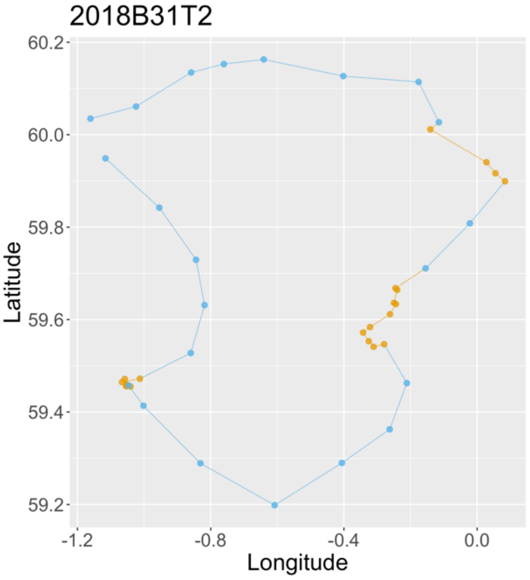
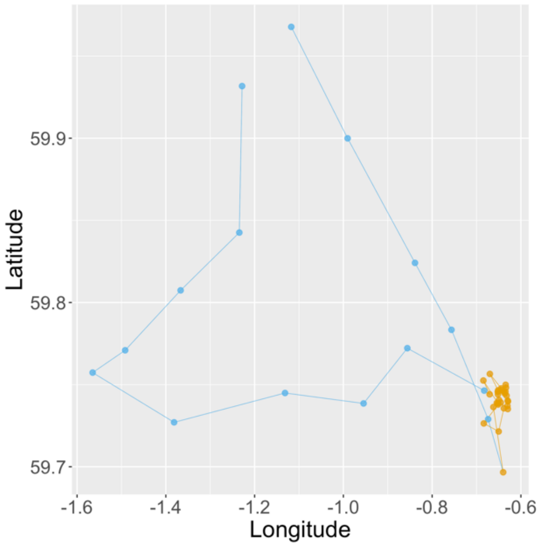
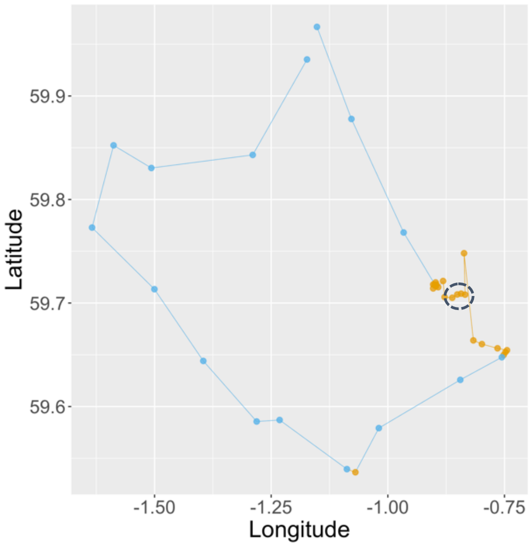

2018B31T2

2018B50T1



2018B50T2



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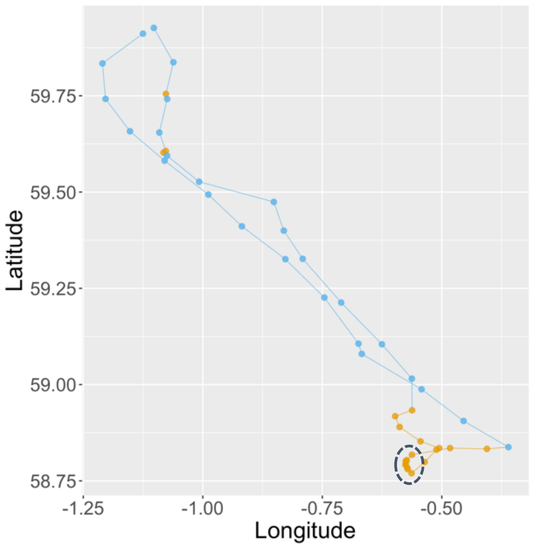

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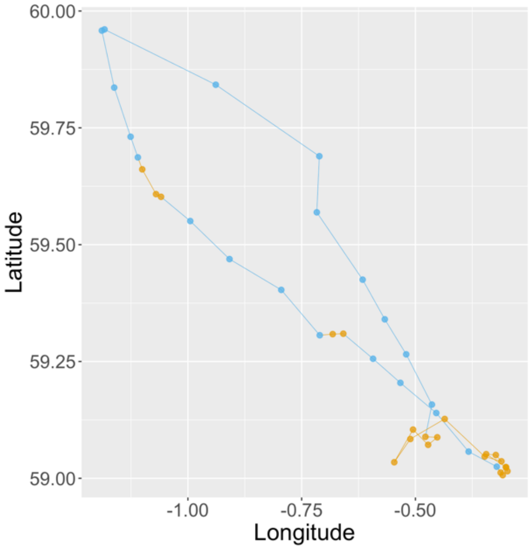

2018B232bT1