TERRESTRIAL AND MARINE RISKS FOR LEACH'S STORM-PETRELS DURING THE BREEDING SEASON

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ABSTRACT

Globally, seabirds are in decline, so comprehensive efforts are needed to understand risks facing these species. Leach's Storm-Petrels are globally identified as 'Threatened', and my thesis addresses two factors which pose risk during the breeding season for the population breeding at Gull Island, Newfoundland: predation and light attraction. Chapter 2 investigates activity associations between breeding storm-petrels and nearby predatory Herring Gulls to gauge predation risk. Herring Gull activity was negatively associated with, and was the most important predictor of, Leach's Storm-Petrel activity, suggesting that storm-petrels modify their colony activity in response to their top predator. Chapter 3 examines foraging tracks of parental storm-petrels to assess risk from light attraction to offshore oil platforms. This population of storm-petrels was consistent in foraging trip duration, distance, behaviour, and location. They transited past oil platforms during the day, thereby minimising risk. Breeding season risks from predation and light attraction are minimised by existing constraints on behaviour, so future research should focus on other risks to adults along with the juvenile and immature phases of the life cycle. Overall, I demonstrate that a comprehensive examination of risks facing seabirds throughout their life cycle is vital for informing effective mitigation efforts.

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CHAPTER 1:THE LEACH'S STORM-PETREL POPULATION CRISIS AND RISK

1.1 RISK ASSESSMENT

Risk assessment is an important tool for conservation biology (Harwood 2000). 'Risk' implies uncertainty in an outcome, so detailed analyses of the risks/hazards (objects or events that could harm a species) and their potential effects on the species requires assessment (Harwood 2000). As outlined in Chapter 2 of *Risk Assessment: A Practical Guide to Assessing Operational Risks* (Hollcroft and Lyon 2016), the process of risk assessment requires the following steps:

1. Identification
2. Analysis
3. Evaluation
4. Treatment

Risk/hazard identification involves pinpointing and describing specific hazards (Hollcroft and Lyon 2016). In conservation biology, this concept is extended to examine the probability of risk exposure (Harwood 2000). **Risk analysis** involves identifying the level of risk posed by an identified hazard, which can be scored qualitatively - based on subjective ratings, or quantitatively - based on numerical evidence (Hollcroft and Lyon 2016). **Risk evaluation** involves comparing the results of risk analysis to predetermined acceptable levels of risk (Hollcroft and Lyon 2016). Although the acceptable level of risk is rarely known in conservation biology, there are strategies that can be used to inform decision-making. Some examples of these strategies include cost-benefit analyses (which are especially important when the risk itself has ties to economics or industry), assessment of relative risk, which compares the probability of damage to the population between those exposed to the risk and those not exposed, and modelling, which can objectively evaluate the associations between the hazard and the health of the species and can even be used to predict future outcomes under different conditions (Burgman and Yemshanov 2013). **Risk treatment** requires creating and implementing mitigation strategies to reduce the observed level of risk below the determined acceptable level (Hollcroft and Lyon 2016).

1.2 SPECIES INFORMATION

1.2.1 Leach's Storm-Petrel

The Leach's Storm-Petrel (*Hydrobates leucorhous*) is a small Procellariform that breeds largely on islands in the Northern Atlantic and Pacific Oceans (BirdLife International 2017). These burrowing seabirds build nests in soil or substrate when possible, or uncommonly nest in rock crevasses (Pollet et al. 2020). Burrow architecture, the shape and size of the interior of the underground nesting chamber, can vary dramatically between burrows (Grimmer 1980).

Leach's Storm-Petrels, like all Procellariforms, exhibit high social and genetic monogamy (Mauck et al. 1995, Bried et al. 2003), which may be explained by their high nest fidelity (Morse and Kress 1984). Leach's Storm-Petrels exhibit biparental care, however, possibly due to the female’s large initial investment in the egg (the single annual egg makes up more than 20% of female body mass; Montevecchi et al. 1983), the male tends to spend a higher proportion of time incubating and makes more parental food deliveries (Mauck et al. 2011).

1.3 THE POPULATION CRISIS AND RISKS TO THE LEACH'S STORM-PETREL

Leach's Storm-Petrels (*Hydrobates leucorhous*) are the most abundant breeding seabird in the Northwest Atlantic, with population estimates in the millions (Pollet et al. 2020). Yet, surveys and modeling indicate an alarming decline of 54% across Atlantic colonies over the past few decades (COSEWIC 2020, Duda et al. 2020b, Wilhelm et al. 2020). In 2016, they were classified as Globally Threatened and uplisted to 'Vulnerable' on the International Union for the Conservation of Nature (IUCN) RedList, and in 2020 they were assessed as Threatened by the Committee on the Status of Endangered Wildlife in Canada (COSEWIC) (Newson et al. 2008, BirdLife International 2017, COSEWIC 2020, Duda et al. 2020b, Wilhelm et al. 2020).

Although reproductive success tends to be high in this species (70-90%; A. Hedd unpub., Mauck et al. 2018, Pollet et al. 2020), adult survival in Atlantic Canada (as measured using survival models with capture-mark-recapture data), where the majority of the global population of Leach's Storm-Petrels breed, is much lower than expected for long-lived seabirds (Pollet et al. 2020). Long-lived species tend to be iteroparous and breed once or multiple times during their lifetime, giving them numerous chances to be reproductively successful (Heppell et al. 1999). On average, Leach's Storm-Petrels have about six breeding years, but individuals can live to be over 30 years old, so this number can be much higher (Pollet et al. 2020). Thus, a trade off between survival and reproductive success is expected and often observed (e.g. Kitaysky et al. 2010). In two

Eastern Pacific colonies, annual survival is estimated to be 98%, contrasting with estimates for Western Atlantic colonies which tend to be less than 80% (Fife et al. 2015, Rennie et al. 2020, Pollet et al. 2020). Numerous risks for these birds have been identified including mercury and plastic pollution, climate change and low food availability, habitat change and loss, fatal light attraction, and predation (Montevecchi and McFarlane Tranquilla 2019, Dias et al. 2019, Pollet et al. 2020). This thesis analyzes and evaluates two of these known risks for one large colony in Newfoundland so that better understanding and conservation strategies can be developed.

1.3.1 Change and Destruction of Nesting Habitat

Leach’s Storm-Petrels breed in island dense colonies from May to October each year. They exhibit clear habitat preferences, and factors such as slope and fern cover are associated with the weight of chicks (Grimmer 1980). Although they spend most of their lives at sea, changes in terrestrial habitat that modify the quality or availability of preferred habitat types can influence their reproductive success. Recent studies have found associations between habitat changes and changes in colony size (d’Entremont et al. 2020, Duda et al. 2020a, 2020b). Decline in total forest cover in large colonies, most likely driven by climate change and invasive species, has been associated with long-term declines in Leach's Storm-Petrels on Kent Island, New Brunswick (d’Entremont et al. 2020). Contrastingly, on Baccalieu Island, Newfoundland and Labrador (the species’ largest colony), forested habitat area has shown little change yet there has been a disproportionately large decline in occupied burrow density in forest, and the storm-petrel’s preferred habitat of fern has increased, coincident with the population decline

(Wilhelm et al. 2020). Habitat changes are associated with climate change, and habitat and predation risk are inherently linked, as increased cover can obscure storm-petrels from predators' view (Stenhouse et al. 2000), and because specialist predators may select habitat types that overlap with storm-petrel habitat (Pierotti and Annett 1991).

1.3.2 Predation

Predation at colonies can lead to significant loss of breeding adults, which has a large impact on population stability. This predation can be significant, especially in the circumstances of predator introductions, predator population increases, or loss/decrease of other predator food sources. On Bon Portage Island, Nova Scotia, Leach's Storm-Petrels appeared in 79% Great Horned Owl (*Bubo virginianus*) pellets, accounting for annual predation of 1% of the total population (Pollet and Shutler 2019, Hoeg et al. 2021). River otter (*Lontra canadensis*) predation of Fork-tailed (*H. furcatus*) and Leach's Storm-Petrels has also been documented, where annual predation of the latter was estimated to be 8% of banded breeding adults (Quinlan 1983). Skuas (*Stercorarius* spp.) and gulls (*Larus* spp.) are significant predators of Leach's Storm-Petrels in the Eastern Atlantic. In St. Kilda, the population of Skuas has grown exponentially since the 1990's and high predation of Leach's Storm-Petrels (an estimated 21 000 individuals consumed annually, most of which were non-breeders) has been linked to this decline (Miles 2010). On Elliðaey Island, Iceland, a small population of Gulls (<200 individuals) consumed an estimated two Leach's Storm-Petrels per day, which is significant for this small colony (Hey et al. 2019). At other breeding colonies, species introductions have increased adult mortality and reduced reproductive success via chick predation (St Kilda Field Mice *Apodemus* *sylvaticus hirtensis*; Bicknell et al. 2009) or by driving chicks from their burrows (tramp ants *Monomorium pharaonis* and Tristam's Storm-Petrels *Oceanodroma tristani;* McClelland and Jones 2008). Historically, some species introductions (e.g. foxes, rats, cats, dogs, rabbits, sheep, goats, etc.) have even caused the extirpation of entire Leach's Storm-Petrel colonies (McChesney and Tershy 1998), but eradications of these species have led to the recolonization of some Leach's Storm-Petrel populations (Buxton and Jones 2012, Croll et al. 2016).

Gulls (*Larus* spp.) are the dominant predators of Leach's Storm-Petrels during the breeding season in many Western Atlantic colonies (Stenhouse et al. 2000, Hoeg et al. 2021). The Northern Cod Moratorium in 1992 terminated the source of offal and discards that historically provisioned gull populations in the Northwest Atlantic (Stenhouse and Montevecchi 1999), and while gull populations have decreased significantly (Regular et al. 2013), predation pressures on Leach's Storm-Petrels remains intense at some colonies (Stenhouse and Montevecchi 1999, Bond 2016). Colonies in the Witless Bay Ecological Reserve in Newfoundland, Canada provide a staggering example: an estimated 110 000 individual storm-petrels were killed by gulls on Gull Island in 2012 (Bond unpubl. data), and annual predation at Great Island has been estimated at around 9% of the population (Pierotti 1982, Stenhouse et al. 2000). In other colonies, however, predation does not seem to be as significant a risk. Very few gulls nest on Baccalieu Island, the species' largest colony (Sklepkovych and Montevecchi 1989, Duda et al. 2020b, Wilhelm et al. 2020), which is experiencing the largest and most globally significant population decrease. Hence, gull predation does not appear to be a major driver of the decline at all colonies.

1.3.3 Climate Change and Food Availability

Globally, climate change has been associated with range shifts, size reductions, and die offs of key forage fishes and other aquatic prey (e.g. Ottersen et al. 2006, Buren et al. 2019, Freer et al. 2019). Increased water temperatures can result in changes in behaviour, swimming ability, and physiological processes such as metabolic rate and growth of aquatic organisms, all of which may lead to changes in survival and reproduction (Heath et al. 2012). A meta-analysis of 224 fishery stocks showed that the environment has a greater influence on recruitment than spawning biomass at the majority of stocks (Szuwalski et al. 2015), meaning that continued changes in ocean climate will result in continued change in fish recruitment. Climate-induced changes in the quality and abundance of oceanic prey have had dramatic effects on seabird survival; a massive die-off of Cassin's Auklets (*Ptychoramphus aleuticus*) and Common Murres (*Uria aalge*) in the northeast Pacific was attributed to starvation from reduced availability and quality (lipid content) of zooplankton following a marine heatwave (Jones et al. 2018, Piatt et al. 2020). Leach's Storm-Petrels rely heavily on lantern fish (Myctophids) and, to a lesser extent, capelin (*Mallotus villosus*), amphipods and other crustaceans (Hedd and Montevecchi 2006, Hedd et al. 2009), so decreasing availability of these key prey items is cause for concern. In addition, the field metabolic rates of Leach's Storm-Petrels breeding in Newfoundland are higher than those of conspecifics in the more southerly parts of their range, so birds breeding at Newfoundland colonies may be particularly affected by reduced prey availability (Montevecchi et al. 1992).

Additionally, global climate has been negatively associated with reproductive success of storm-petrels at Kent Island in the Bay of Fundy (Mauck et al. 2018), so higher global temperatures caused by climate change will likely result in reduced future reproductive success and increased food stress. This could be critical as Marine Heat Waves and extreme weather events are predicted to increase (Oliver et al. 2019).

1.3.4 Pollutants

Globally, oceanic pollutants concentrate within seabird tissues, and concentrations are increasing in many cases (Braune 2007, Wilcox et al. 2015). Leach's Storm-Petrels have relatively high tissue concentrations of mercury compared to other seabirds (Provencher et al. 2014, Burgess et al. 2017, Pollet et al. 2017). Surprisingly, the observed blood mercury concentrations did not associate with reproductive success or adult return rate for breeders on Bon Portage Island, Nova Scotia, Canada (Pollet et al. 2017). There may, however, be significant differences between colonies in diet and foraging location which influences mercury exposure, and birds from Bon Portage have lower mercury concentrations than birds from Newfoundland colonies (Burgess et al. 2019, Frith et al. 2020). The effects of mercury and the threshold for negative impacts needs further investigation.

Leach's Storm-Petrels ingest plastic (Frith et al. 2020, d'Entremont et al. 2021), and almost 50% of birds assayed have ingested plastic levels above the Ecological Quality Objective – the level of plastic ingestion that was determined to be harmful (van

Franeker et al. 2005, Bond and Lavers 2013). High accumulation of stomach plastic and blood mercury levels have even been observed among stranded fledglings, suggesting that chicks may accrue pollutants from their parents before fledging (Krug et al. 2021). While the effects of high plastic levels on Leach's Storm-Petrels are poorly understood, high plastic levels have been associated with poor body condition in Flesh-footed Shearwaters (*Puffinus carneipes*) (Lavers et al. 2014), Pacific Northern Fulmars (*Fulmarus glacialis rogersii*) (Donnelly-Greenan et al. 2014), and albatross fledglings (Sievert and Sileo 1993).

1.3.5 Fatal Light Attraction

Attraction to coastal, ship and offshore hydrocarbon platform night-lighting is a major issue that requires study and mitigation. Birds can die from collisions with the structure and incineration in gas flares (Burke et al. 2012). If stranded live, they can be oiled or injured by machinery or experience an elevated predation risk following exposure and disorientation from offshore night lighting (Burke et al. 2012). The Leach's Storm-Petrel's foraging area often overlaps with offshore oil platforms (Hedd et al. 2018), where there are ongoing episodic mortality events (Wiese et al. 2001, Hedd and Montevecchi 2006, Burke et al. 2012, Ronconi et al. 2015, Davis et al. 2017). In addition, light attraction can alter foraging and migration paths of marine birds, resulting in increased energy expenditure (McLaren et al. 2018). Northerly breeding Leach's Storm-Petrels have higher energetic requirements during breeding than birds nesting in more southerly locations (Montevecchi et al. 1992), so the potential increased energy expenditure associated with anthropogenic light could be more stressful.

1.3.6 Primary Risks during the Breeding Season

The risks to Leach’s Storm-Petrels are numerous and widespread. In this thesis, I focus on risks during the breeding season as this is when the birds breed in burrows on islands in large colonies (Pollet et al. 2020) and are therefore concentrated within a specific area. Certain factors pose a greater risk during the breeding season due to temporal and geographical scales of risk.

Climate change has arguably the most pervasive and complex effects on species survival. Its effects are felt globally and over extended periods, as well as abruptly in the form of regime shifts (Buren et al. 2014) and marine heatwaves (Piatt et al. 2020, d’Entremont et al. 2021). Ocean climate change is also integrated with and can synergize other survival risks. Hence, the independent effects of climate change are difficult to assess, especially within a single breeding season.

Fish populations and food availability are changing globally over broad geographic scales (e.g. Buren et al. 2019, Freer et al. 2019). Because Leach's Storm-Petrels are trans-Atlantic migrants, with some individuals wintering as far from their Northern breeding colonies as southern Africa (Pollet et al. 2014, 2019, Hedd et al. unpubl.), they will be exposed to and affected by these changes on a global scale. Although I can investigate the effects of food availability during the breeding season on these birds, this is generally more relevant for reproductive success than for adult survival because, as predicted by life-history theory, long-lived organisms tend to reduce reproductive success in favour of preserving their own life when faced with sub-optimal conditions (Chastel et al. 1995, Oro and Furness 2002, Santos and Nakagawa 2012). In addition, adults which are food stressed at the colony may choose not to return to the colony, thus reducing the reproductive output of that colony as a whole. The effects of long-term food stress on adult survival and on reproductive success require further investigation over a broad timescale.

Oceanic pollutants such as mercury and plastics are prevalent globally (Pollet et al. 2017, Shoji et al. 2021), so Leach's Storm-Petrels are likely exposed to these risks throughout the year. Mercury can also take time to bioaccumulate to levels that pose a risk (Stenhouse et al. 2018). Pollutant risk is not concentrated within a single breeding season and is beyond the scope of this study.

Gradual change in nesting habitat for Leach's Storm-Petrels has been documented in some Western Atlantic colonies (d'Entremont et al. 2020, Duda et al. 2020a). Decadal change in preferred habitat has been associated with population declines (d'Entremont et al. 2020). Over millennial scales, increases in Leach's Storm-Petrel populations have been shown to cause an increase in preferred nesting habitat. Over short time scales (within a breeding season or between one or two breeding seasons), it is unlikely that obvious changes in habitat would occur unless there was a significant disturbance event (such as natural disasters). Events such as these are rare and difficult to predict, so assessing the long-term effects of this risk factor is more valuable than assessing effects within a few breeding seasons (see Duda et al. 2020a).

Although migrating petrels are likely exposed to predators on the ocean, they live among dense colonies of their primary predators during the breeding season and are obligated to return to their nest burrows, making them highly vulnerable (Stenhouse et al.

2000, Pollet et al. 2020). The risk from predation is therefore considered to be most concentrated within a breeding season for colonies where Leach’s Storm-Petrels coexist with their predators. This is also true for light attraction. Because oil platforms on the Grand Banks intersect foraging paths (Hedd et al. 2018), birds will likely be highly exposed to light pollution from offshore oil platforms during the breeding season (Hedd et al. 2018). Exposure to oceanic light pollution during migration requires investigation that is beyond the scope of this thesis. Because of the relative consistency of the risks posed by predation and light pollution during the breeding season, my thesis focuses on these risks in a colony with known exposure to both.

1.4 STUDY SITE

I studied the Leach's Storm-Petrel population on Gull Island (47.26265, -52.77187) in the Witless Bay Ecological Reserve, Newfoundland and Labrador, Canada (Figure 1.1). The most recent population estimate for this colony (2017) is 179 743 pairs, down from a 2001 estimate of 351 866 pairs (Robertson et al. 2006, Wilhelm 2017). This colony has been monitored for more than 10 years for dietary trends, foraging and migratory behaviour, survival, reproductive success, and more.

Figure 1.1. Map of the Witless Bay Ecological Reserve, NL, Canada.

1.5 OBJECTIVES

The goal of this thesis is to examine the exposure of Leach's Storm-Petrels to marine and terrestrial risks during the breeding season. In Chapter 2, I (1) assess the level of temporal overlap in the colony activity of Leach's Storm-Petrels and their main predator, the Herring Gull, and (2) investigate the interactive associations between predator activity and weather and habitat factors on the nocturnal terrestrial activity of Leach's Storm-Petrels to better understand constraints on their activity during the breeding season. In Chapter 3, and with these constraints in mind, I (3) determine the temporal and behavioural foraging track structure of parental storm-petrels and (4) determine their temporal and spatial associations with offshore oil platforms during the breeding season. Finally, in Chapter 4 and throughout the thesis, I (5) evaluate the risk imposed on adult Leach's Storm-Petrels by gull predation and oil platforms during the breeding season, and how these pressures have and could change over time to (6) make recommendations for future research and potential conservation strategies for this at-risk species.

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CHAPTER 2: TERRESTRIAL RISK AND COLONY ACTIVITY OF THE LEACH'S STORM-PETREL

2.1 ABSTRACT

Leach's Storm-Petrels are experiencing dramatic population declines, to which high levels of predation during the breeding season may contribute at some colonies. These tiny seabirds nest in burrows on island colonies where they coexist with their predators. They are nocturnal at the colony, being present in the burrow during the day and only leaving or returning to the burrow at night. The nest burrows offer protection for the adults and chicks, though adults are vulnerable to predation when they depart and return to the burrow. In the Witless Bay Ecological Reserve, Newfoundland and Labrador, Canada, diurnal Herring Gulls are the dominant predator of Leach's Storm-Petrels. Although they are active at the colony at opposite times, storm-petrels are vulnerable to gull predation during crepuscular periods when both species may be active. Predation risk may vary with weather, such as when environmental light and the ease of movement (due to factors such as high winds, etc.) of birds may affect the colony activity and interactions of the species. The present study gauges predation risk on Gull Island by measuring colony activity overlap between storm-petrels and gulls. Vocal activity, as measured using sound recorders, was used as a proxy for colony activity for both species to minimize disturbance and to capture nocturnal activity throughout the breeding season. Herring Gull vocal activity was associated with time of day and date. Leach's Storm-Petrel vocal activity was associated with time of day, habitat, cloud cover, and Herring Gull vocal activity, the latter being the most important predictor. Though Leach's Storm-Petrels are constrained by their nocturnality at the colony, they appear to structure their nocturnal colony activity around that of their top predator. This behavioural adaptation may bolster adult survival during the breeding season.

2.2 INTRODUCTION

The Leach's Storm-Petrel (*Hydrobates leucorhous*) is the smallest, most abundant breeding seabird in the North Atlantic (Montevecchi et al. 1992). Despite their abundance, a massive population crash has resulted in the loss of about 54% of the Atlantic Canadian population in just 44 years (BirdLife International 2017, Montevecchi and McFarlane Tranquilla 2019, COSEWIC 2020, Duda et al. 2020c, Wilhelm et al. 2020). Consequently, the species has been listed as 'Vulnerable' on the International Union for Conservation of Nature (IUCN) Red List and 'Threatened' by the Committee on the Status of Endangered Wildlife In Canada (COSEWIC) (BirdLife International 2017, COSEWIC 2020). Recent paleoenvironmental research has revealed fluctuations in storm-petrel populations over the last 1700 years, though unusually sharp modern decreases may be attributed to anthropogenic and natural factors and limited gene flow among colonies, emphasizing the need for a wider network of ecological reserves (Duda et al. 2020a, 2020c).

Several non-independent factors are likely contributing to the population decline, including prey declines, marine habitat disruptions and declines in reproductive success linked to climate change (Mauck et al. 2018, Buren et al. 2019, Freer et al. 2019), changes in terrestrial breeding habitat (d'Entremont et al. 2020, Duda et al. 2020a, 2020b), high mercury and plastic body-burdens (Bond and Lavers 2013, Provencher et al. 2014, Burgess et al. 2017, Pollet et al. 2017), and fatal attraction to coastal and oceanic light pollution (Wiese et al. 2001, Montevecchi 2006, Burke et al. 2012, Ronconi et al. 2015, Davis et al. 2017).

Predation risk at the breeding colony may also be at play. While many of the world's largest colonies, located off the eastern coast of Newfoundland, Canada, are relatively free from invasive species that prey on Leach's Storm-Petrels, these colonies are also the site of the most globally significant population losses (Robertson et al. 2006, Duda et al. 2020c, Wilhelm et al. 2020). It is therefore important to assess how natural predators are impacting populations during the breeding season. In some Newfoundland colonies, Herring Gulls are the dominant predators of Leach's Storm-Petrels during the breeding season (Stenhouse et al. 2000), and gull predation may be contributing to local population declines (Stenhouse and Montevecchi 1999, Wilhelm et al. 2020). In an Icelandic colony of approximately 160 gulls, an average of two adult Leach's Storm-Petrels total were eaten per day, and they appeared in about 20% of gull pellets (Hey et al. 2019). On Bon Portage Island, gulls were responsible for annual predation of up to 5% of that colony's total population (Hoeg et al. 2021). Two studies on Great Island, Newfoundland and Labrador, Canada, estimated the annual predation of Leach's Storm-Petrels by gulls at nearly 50 000 individuals in both 1976 and 1997, accounting for 9% of the island's total population (Pierotti 1982, Stenhouse et al. 2000). In 2012, a staggering estimate of 110 000 adult Leach's Storm-Petrels were taken by gulls on Gull Island, Newfoundland and Labrador, Canada (Bond unpubl. data).

Given that predation can be significant, understanding the interactions between predator and prey can be useful for conservation efforts. Leach's Storm-Petrels are nocturnally active at the colony. Herring Gulls are diurnally active, and although they will prey upon storm-petrels who leave their burrows at dawn (Weseloh et al. 2020), fly close to the colony during the day (Watanuki 1986), or are trapped inshore during the day as wrecks (d'Entremont et al. 2021), they must primarily prey on storm-petrels at the colony at night (Watanuki 1986, Bryant 1993, Weseloh et al. 2020). In this study, I investigate the periods of overlap in nocturnal activity between these predator and prey, as this is when Leach's Storm-Petrels are most vulnerable to predation. I also investigate sources of the variation in timing and extent of overlap to better understand factors that may constrain storm-petrel behaviour and influence their vulnerability to gull predation.

Numerous environmental factors influence the activity of storm-petrels and gulls. Many studies have identified the negative association between lunar illumination and activity level of nocturnal seabirds (e.g. Watanuki 1986, Bryant 1993, Mougeot and Bretagnolle 2000, Keitt et al. 2004, Riou and Hamer 2008). Gulls tend to be more nocturnally active on brighter nights (Burger and Staine 1993), so storm-petrels may be at higher risk of predation on nights with greater moon illumination (e.g. Watanuki 1986, Bryant 1993). Weather factors, like fog, that influence the illumination levels of moonlight also influence colony attendance outside the burrow and the time individuals return to the colony (Bryant 1993). Fog affects coastal Herring Gull foraging (Hebert 1987), and dense cloud cover reduces nocturnal foraging activity by Laughing Gulls (*Leucophaeus atricilla*) and Ring-billed Gulls (*Larus delawarensis*; Burger and Staine 1993). Wind speed and direction have been associated with storm-petrel activity and colony attendance (Furness and Baillie 1981, Gladwell et al. 2019). Windspeed may also influence the gulls' activity, as higher winds can facilitate searching and hovering when attacking prey (Gilchrist et al. 1998). Nesting location and habitat is also important;

Herring Gull foraging may be affected by nesting habitat, as adults that nest closer to storm-petrel burrow habitat tend to prey more on storm-petrels than gulls that breed in other habitats on the same island (Pierotti and Annett 1991). Habitat can also affect the number of storm-petrels in an area, as storm-petrels show preferences for forested and dense fern areas, so burrow density and therefore colony attendance may differ significantly among habitat types (Grimmer 1980, Stenhouse 1998). Additionally, storm-petrels may be more visible and in closer proximity to nesting predators in open areas (Stenhouse 1998), although one study found no differences between forested and open habitats in the number of petrel carcasses found (Stenhouse and Montevecchi 1999).

Nocturnal, burrowing seabirds are difficult to monitor and are sensitive to researcher disturbance (Blackmer et al. 2004, Carey 2009, Fiske et al. 2013), as traditional census and monitoring techniques are invasive and destructive to habitat (Ambagis 2004). In this study, I use acoustic monitoring – the recording of vocalizations of target species for the purposes of quantifying population size, active periods, etc. – to assess the variation in activity overlap of storm-petrels and gulls. Leach's Storm-Petrels produce most of their calls when they are outside the burrow (Gladwell et al. 2019, Pollet et al. 2020) where they are vulnerable to predation by Herring Gulls, so the frequency of Leach's Storm-Petrel calls can be used to inform the number of potentially vulnerable individuals in an area at a particular time. Herring Gulls produce mew and long calls, their most common call types, when defending a feeding territory (Drury and Smith 1968, Weseloh et al. 2020). In addition, Herring Gulls vocalize frequently when they are awake/alert, and opportunistic predation by Herring Gulls of other birds can be significant

(Ingraham et al. 2020), so any awake Herring Gull could be a potential danger. The number of vocalizing Herring Gulls can therefore inform the level of predation risk to active Leach's Storm-Petrels.

Both Leach's Storm-Petrels and Herring Gulls are good candidate species for acoustic monitoring. Leach's Storm-Petrels of both sexes call frequently and produce numerous distinctive and repetitive calls (Pollet et al. 2020). Acoustic monitoring studies have been used to monitor declining populations of Leach's Storm-Petrels (Orben et al. 2019), their burrow occupancy (Ambagis 2004), and hourly, nightly, and seasonal variation in their activity (Buxton and Jones 2012, Gladwell et al. 2019). Herring Gulls also produce a variety of distinctive calls that can be identified in acoustic monitoring studies (Weseloh et al. 2020), so this technique is useful for monitoring the activity overlap of Leach's Storm-Petrels and their primary terrestrial predator.

In the present study, I use storm-petrel call frequency as a proxy for colony attendance outside the burrow. I use Herring Gull call frequency as a proxy for colony attendance of awake gulls. For both species, I refer to this measurement as colony activity, which approximates the number of active individuals at the colony. When combined, these data inform the level and timing of overlap in colony activity between storm-petrels and gulls, and therefore the level of predation risk to storm-petrels. I incorporate environmental and temporal factors into these analyses to help explain the variation in the level of colony activity overlap by these species. I hypothesize that Leach's Storm-Petrels act to reduce predation risk at the colony by exiting the burrow or returning to the island from the sea at specific times, and I predict that there will be a negative correlation between the colony activity levels of Leach’s Storm-Petrels and Herring Gulls.

2.2.1 Chapter Objectives

1. To describe temporal patterns of Leach’s Storm-Petrel colony activity in relation to time of day, time of year, and environmental factors.
2. To describe the temporal patterns of Herring Gull colony activity in relation to time of day, time of year, and environmental factors.
3. To determine the timing, degree, and variation in overlap of colony activity of Leach’s Storm-Petrels and Herring Gulls to better assess predation risk.

2.3 METHODS

2.3.1 Field Methods

2.3.1.1 Study Site

This study was conducted on Gull Island in the Newfoundland and Labrador Witless Bay Ecological Reserve on (47.26265, -52.77187; Figure 2.1), which has been studied extensively for more than 10 years (Wilhelm 2017). The island is mainly forested with open areas around the perimeter, and my work was done in both habitat types. Differences in habitat variables between the two plots are presented in Figure S 1 in Appendix B. The forested plot had generally high (>50%) canopy cover, and ground cover was mostly fern or pine needles. A Herring Gull nesting colony was about 10 meters east of the forested plot. The second plot was much more open, with no canopy cover over most of the plot. Ground cover was much more diverse in the open plot, where fern and raspberry were common. Breeding Herring Gulls surrounded the open plot on all sides, with most nesting gulls east of the plot. Although no gull nests were found within the open plot, adults commonly flew directly over the plot or rested on dead trees within and immediately surrounding it. Much of Gull Island is forested, and this habitat tends to have the highest density of occupied Leach's Storm-Petrel burrows (Grimmer 1980). I did not directly assess occupied burrow density because the microphone arrays (see below) overlapped with plots that were being used for other research that does not allow intervention in the burrows. However, a similar number of occupied burrows were found and regularly monitored in each of these plots using Passive Integrated Transponder (PIT) tags.

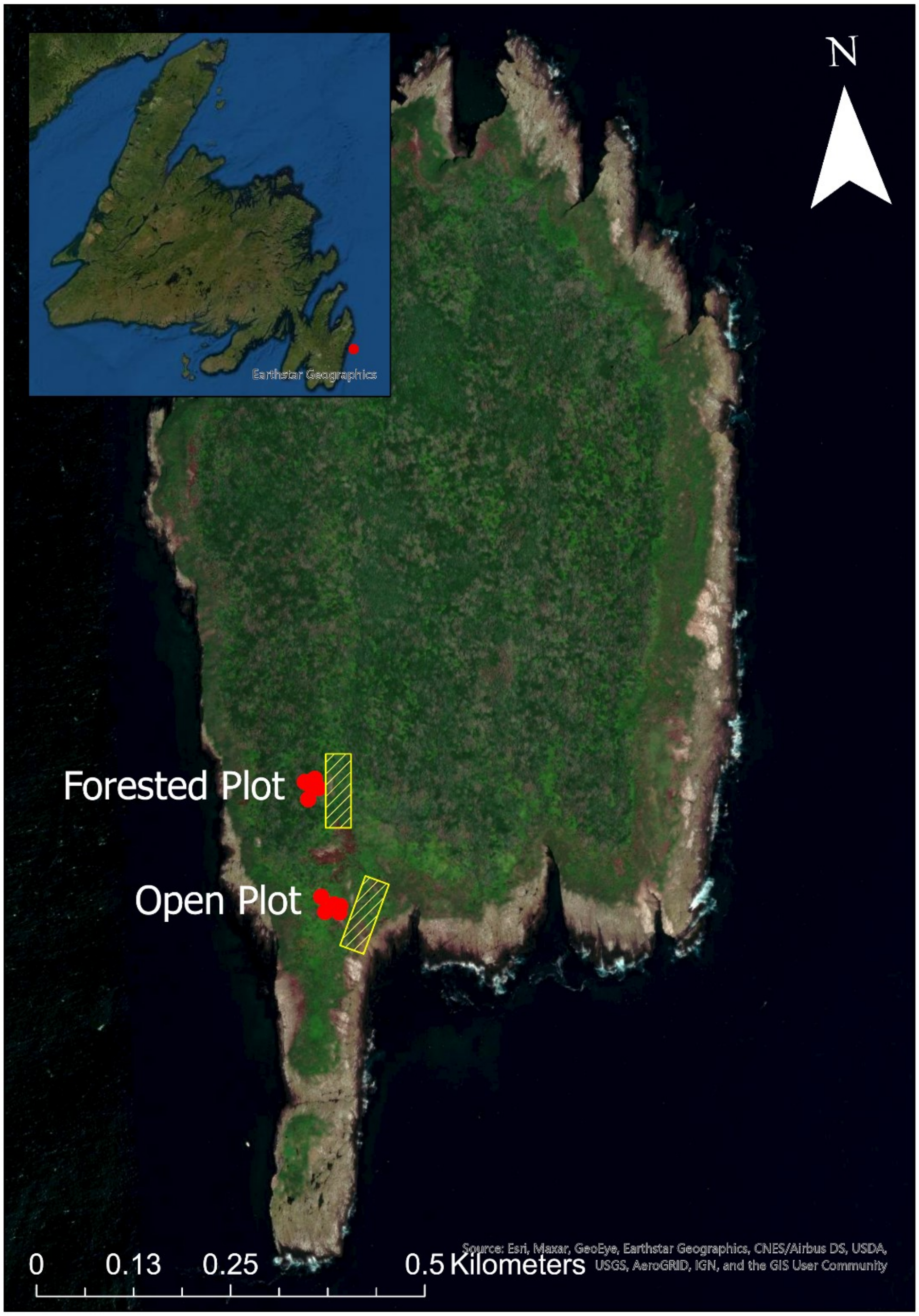

Figure 2.1. Locations of recording plots on Gull Island. Red dots represent the location of each microphone in the microphone arrays. Yellow hatched boxes show approximate locations of dense Herring Gull nesting habitat. Forests appear as dark green; meadows and grassy slopes are lighter green around the island perimeter.

2.3.1.2 Vocal Recordings

I measured call frequency in forested and open habitat (Figure 2.1) using autonomous audio recorders (WAVE format, 24 kHz sampling rate, 16-bit amplitude encoding; Wildlife Acoustics Song Meters, model SM3; Wildlife Acoustics, Concord, MA) set to record each day (20:00 to 08:00 h) from 25 June until 10 August 2019. Recording began before sunset and ended after sunrise on all days and produced six 2-hour stereo files for each recorder for each night. This is the period when Leach's Storm-Petrels have the highest calling rates (Huntington et al. 1996). Two recorders were placed in each habitat, and each recorder had two microphones, including one attached to the recorder and one that extended outward on a cable, also attached to the recorder. The four microphones were arranged in a 40 x 40 m array, which allowed me to expand the area covered at each site. The recorders and microphones were secured to trees approximately 1.5 m above the ground. The omnidirectional microphones captured all calls produced within the area bounded by the microphone array, and within the 10-m area surrounding the array (Hennigar et al. 2019, Ethier and Wilson 2020, Fahmy and Wilson 2020).

Logistical constraints precluded changing the recorders' batteries regularly, resulting in inconsistent gaps in the recordings. To examine plot differences, I only analyzed days for which all four recording channels in both plots produced a recording and when the recordings were not obscured by high winds or rain. I analyzed a sample of 8 days (27 June, July 1, 5, 8, 15, 17, 24, 28) that met these criteria and that maximized the time interval between days. This sampling period covered the bulk of the storm-petrels' incubation period (For Gull Island: mid June to ~ July 21; A. Hedd. unpub. data). Only a few pairs would have been leaving their burrows to forage for chicks on the last day of the sample of recordings.

2.3.1.3 Weather Data

Weather data for 2019 were collected using a Kestrel 5500 Weather Meter (Kestrel Meters, Boothwyn, PA), which measured 19 weather variables every 20 minutes including temperature (^{o}C, accuracy ±0.5°C), wind speed (m/s, accuracy larger of 3% of reading, least significant digit or 20 ft/min), and true wind direction (^{o} relative to North, accuracy ± 5°). Moon Illumination (percentage of moon visible representing the stage in the lunar cycle) and times of moonrise/moonset were obtained from timeanddate.com (Thorsen 2020). Cloud cover (%) for Gull Island in 2019 is from Weather Source, LLC (2020).

2.3.2 Sound Analysis

I used vocalization recordings to measure the calling frequency of Leach's Storm-Petrels and Herring Gulls. All Herring Gull call types were considered in these analyses (Table S 1), but I only counted chatter calls for Leach's Storm-Petrels. Herring Gull calls are produced either on the ground or while flying (Weseloh et al. 2020), and their calls are much louder and cover a broader frequency range than Leach's Storm-Petrel calls (Shah et al. 2015, Yip et al. 2017), so all calls types produced within range of the microphones are likely to be detected. The most common call types produced by adult Leach's Storm-Petrels are purr and chatter calls; purr calls are produced almost exclusively from within the burrow, and although chatter calls may sometimes be produced from the burrow, they are more often produced by individuals while flying or on the ground (Pollet et al. 2020), making this call type easily detectable (Gladwell et al. 2019). Counts of chatter calls can therefore provide information on the number of storm-petrels present at the colony in the assessed location. Descriptions and functions of all call types of Leach's Storm-Petrels are outlined in Table S 2, and Herring Gull call types and their functions are outlined in Table S 1.

The recordings were analyzed using Audacity 2.3.3, which allows the user to both listen to and visualize the spectrogram for recordings (Audacity Team 2019). A high pass filter of 1000 Hz and a noise gate of -50 dB were applied to every channel of every recording; the calls of both Leach's Storm-Petrels (Taoka et al. 1989) and Herring Gulls (Shah et al. 2015) have a median frequency above 1000 Hz. The Noise Gate of -50 dB was chosen based on the calculated Noise Floor (lowest decibel level in the recording) and average decibel level of every three-minute recording. To standardize the area over which calls were detected, all calls detected on at least three of the four channels from the recorders were included (Fahmy and Wilson 2020). A "detected" call was one that the I could either see or hear on the recording. See Figure S 2 for example spectrograms that visualize Leach's Storm-Petrel and Herring Gull calls.

To investigate the association of the onset and termination of Leach's Storm-Petrel colony activity with sunrise, and to better understand the variation in the onset and termination of their colony activity with date, the first and last 30 Leach's Storm-Petrel calls were counted for each sample day. I chose 30 calls because, based on personal observation of the recordings, this captured outliers that called especially early or late, as well as the period when storm-petrels began calling regularly (every few seconds). I viewed each 3-minute recording as 4-channel spectrograms in Audacity (Audacity Team 2019). I began looking for calls at the start of the recording period (20:00:00) and stopped when I identified the first 30 Leach's Storm-Petrel calls. The 30 terminal calls were identified by starting at the end of the recording period (07:59:59), moving backwards through the recording, and stopping when the last 30 calls were detected. An assistant (Mackenzie Grace) and I conducted all first and last call analyses. I provided extensive training to the assistant and checked all analyzed files to ensure calls were not missed or misidentified.

I analyzed the first three minutes of each hour of each recording to test for possible associations between the calling frequencies of Leach's Storm-Petrels and Herring Gulls, and to describe variation in calling frequencies throughout and between nights. I counted every Leach's Storm-Petrel chatter call and every Herring Gull call within the three-minute recording sample that could be seen on the spectrogram or heard in the playback in three of the four audio channels. In some instances, there were too many gull calls occurring simultaneously throughout the three-minute recording to count. These instances were given a ceiling value of 350 calls for the three-minute window, based on the maximum number of calls that I was able to count in clearer recordings. An assistant (Eleanor Kenyon) and I counted calls, and I checked all completed files to ensure calls were not missed or misidentified.

2.3.3 Statistical Analyses

Model construction followed the steps for conducting regression analyses outlined in Zuur and Ieno (2016) using the R package "glmmTMB" (Brooks et al. 2017) and models were compared with Akaike Information Criterion tests (AIC). All assumptions and model fits were tested using the “DHARMa” R package (Hartig 2020). I tested for over/underdispersion, zero-inflation, and temporal autocorrelation. The DHARMa package tests for over/underdispersion by testing the standard deviation of the observed data against the standard deviation of the data simulated from the specified model. Zero-inflation is tested by comparing the observed number of zeros to the predicted number of zeros based on the specified model. A Conditional Inference Tree was created for the models of Herring Gull and Leach’s Storm-Petrel colony activity using the R package “party” (Hothorn et al. 2006) to further examine each predictor's influence on calling frequency. Relative importance of predictors for all models was calculated for a covariance matrix of all model variables using the ‘lmg’ method of the ‘relaimpo’ R package (Grömping 2006). This method calculates how much variation can be explained by each predictor out of the proportion of variance in the response variable that is explained by the full model and is the recommended method for calculating relative importance (Grömping 2006, Zhang and Wang 2017). Because the sample days were not equidistant from one another, the Julian day of the year (assigned as the date the sample started) was used to represent the *Date* for all models.

2.3.3.1 Models describing onset and terminal Leach’s Storm-Petrel calls

I ran four models which investigated the change in the timing of the onset and termination of Leach’s Storm-Petrel calls throughout the season. The first two models, one each for onset and terminal calls, assessed the change in the average time of the first or last 30 detected storm-petrel calls ($n_{nights} = 10$, $n_{plots} = 2$, $N = 20$). The response variable, average time, was represented as minutes after 20:00 for each night and was modelled with the explanatory variables Date and Plot. The second two models were the same as the first but I used the corrected time of day, which was the minutes past sunset or before sunrise, as the timing of calls to determine the association with date independent of the effect of sunrise or sunset. These models improved the residual versus fit plots for *Date* without changing the dispersion estimates, so are therefore better fitting models.

2.3.3.2 Models for Herring Gull and Leach's Storm-Petrel Call Frequency

I used a modelling approach to examine the potential influence of Herring Gull activity, along with temporal and environmental factors, on Leach's Storm-Petrel activity. Because Herring Gull activity may also be influenced by temporal and environmental factors, I also modelled variation in their activity to identify potential interactive effects on storm-petrel activity. From the analyses of the onset and terminal calls of storm-petrels, I determined that Leach's Storm-Petrels were not active at the colony before 22:00 or after 5:00, so data points from 20:00, 21:00, 05:00, 06:00, and 07:00 were removed from the dataset for these models to reduce zero-inflation and control for effects of sunlight on activity of both species. The unit of replication in this second set of models was the number of counted calls within each three-minute recording for each hour of each night in each plot ($n_{\text{hours}} = 7$, $n_{\text{nights}} = 8$, $n_{\text{plots}} = 2$, $N = 112$). A limitation of these analyses is that I had no way to differentiate between calling individuals. It is likely that numerous counted calls were produced by the same individual within and between nights. I acknowledge that the measurement used here is not a true indication of the number of active individuals. Because these data were collected at regular time intervals, there is also a possibility for autocorrelation, however a test for autocorrelation revealed that it was not present in these data.

The call frequency models for Leach’s Storm-Petrels and Herring Gulls required transformation of some predictors. This dataset contained two circular variables (*Hour* and *Wind Direction*) that needed transformation to be included in the models. While it is possible to apply linear transformations to these variables, a linear transformation of direction, such as degrees from North, does not allow for differentiation between East and West whereas the pair of transformed variables does. High positive values of cos(*Wind Direction*) represent North and negative values of cos(*Wind Direction*) represent South. Positive values of sin(*Wind Direction*) represent West, and negative values of sin(*Wind Direction*) represent East. Although time could also be transformed to linear, the relationship of calling frequency with time is clearly non-linear for both species (Figure 2.2). Values of sin(*Hour*) above 0.5 are times in the morning (04:00 – 07:00) and values below -0.5 are in the evening (20:00 – 21:00). cos(*Hour*) is harder to interpret, however, values less than 0.5 represent 05:00 – 07:00. *Hour* and *Wind Direction* were trigonometrically transformed into pairs of variables using Equation 2.1 and Equation 2.2.

$$sin\left(\frac{2\pi \cdot Hour}{24}\right), \quad cos\left(\frac{2\pi \cdot Hour}{24}\right)$$

Equation 2.1. Trigonometric functions to transform the circular hour of the day variable into a pair of predictors.

$$sin\left(\frac{2\pi \cdot Wind\ Direction}{360}\right), \quad cos\left(\frac{2\pi \cdot Wind\ Direction}{360}\right)$$

Equation 2.2. Trigonometric functions to transform the circular Wind Direction variable into a pair of predictors.

Because weather variables can interact to influence individual activity and sound transmission, I examined the entire complex of measured weather variables and chose those for inclusion in our model based on variance inflation factors (VIFs). Between weather variables, there is a risk of multicollinearity, and analysis of VIFs test for this. I conducted a VIF test using the “corvif” function (Zuur et al. 2009, 2010). The predictor with the highest VIF score was eliminated and the VIFs were recalculated until all VIFs were less than three. An exception was the *cos(Hour)* variable, which was correlated with *HERG* (Herring Gull call frequency) and resulted in moderate variance inflation (<10). This variable was not removed because circular variables must be included as a sine and cosine pair (Pewsey et al. 2013). Non-convergence of the model prompted me to create a correlation plot of the remaining predictors using the “Mypairs” function (Zuur et al. 2009), which revealed a relatively strong correlation ($\rho = 0.57$) between *Headwind* and *Wind Direction,* so *Headwind* was also eliminated, leaving the following variables: *HERG*, *Wind Speed*, *sin(Wind Direction)*, *cos(Wind Direction)*, *Cloud Cover*, *Moon Illumination*, *sin(Hour)*, *cos(Hour)*, *Plot*, and *Date*.

The association of Herring Gull call frequency with environmental and temporal factors was assessed using a negative binomial model. The association of Leach’s Storm-Petrel call frequency with Herring Gull call frequency and environmental and temporal factors was assessed using a zero-inflated, negative binomial model with additional specifications to account for overdispersion and zero-inflation. Tests of the assumptions for both models (homogeneity of variance, normality of residuals, overdispersion, zero-inflation, temporal autocorrelation) showed no violations. Equations 2.3 and 2.4 show the final model for Herring Gull call frequency and Leach's Storm-Petrel call frequency.

$$HERG_i \sim Negative\ Binomial(\mu_i, k)$$

$$\mu_i = E(HERG_i) = \quad \text{and} \quad var(HERG_i) = \mu_i(1+k)$$

$$\begin{aligned} log\ (\mu_i) &= \alpha + \beta 1 \cdot Wind\ Speed + \beta 2 \cdot \sin(Wind\ Direction) + \beta 3 \\ &\cdot \cos(Wind\ Direction) + \beta 4 \cdot Cloud\ Cover + \beta 5 \cdot Moon\ Illumination \\ &+ \beta 6 \cdot \sin\ (Hour) + \beta 7 \cdot \cos\ (Hour) + \beta 8 \cdot Plot + \beta 9 Date \end{aligned}$$

Equation 2.3. The final statistical model of Herring Gull call frequency varying with all selected predictors, where HERG$_i$ is the *i*th observation of Herring Gull call frequency, α is the intercept, βx are the calculated regression intercepts, and $i = 1,\ldots,112$.

$$LESP_i \sim Negative\ Binomial(\mu_i, k)$$

$$\mu_i = E(LESP_i,\ NSZ) \quad \text{and} \quad var(LESP_i,\ NSZ) = \mu_i(1+k)$$

$$\begin{aligned} log\ (\mu_i) &= \alpha + \beta 1 \cdot HERG + \beta 2 \cdot Wind\ Speed + \beta 3 \cdot \sin(Wind\ Direction) + \beta 4 \\ &\cdot \cos(Wind\ Direction) + \beta 5 \cdot Cloud\ Cover + \beta 6 \cdot Moon\ Illumination \\ &+ \beta 7 \cdot \sin(Hour) + \beta 8 \cdot \cos(Hour) + \beta 9 \cdot Plot + \beta 10 \cdot Date \end{aligned}$$

$$(\pi_i) = \alpha_\pi + \beta_{\pi 1} \cdot HERG$$

$$log\ (k) = \alpha_k + \beta_{k1} \cdot HERG + \beta_{k2} \cdot \sin(Hour)$$

Equation 2.4 The final statistical model of Leach's Storm-Petrel call frequency varying with all selected predictors, where LESP_i is the *i*th observation of Leach's Storm-Petrel call frequency, *NSZ* is the event "non-structural zero", α is the intercept, βx are the calculated regression intercepts, π_i is the probability of *NSZ*, k is the variance, and $i = 1,\ldots,112$.

2.4 RESULTS

2.4.1 Nocturnal Vocal Activity

Leach's Storm-Petrels were most vocally active between 02:00 and 03:00 h when Herring Gulls were the least vocally active (00:00 and 03:00 h; Figure 2.2, Figure 2.3). There was no change in storm-petrel colony activity associated with date (Table 2.1), but, as anticipated with the increase in night length with Julian Date, they began calling earlier and finish calling later in the night as the season progressed (Figure 2.4,

Table S 3). Herring Gull colony activity peaked in the middle of the study period (Table 2.1).

Table 2.1. Means and standard deviations, calculated by averaging the calls from the hourly samples on each night, of the frequency of Herring Gull and Leach's Storm-Petrel calls on Gull Island, Witless Bay, Newfoundland, Canada during eight nights of the 2019 breeding season.

Date	LESP mean	HERG mean	LESP sd	HERG sd
June 26 – 27	87.143	69.929	70.512	63.966
June 30 – July 1	73.571	56.857	65.601	53.591
July 4 – 5	86.857	67.143	65.937	86.322
July 7 – 8	85.929	72.857	78.262	73.591
July 14 – 15	87.286	82.357	55.670	58.665
July 16 – 17	78.071	63.071	62.929	36.607
July 23 – 24	69.500	37.071	41.547	35.319
July 27 – 28	116.714	56.071	62.870	58.267

The first 30 storm-petrel calls were heard, on average, between 22:04 and 22:26, and the last 30 calls were heard, on average, between 03:59 and 04:14 (see Figure S 3 in Appendix B). Neither the timing of onset nor terminal calls varied between plots (

Table S 3). Onset calls started earlier, and terminal calls finished later as the season progressed, but these patterns were considerably weakened when considering the time since sunset or time before sunrise that the calls began (Figure 2.4). There was, however, a significant negative relationship between the average time of terminal calls before sunrise and date (

Table S 3). The duration of night increased throughout the season, and storm-petrels were active at the colony for longer later in the season. Because the timing of sunrise and sunset is so important for the onset and termination of activity of Leach's Storm-Petrels, we only consider nocturnal activity of both storm-petrels and gulls in all other analyses.

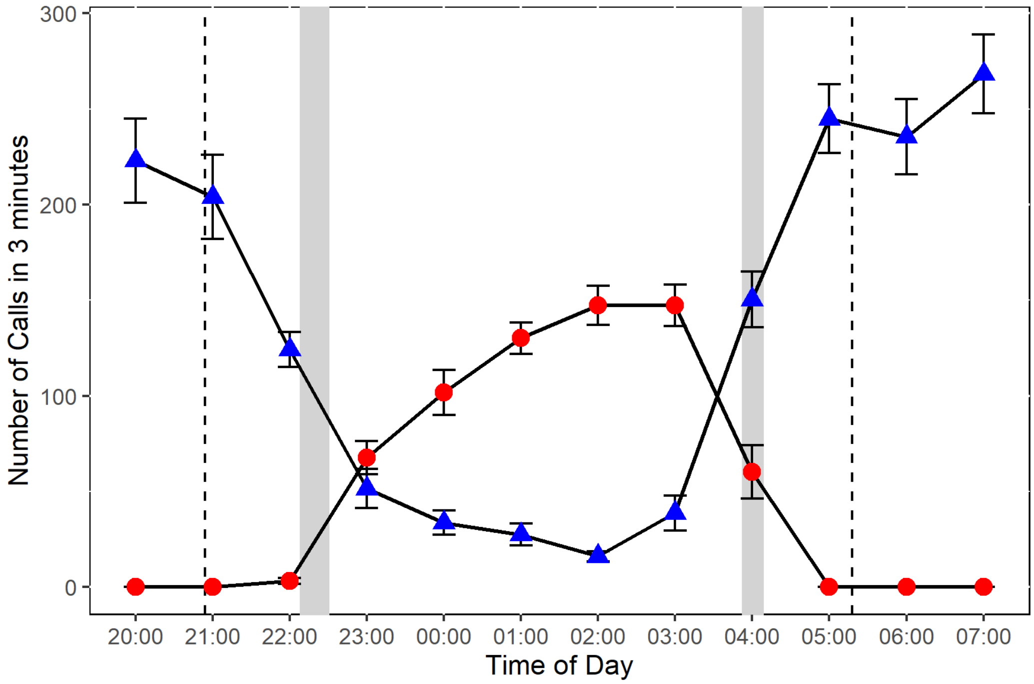

Figure 2.2. Line plot of the average (+SE) hourly frequency of Leach's Storm-Petrel (red circles) and Herring Gull (blue triangles) calls during the 2019 breeding season on Gull Island, Witless Bay Ecological Reserve, NL. Vertical dashed lines represent the average sunset and sunrise times and grey vertical bars represent the average timing of the onset and terminal 30 Leach's Storm-Petrel calls throughout the season.

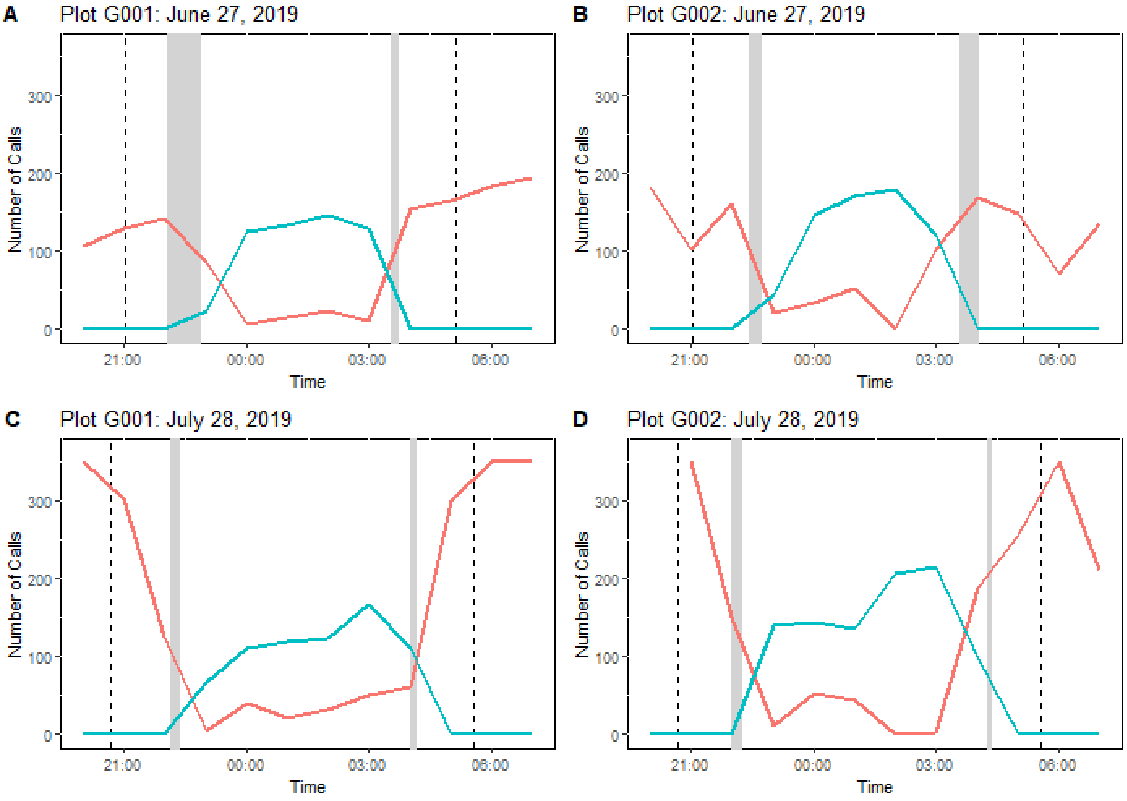

Figure 2.3. Line graphs showing the relationship between call frequency of Leach's Storm-Petrels (blue) and Herring Gulls (orange). Grey bars represent the times of the first and last 30 calls for each day in each plot. Dotted lines represent the times of sunrise and sunset. See Figure S 3 in Supplementary Material for the full set of line graphs for each day and plot in the sample.

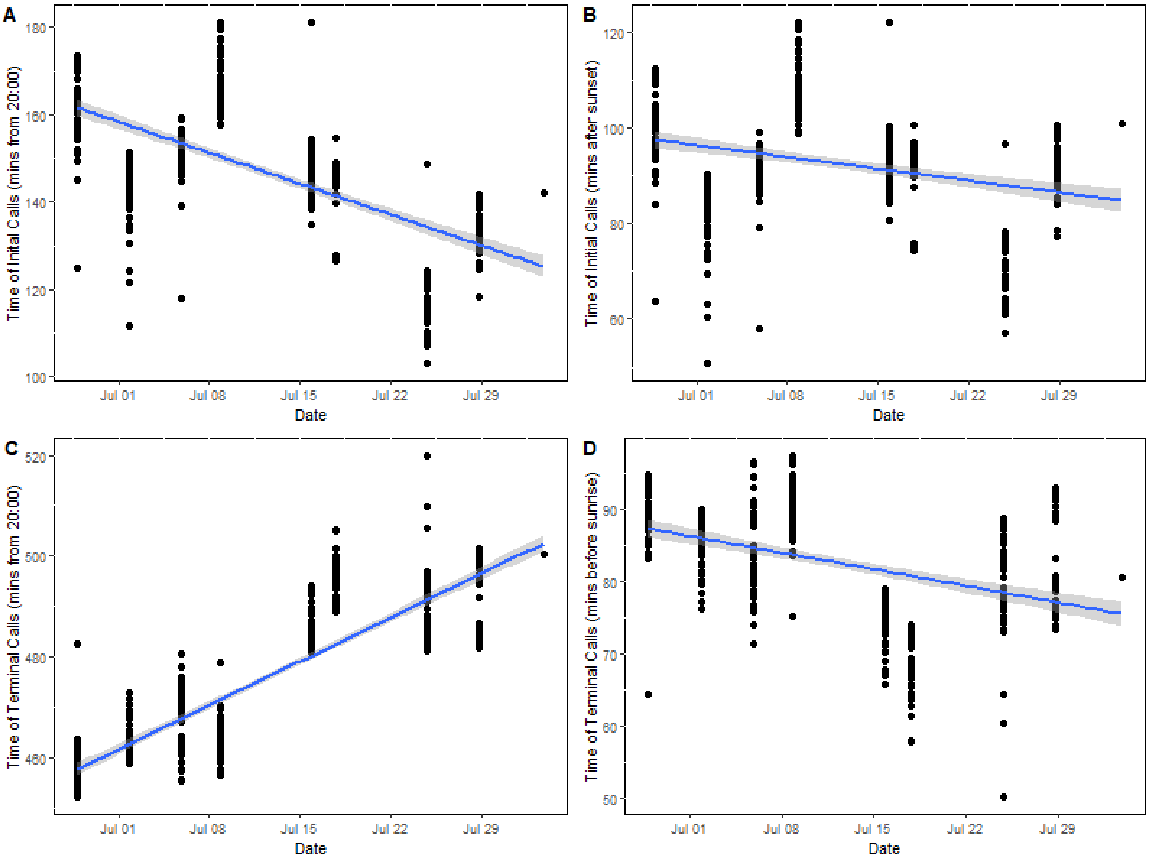

Figure 2.4. Change in the timing of a) the onset and c) the terminal 30 Leach's Storm-Petrel calls throughout the breeding season. The strength of the relationship between date and time of day is reduced when accounting for the timing of b) the first 30 calls after sunset and d) the last 30 calls before sunrise.

2.4.2 Factors Associated with Leach's Storm-Petrel Colony Activity

The trigonometric transformations of hour of the day ($z_{sin(Hour)} = 5.668$, $z_{cos(Hour)} = 3.299$, both $p < 0.001$) were significant predictors of Leach's Storm-Petrel call frequency (Table 2.2). As is evident in Figure 2.2, call frequency was greatest in the middle hours of the night. Leach's Storm-Petrels called more in the open plot than in the forested plot ($\underline{x}_{forest} = 70.291$ calls/3 minutes, $\underline{x}_{open} = 101.054$ calls/3 minutes, $z = 5.962$, $p < 0.001$), and their call frequency was negatively associated with Herring Gull call frequency (z = -

2.720, p = 0.007). Herring Gull activity was the most important predictor of Leach's Storm-Petrel activity, followed by the sine and cosine of Hour (Table 2.3). Although there was a significant, negative association between cloud cover and Leach's Storm-Petrel activity, cloud cover was one of the least important predictors (Table 2.2, Table 2.3). The conditional inference tree showed that the highest Leach's Storm-Petrel call frequencies occurred in the open plot after midnight when Herring Gull call frequency was less than 60 calls (Figure 2.5). Plots of the call frequency of Leach's Storm-Petrels associated with each untransformed variable can be seen in Figure S 4 in Appendix B.

The data were significantly zero-inflated (zero Leach's Storm-Petrel calls detected in the 3-minute acoustic survey) and overdispersed. The probability of detecting zero Leach's Storm-Petrel calls in a 3-minute acoustic survey increased with increasing Herring Gull call frequency. Variance of Leach's Storm-Petrel call frequency was significantly predicted by the number of Herring Gull calls, and by sin(Hour) (Table 2.2).

Table 2.2. Results of the zero-inflated negative binomial model for the variation of Leach's Storm-Petrel call frequency with Herring Gull call frequency, time, date, location, and various weather factors. Significant predictors in the models are in **bold** text.

Model Type	Predictor	Estimate	Standard Error	z value	p value
Conditional model:	**(Intercept)**	**3.060**	**1.618**	**1.891**	**0.059**
	HERG	**-0.004**	**0.002**	**-2.720**	**0.007**
	Wind Speed	0.077	0.072	1.067	0.286
	sin(Wind Direction)	0.017	0.466	0.370	0.711
	cos(Wind Direction)	0.039	0.071	0.550	0.582
	Cloud Cover	**-0.002**	**0.001**	**-2.150**	**0.032**
	Moon Illumination	-0.001	0.001	-1.060	0.289
	sin(Hour)	**1.538**	**0.271**	**5.668**	**<0.001**
	cos(Hour)	**1.933**	**0.586**	**3.299**	**<0.001**
	Open Plot	**0.318**	**0.053**	**5.962**	**<0.001**
	Date	-0.002	0.006	-0.356	0.722
Zero-inflation model:	**(Intercept)**	**-7.881**	**2.728**	**-2.889**	**0.004**
	HERG	**0.049**	**0.018**	**2.665**	**0.008**
Dispersion model:	**(Intercept)**	**1.666**	**0.436**	**3.825**	**<0.001**
	HERG	**0.027**	**0.007**	**3.993**	**<0.001**
	sin(Hour)	**-1.640**	**0.587**	**-2.793**	**0.005**

Table 2.3. Relative Importance of each predictor in the model for nocturnal colony activity of the Leach's Storm-Petrel, measured as the amount of variation that can be explained by each predictor out of the proportion of variance in the response variable that is explained by the full model.

Predictor	Relative Importance
Herring Gull Activity	0.364
Plot	0.065
Wind Speed	0.005
Cloud Cover	0.002
Moon Illumination	0.002
sin(Hour)	0.223
cos(Hour)	0.093
cos(Wind Direction)	0.001
sin(Wind Direction)	0.007
Date	0.004

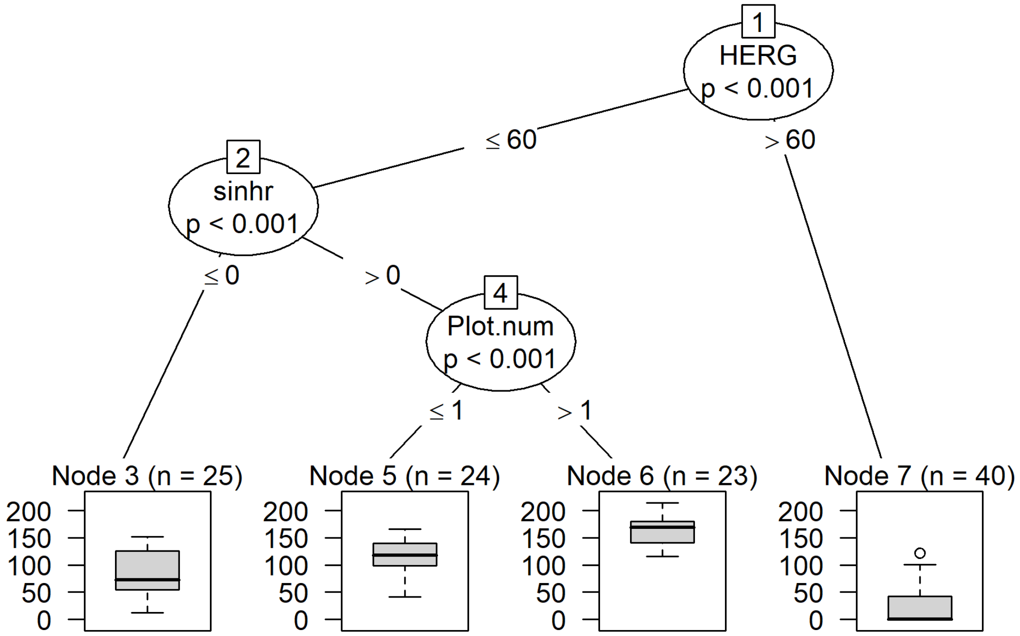

Figure 2.5. Conditional Inference Tree for the Leach's Storm-Petrel model. Conditional Inference Trees are created using recursive binary partitioning, which creates groups within the population or sample based on important predictors in a model. The order of nodes for partitioning is indicated in squares above each circle, and above each boxplot. The variable on which each node is based is contained within the circles, where HERG is the frequency of Herring Gull calls per three minutes, sinhr is the sine of hour of the night, and Plot.num is the ID of the plot where 1 represents the forested plot and >1 represents the open plot. The numbers contained within each line connecting each node indicate the value of the predictor that separates nodes.

2.4.3 Factors Associated with Herring Gull Colony Activity

Herring Gull call frequency was the most important predictor of Leach's Storm-Petrel activity. Therefore, I wanted to investigate sources of variation in Herring Gull activity to inform potential interactions between factors that influence storm-petrel activity. Herring Gull call frequency was negatively associated with time (called most frequently in the evening and in the morning; $z_{\sin(\mathrm{Hour})} = -11.136$, $z_{\cos(\mathrm{Hour})} = -12.469$, both $p < 0.001$). Plots of Herring Gull call frequency against each untransformed variable can be seen in Figure S 5 in Appendix B. The test of relative importance of each predictor in the model showed that the circular time variables were the most important predictors of

Herring Gull activity (Table 2.4). Herring Gulls called less frequently at night than during sunlit hours (Figure 2.2). Conditional on the time of day, Herring Gulls tended to call more when the moon was more full (Figure 2.6).

Table 2.4. The negative binomial model results for the variation of Herring Gull call frequency with time, date, location, and various weather factors. Significant predictors in the models are in **bold** text.

Model	Predictor	Estimate	Standard Error	z value	p value
Conditional model	**(Intercept)**	**12.869**	**1.293**	**9.951**	**<0.001**
	Wind Speed	0.045	0.084	0.534	0.594
	sin(Wind Direction)	0.133	0.084	1.575	0.115
	cos(Wind Direction)	0.041	0.138	0.295	0.768
	Cloud Cover	-0.002	0.001	-1.614	0.107
	Moon Illumination	0.002	0.001	1.100	0.271
	Date	**-0.017**	**0.006**	**-2.741**	**0.006**
	sin(Hour)	**-1.644**	**0.148**	**-11.136**	**<0.001**
	cos(Hour)	**-6.346**	**0.509**	**-12.469**	**<0.001**
	Open Plot	0.077	0.102	0.756	0.450

Table 2.5. Relative Importance of each predictor in the model for nocturnal colony activity of the Herring Gull, measured as the amount of variation that can be explained by each predictor out of the proportion of variance in the response variable that is explained by the full model.

Predictor	Relative Importance
Plot	0.001
Wind Speed	0.009
Cloud Cover	0.004
Moon Illumination	0.003
sin(Hour)	0.143
cos(Hour)	0.428
cos(Wind Direction)	0.005
sin(Wind Direction)	0.029
Date	0.018

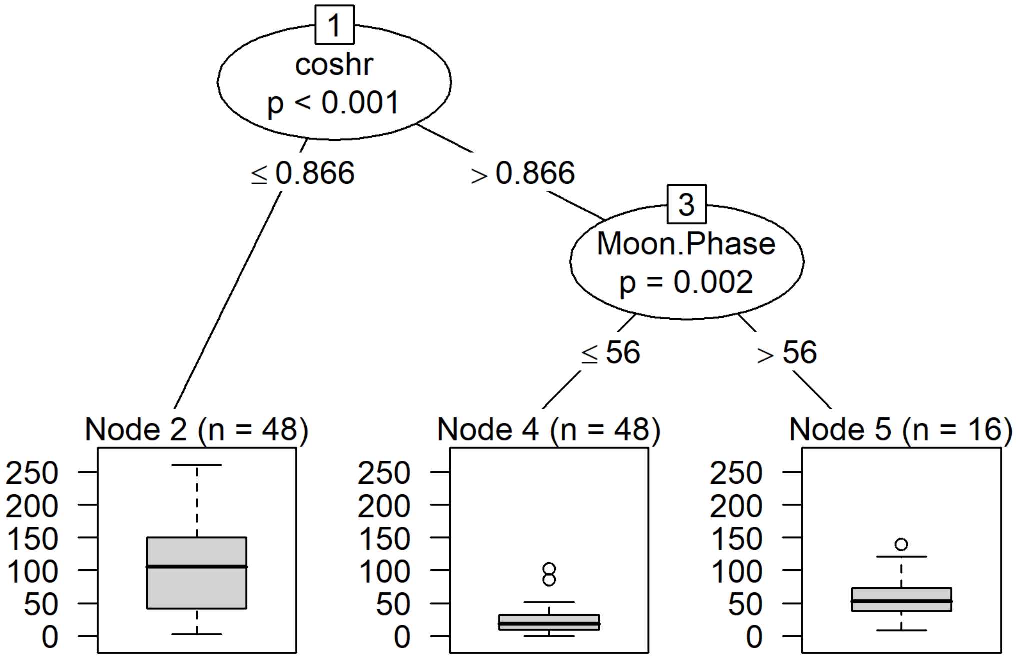

Figure 2.6. Conditional Inference Tree for the Herring Gull model. Conditional Inference Trees are created using recursive binary partitioning, which creates groups within the population or sample based on important predictors in a model. The order of nodes for partitioning is indicated in squares above each circle, and above each boxplot. The variable on which each node is based in contained within the circles, where, coshr is the cosine of hour of the night and Moon.Phase is the percentage of the moon visible. The numbers contained within each line connecting each node indicate the value of the predictor that separates nodes.

2.5 DISCUSSION

In this study, I investigated the patterns and overlap in nocturnal colony activity of Leach's Storm-Petrels and their top predator, Herring Gulls. Leach's Storm-Petrels were exclusively nocturnal at the colony during the study period (see Figure S 3 in Appendix B for precise timing of onset and terminal calls each night) which is unsurprising, as they are known to be nocturnal at the colony and infrequently call from their burrows during the day, when they do not leave or return to their burrows (Pollet et al. 2020). Herring Gulls were active at all times but reduced their colony activity levels at night (Figure 2.2). Nocturnally, Herring Gull activity was highest right after sunset and right before sunrise. This could mean both that more gulls were attending the colony and more gulls were alert, as colony attendance of Herring Gulls at Walney Island, England peaks around sunrise and sunset, and the fewest proportion of gulls were sleeping at these times (Galusha Jr and Amlaner Jr 1978). In my study, Herring Gull activity was lowest between midnight and 03:00. Herring Gulls are usually diurnal, although they are commonly nocturnally active (Garthe and Huppop 1996, Weseloh et al. 2020). That being said, they likely cannot see as well in darkness as they can in well-lit conditions; the retinas of Herring Gulls have not yet been studied, but other nocturnally active gull species (*Larus michahellis*, *Larus delawarensis, Larus modestus*) have enough rods to enable some night vision (Emond et al. 2006, Vidal et al. 2018). However, unlike nocturnal animals that can see well in the dark, these gull species have more cones than rods, suggesting that they are better adapted to seeing in daylight than in poorly lit conditions (Emond et al. 2006, Vidal et al. 2018). Further study on the nocturnal vision of Herring Gulls is required to better understand their nocturnal hunting behaviour.

Within the breeding season, I observed changes in the duration and timing of active periods. Nocturnal Herring Gull colony activity peaked in the middle of the study period (Table 2.1). Leach’s Storm-Petrel colony activity levels did not change with date (Table 2.1, Table 2.2), however, they began vocalizing earlier and stopped vocalizing later as the season progressed (Figure 2.4,

Table S 3), consistent with the timing of sunrise and sunset (Figure 2.4).

The mid-season peak in Herring Gull colony activity may relate to their breeding state. Parental gulls communicate with their chicks through vocalizations, and chicks recognize their parents' specific vocalizations soon after hatching (Knudsen and Evans 1986). Peak Herring Gull hatching dates on Gull Island occur in the second week of June (Haycock and Threlfall 1975, Weseloh et al. 2020), so most Herring Gull chicks would have hatched before the start of this study. Herring Gull chicks are semiprecocial and generally remain near the nest for a week after hatching (Weseloh et al. 2020). Parental gulls need to communicate with their chicks more often when they are not near the nest, explaining the increase in calls throughout the season. In addition, wandering chicks may enter the breeding territory of another pair of parental Herring Gulls, eliciting loud alarm calls from the territorial adults (Weseloh et al. 2020). Herring Gulls are naturally cannibalistic, with some adults actively searching out live chicks and others attacking and eating chicks who wander into their territory (Parsons 1971). The occurrence of parental alarm calls is likely to increase as the chicks age and begin to wander. At least one parent will continuously watch over the chicks until they are about 30 days old, at which point parental vigilance decreases significantly (Weseloh et al. 2020). This pattern of parental care matches the pattern of activity I observed in this study.

My key finding was that Herring Gull colony activity was the most important predictor of Leach’s Storm-Petrel colony activity (Table 2.3). Leach’s Storm-Petrel colony activity was lower when Herring Gull colony activity was high (Figure 2.2, Figure S 6). Both Leach’s Storm-Petrel and Herring Gull colony activity were inversely associated with time of day (Figure 2.2), and time was an important predictor of colony activity for both species (

Table 2.5, Table 2.3). While I cannot say with any certainty that changes in Herring Gull vocal activity caused the observed patterns of Leach’s Storm-Petrel vocal activity, I can conclude that there is a strong inverse association between them. Leach’s Storm-Petrels may, therefore, respond both to time of day and Herring Gull vocal activity. These results concur with a recent study on Kent Island, New Brunswick, which found that the call rates of Leach’s Storm-Petrels and Herring Gulls were inversely associated, though the relationship varied with nesting habitat (Gladwell et al. 2019).

A potential methodological problem that might contribute to the strong correlation between storm-petrel and gull activity is the researcher's ability to detect calls. Herring Gull calls are much louder and cover a broader frequency range than Leach’s Storm-Petrel calls (Taoka et al. 1989, Shah et al. 2015), so it is likely that some storm-petrel calls were missed during particularly busy Herring Gull periods. However, there were times when both Herring Gulls and Leach’s Storm-Petrels were calling together, and the calls of both species were discernable to a trained researcher, albeit not as precisely as when only one species was calling (Figure S 2).

In addition to variation with date and time, habitat was associated with colony activity. Leach's Storm-Petrels had greater colony activity in the open habitat (~101 calls/3 minutes) than in the forested habitat (~79 calls/3 minutes), whereas Herring Gull colony activity did not differ between habitats (Table 2.4, Figure S 5). Differences in occupied burrow density and habitat suitability between the two plots (Figure S 1) might account for this difference in activity (Stenhouse and Montevecchi 2000, Gladwell et al. 2019), or the difference could be due to the differences in attenuation of sound in forested versus open environments (Yip et al. 2017a). My acoustic arrays overlap with plots used for a PIT tag study that requires minimum disturbance, so I did not directly assess occupied burrow density in either plot, however, a similar number of burrows were located and continually monitored with PIT tags in these plots, so occupied burrow density within my acoustic arrays is likely similar. While I did not find plot differences in Herring Gull vocal activity, they were located in high densities in approximately equal distances from each microphone array (Figure 2.1) and their calls cover a broader frequency spectrum and tend to be louder than Leach's Storm-Petrel calls, which will result in less attenuation (Yip et al. 2017b). Finally, adult Leach's Storm-Petrels may fly through the open plot when returning to their burrows elsewhere, so the higher rate of vocalizations may be from birds flying overhead. This explanation is supported by a recent, similar study that utilized acoustic monitoring and GPS tracks of Manx

Shearwaters (*Puffinus puffinus*) to show that many calls detected in certain plots were from individuals flying over the plot (Arneill et al. 2020).

Variation in weather seemed to be the least important predictor of nocturnal colony activity in both species. No weather variables were significantly associated with Herring Gull activity in the model (Table 2.4), but between 23:00 and 01:00, gulls tended to call more when the moon was more full (Figure 2.6). Still, Moon Phase was an unimportant predictor of Herring Gull activity (Table 2.5). Cloud cover had a significant negative relationship with storm-petrel activity, however, it was also deemed one of the least important predictors (Table 2.2, Table 2.3). The lack of strong association with moon phase is unexpected because many studies have found associations between moon illumination and the activity of nocturnal seabirds (Watanuki 1986, Bryant 1993, Burger and Staine 1993, Mougeot and Bretagnolle 2000, Keitt et al. 2004, Riou and Hamer 2008). Cloud cover was higher when the moon was fuller during our study (see Figure S 7 in Supplementary Material), which may have mediated the effects of moon illumination as cloud cover attenuates moonlight. A study of gull foraging activity by Burger and Staine (1993) treated cloud cover as a proxy for available environmental light and found reduced foraging activity with higher cloud cover in two gull species. The by-chance associations in moon phase and cloud cover may explain our observed lack of association between moon illumination and activity, so the effects of moon illumination should not be ruled out for future studies. This also emphasizes that the amount of environmental light rather than strictly the phase of the moon, may be what is most important for mediating nocturnal colony activity levels of storm-petrels and gulls.

2.6 CONCLUSIONS: IMPLICATIONS FOR RISK ASSESSMENT AND CONSERVATION

Leach's Storm-Petrels are experiencing rapid global declines (Wilhelm et al. 2020), and it is vitally important to assess potential contributing risks. Predation has, historically, had disastrous local effects on Leach's Storm-Petrel breeding colonies (Pierotti 1982, McChesney and Tershy 1998, Stenhouse et al. 2000, Miles 2010, Hoeg et al. 2021), and changes in food availability for predators of storm-petrels is likely increasing predation pressure at colonies in which these species coexist (Stenhouse and Montevecchi 1999, Oro et al. 2005). To gauge risk of predation to storm-petrels during the breeding season, I examined the patterns and level of overlap in colony activity between Leach's Storm-Petrels and their primary predator, the Herring Gull. These two species had inverse activity patterns, and the overlap of colony activity was generally low, as storm-petrels began calling after a reduction of activity of Herring Gulls (Figure 2.2). While temporal and weather variables showed some associations with colony activity for both species, my key finding is that Herring Gull colony activity was the most important predictor of Leach's Storm-Petrel colony activity. I cannot conclude from this study whether it is Herring Gull vocal activity, the hour of the day, the amount of nocturnal light, or a combination of these factors that influence the nocturnal colony activity of Leach's Storm-Petrels. However, because storm-petrels are killed by Herring Gulls and not by nocturnal light, the biological signal can be expected to override the physical signal and storm-petrels will respond primarily to their predators. As evidenced in this study, Leach's Storm-Petrels likely predicate their activity patterns on time of day but alter activity levels according to their dominant predator's activity. Future playback studies and studies of storm-petrel colony activity in colonies where gulls are not present could examine potential causative effects of Herring Gull vocal activity on variation in Leach's Storm-Petrel colony activity.

Although I show here that colony activity overlap is relatively low, it is still important to gauge actual predation levels. In some colonies, predation of Leach's Storm-Petrels by Herring Gulls is steady (Stenhouse and Montevecchi 1999, Oro et al. 2005, Hey et al. 2019), but Baccalieu Island, the site of the most dramatic global population decline (Wilhelm et al. 2020), is relatively free from nesting gulls (Cairns et al. 1986). Storm-petrels breeding in different colonies may face significantly different risks, so predation could be causing declines in some colonies but not others. Estimates of predation rates at more colonies are needed to better understand the impact of predation on storm-petrels globally. An updated estimate of predation by gulls on Leach's Storm-Petrels in Witless Bay would also be valuable, as the latest estimate was conducted on Gull Island in 2012 (Bond unpubl. data) and is more than double the estimates on Great Island from 1976 and 1997 (Pierotti 1982, Stenhouse et al. 2000).

Climate change induced environmental stochasticity makes the future effects of predation uncertain, but existing trends suggest that the risk from predation may increase. The closure of the northern cod fishery in the early 1990s terminated massive amounts of artificial food provided by fishery discards and offal, with a resultant decline in the populations of Herring Gulls and other scavenging seabirds (Regular et al. 2013). Surviving gulls, however, intensified the predation pressure on smaller nesting seabirds (storm-petrels, puffins, and kittiwakes; Russell and Montevecchi 1996, Regehr and Montevecchi 1997, Stenhouse and Montevecchi 1999). The concurrent crash of the capelin stock, the main forage prey of breeding seabirds in Newfoundland, has likely exacerbated these circumstances (Buren et al. 2014, 2019). Ocean climate perturbations are projected to increase (Oliver et al. 2019), and indirect physical effects on top-down (predation) and bottom-up (prey availability) processes will influence the population dynamics and modify the risks with which Leach's Storm-Petrels will have to cope.

I show in this study that Leach's Storm-Petrels are entirely nocturnal at the colony, and gull predation may influence their activity patterns at the colony. This nocturnality extends beyond colony activity. These birds are also nocturnally active (albeit not exclusively) at foraging areas (see Chapter 3) due to the dial vertical migration patterns of their primary food source (Watanuki 1985, Hedd et al. 2009), and are one of the most nocturnally active tube-nose species during winter migration (Bonnet-Lebrun et al. 2021). Nocturnal activity patters may affect their exposure to other risks. In my next chapter, I investigate exposure of foraging Leach's Storm-Petrels to anthropogenically lit oil platforms, and how the timing and behaviour near these platforms, and therefore the risk imposed by them, may be influenced by their nocturnality at the colony and at sea.

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CHAPTER 3: MARINE RISK AND FORAGING ACTIVITY OF LEACH'S STORM-PETRELS DURING THE BREEDING SEASON

3.1 ABSTRACT

The global population of Leach's Storm-Petrels, the smallest and most abundant breeding seabird species in eastern Canada, has declined substantially in recent decades. The largest colonies of these seabirds, located off the east coast of Newfoundland and Labrador, Canada, are experiencing the most dramatic declines. The International Union for the Conservation of Nature (IUCN) list the species as Vulnerable. Fatal attraction to anthropogenic light is a known risk for seabirds globally and for Leach's Storm-Petrels in particular. Brightly lit oil and gas production platforms intersect the foraging paths of storm-petrels from the species' largest colonies, and the level of risk posed by attraction to these platforms is poorly understood. Using a GPS tracking dataset from Gull Island, Witless Bay, Newfoundland and Labrador, Canada (2016 to 2021), we show considerable similarity in foraging trip distance, location, and behaviour among years, and a decrease in trip distance and duration from egg incubation to chick rearing. Although oil platforms were within the core foraging area of parental storm-petrels from this colony, owing to their constraints of nocturnality at the colony and in offshore foraging areas, the storm-petrels tended to transit rapidly past platforms during the day when light attraction is minimized. This research helps focus conservation efforts on risks outside the breeding season, during migration and winter.

3.2 INTRODUCTION

Globally, seabirds are in decline. Nearly 50% of seabird species are classified as Near Threatened or worse, and 50% of these species have earned this classification due to recent rapid declines (Croxall et al. 2012, Dias et al. 2019). The Leach's Storm-Petrel (*Hydrobates leucorhous*) has recently been listed as 'Vulnerable' on the International Union on the Conservation of Nature (IUCN) Red List and 'Threatened' by the Committee On the Status of Endangered Wildlife In Canada (COSEWIC) as a result of a 54% decline in the Eastern population in just three generations, approximately 44 years (BirdLife International 2017, COSEWIC 2020). Their largest colonies, located in Atlantic Canada, are those that are experiencing the most dramatic declines (d'Entremont et al. 2020, Duda et al. 2020, Wilhelm et al. 2020). They have lower estimated annual survival than colonies in the Pacific (Fife et al. 2015, Rennie et al. 2020), so it is vital to better understand the risks facing these colonies. Leach's Storm-Petrels are highly pelagic, spending the nonbreeding period at sea and only coming on land to breed in large colonies during summer (Pollet et al. 2020). They also spend days on extensive foraging trips during the breeding season. Because they spend so much time at sea, investigation of marine risks is a priority.

During the breeding season, the foraging activity and trip structure of Leach's Storm-Petrels is constrained. Like all seabird species, breeding storm-petrels are central-place foragers (Halpin et al. 2018). Central Place Foraging Theory describes the foraging options and constraints of animals who must return to a specific breeding site after each foraging trip (Orians and Pearson 1979). A foraging trip can include finding then capturing prey for self and/or chick, digestion, and the time and distance travelled to and from the breeding site, resulting in additive energy expenditure (Elliott et al. 2009). These animals are expected to minimize effort and maximise gain from each trip (Burke and Montevecchi 2009), though birds may extend their efforts to work in energy deficit for periods of time (Regular et al. 2014). The foraging behaviour of Leach's Storm-Petrels is further constrained by their nocturnality. They are exclusively nocturnal at the colony, and the time at which they depart from and return to the burrow may be further constrained by weather and the activity of predators at some colonies (Watanuki 1986, Gladwell et al. 2019; chapter 2 of this thesis). Being obligated to return to and depart from the colony at night strongly influences the temporal structure of the Leach's Storm-Petrel's foraging trips, which may, in turn, influence their exposure to marine risks.

Foraging information for Leach's Storm-Petrels during incubation is available from many colonies in the Atlantic (Pollet et al. 2014b, Hedd et al. 2018). Although information on the foraging strategies and locations of Leach's Storm-Petrels during chick rearing is limited, differences in foraging strategies of other Procellariform species are informative. A recent study of European Storm-Petrels (*Hydrobates pelagicus*) found no differences in foraging trip range or trip distance between incubation and chick-rearing, but did find significant differences in trip duration, whereby birds with young chicks had the shortest trips (Bolton 2021). Mediterranean Storm-Petrels (*H. pelagicus melitensus*), change their foraging location with breeding stage, staying closer to the colony and covering much less overall area during chick rearing than during incubation (De Pascalis et al. 2021). Wandering Albatrosses (*Diomedea exulans*) reduce the duration and distance of the foraging trip from incubation to chick rearing to accommodate the chick's needs (Weimerskirch et al. 1993), while Antarctic Prions (*Pachyptila desolata*) and Blue Petrels (*Halobaena caerulea*) alternate between long and short trips while raising young (Chaurand and Weimerskirch 1994, Weimerskirch et al. 1999); short trips function primarily to provision chicks while longer trips are also for self-maintenance. Because Leach's Storm-Petrels exhibit dietary shifts and changes in energetic demands between incubation and chick rearing, it is likely that they, like other Procellariforms, exhibit changes in their foraging trip structure within a breeding season.

Dietary shifts of Leach's Storm-Petrels within a breeding season may associate with changes in their foraging trip structure. Leach's Storm-Petrels can travel more than 2000 km during a single foraging trip to feed in deep Atlantic waters on myctophids, bioluminescent, mesopelagic fish that are globally important in seabird diets (Hedd and Montevecchi 2006, Hedd et al. 2009, 2018, Pollet et al. 2014b, 2020, Watanuki and Thiebot 2018). Myctophids undertake diel vertical migration, being close to the surface of the water at night and deeper during the day (Hedd et al. 2018, Watanuki and Thiebot 2018, Freer et al. 2019). Leach's Storm-Petrels must, therefore, feed on this important food source nocturnally. Small crustaceans, squid, and other fish species also appear in their diet, suggesting that storm-petrels will forage opportunistically and select prey based on size rather than taxa (Watanuki 1985, Vermeer et al. 1988, Montevecchi et al. 1992, Hedd and Montevecchi 2006, Pollet et al. 2020). During a breeding season, the consumption of fish and crustaceans increases during chick rearing (Watanuki 1985, Vermeer et al. 1988). This dietary shift may indicate seasonal changes in prey availability or reflect changes in the energetic needs of adults and chicks, which could influence foraging trip structure.

Breeding involves an enormous energetic demand that changes throughout offspring development. Adults incubate eggs in shifts that usually last three to four days (Pollet et al. 2020), but can last up to six days (Gross 1935). Because of the high initial energetic investment into the egg by females (Montevecchi et al. 1983), males invest more time incubating than females (Mauck et al. 2011). Once hatched, adults rarely stay in the burrow during the day, but return at night to feed their chicks (Pollet et al. 2020). Individual parents will feed their chick every one to four days (Ricklefs et al. 1985), and the inter-feeding interval for chicks by both parents increases as chicks age (Pollet et al. 2020). During chick rearing, adult mass is less and metabolic rate is higher than during incubation (Montevecchi et al. 1992, Niizuma and Watanuki 1997, Niizuma et al. 2001). This change in the energetic requirements of adults and the frequency at which they return to the burrow likely influences the duration and structure of foraging trips, resulting in differences between incubation and chick rearing.

Previous studies have shown considerable variation in the foraging trip distances and durations undertaken by Leach's Storm-Petrels from the same colony (Pollet et al. 2014b, Hedd et al. 2018), and these birds have consistent foraging trip durations, total trip distance, and maximum distance from the colony between early and late incubation (Pollet et al. 2014b). It is unknown, however, if they exhibit any consistent patterns or changes between incubation and chick rearing. This study is, to our knowledge, the first to investigate the foraging location, trip duration, and trip distance of Leach's Storm-Petrels both between breeding stages and among years.

Attraction to coastal, ship and offshore hydrocarbon platform night-lighting is a global issue that requires study and mitigation. The storm-petrel is vulnerable to offshore flaring and lighting (Wiese et al. 2001, Davis et al. 2017, Gjerdrum et al. 2021) and, within eastern Canada, the foraging area of several colonies overlaps with offshore oil platforms (Hedd et al. 2018), where there are ongoing episodic mortality events from collisions with the structure, oiling, and incineration in gas flares, or where birds become lost and disoriented and expend energy circling the platform (Wiese et al. 2001, Montevecchi 2006, Burke et al. 2012, Ronconi et al. 2015, Gjerdrum et al. 2021). In addition, light attraction can alter foraging and migration paths, resulting in increased energy expenditure (Montevecchi 2006, McLaren et al. 2018). Leach's Storm-Petrels breeding at Newfoundland colonies have higher energetic requirements during breeding than birds nesting in a more southerly colony (Montevecchi et al. 1992). Hence, the potential increased energy expenditure associated with anthropogenic light could be more impactful for the Newfoundland populations of Leach's Storm-Petrels, which, incidentally, are the populations experiencing the most dramatic declines (Wilhelm et al. 2020).

Because Leach's Storm-Petrel foraging track structure (trip duration, total trip distance, trip location, and at-sea behaviour) may vary within a season and/or between years, there could be variation in the level of risk posed by oil platforms. Although anthropogenically lit boats can also pose a risk, the light catch basin is not as large, and their position is not as consistent as that of the oil platforms. Here, we investigate the variation in trip structure, overlap with oil platforms, and risk posed by these platforms to Leach's Storm-Petrels during the breeding season. We study the colony at Gull Island, Witless Bay, Newfoundland and Labrador, Canada (47.26265, -52.77187), which has been monitored extensively for more than 10 years. The core foraging area of birds from Gull Island intersects with several oil platforms on the Grand Bank (Hedd et al. 2018). We hypothesize that obligate nocturnality at the colony and at feeding areas on the edge of the continental shelf constrain the foraging activity of Leach's Storm-Petrels. We predict that (1) adult Leach's Storm-Petrels from the Gull Island colony will consistently forage at night in deep offshore waters where myctophids are available. (2) As previous studies have shown changes in the diets, energy requirements, and frequency of burrow visitations throughout the breeding season, foraging track structure of these birds will change during a breeding season. (3) As the most direct route from the colony to foraging areas passes in proximity to offshore oil platforms, Leach's Storm-Petrels will fly close to the platforms frequently. (4) Due to constraints to be nocturnal at the colony and because Leach's Storm-Petrels concentrate offshore foraging efforts at night due to the nocturnal vertical migration of prey, Leach's Storm-Petrels will transit to and from the breeding colony and the foraging ground during the day.

3.3 METHODS

3.3.1 Field Methods: GPS Deployment and Retrieval

GPS units (Pathtrack nanoFix GEO-Mini devices (Figure 3.1), 1.31% – 2.74% body mass) were deployed on adult Leach's Storm-Petrels breeding on Gull Island in the Witless Bay Ecological Reserve, Newfoundland and Labrador, Canada (47.26265, -52.77187) to map at-sea foraging area use. Device deployments in 2016 and 2018 occurred in two plots. These devices were deployed and recovered by April Hedd (Environment and Climate Change Canada). I deployed all devices in 2019 and 2020, distributed evenly among three plots that were separated by less than 200 meters. I also deployed all devices in 2021 among the same three plots and within one new plot that was also within 200 meters of the previous plots. These devices can each log a maximum of 160-200 data points (depending on the year of production) and must be recovered to download the data. All units were set with a continuous sampling interval of two hours, except for units deployed in 2019 (n = 7), which had a continuous sampling interval of three hours because they were initially intended for a different study. When attempting to take a point, the device will turn on to search for a satellite signal for up to 12 seconds (10 seconds in 2016 and 2018) before turning off again to preserve battery power. During incubation, Leach's Storm-Petrels are in the burrow continuously during the day, so I was able to capture adults by reaching into the burrow and carefully guiding the adult out. During chick-rearing, adults are only in the burrow at night, so I deployed burrow traps to safely capture the birds. The units were sutured to the back of the birds or taped to the middle three rectrices. Units were deployed in late June/early July to map foraging during incubation in all years of the study (Table 3.1). Units were deployed a second time on different adults in mid-August to map foraging during chick rearing in 2016, 2020, and 2021 (Table 3.1). I began attempting to recover units after 10 to 14 days of deployment. Deployment durations depended upon researcher access to the field site, weather, and the timing of adults returning to their nest burrow. In 2019-2021, if the chick had hatched prior to retrieval of the GPS device, burrow traps were deployed and checked on a three-day cycle with two daily checks in a row followed by a one-day rest period, or with nightly checks which allowed captured adults to leave before sunrise. This schedule was implemented to ensure the safe recapture and release of the study birds, while minimizing researcher disturbance.

Figure 3.1. Adult Leach's Storm-Petrel with a GPS sutured to the back.

Table 3.1. Summary of the number of deployed, recaptured, and downloaded GPS devices for each year of the study on Gull Island. All GPS tracks from 2016 and 2018 were collected for Environment and Climate Change Canada by April Hedd, and all tracks in 2019 - 2021 were collected by Sydney Collins. All devices were deployed on unique birds with the exception of two individuals who bore devices in two different years. Tracks from these individuals were treated separately.

Year	Breeding Period	GPS Deployed	GPS Recaptured	Tracks Downloaded
2016	Incubation	23	19	18
	Chick Rearing	13	8	8
2018	Incubation	19	16	16
	Chick Rearing	0	0	0
2019	Incubation	10	7	7
	Chick Rearing	0	0	0
2020	Incubation	10	4	4
	Chick Rearing	17	14	13
2021	Incubation	14	8	6
	Chick Rearing	20	15	13
Total	Incubation	77	54	50
	Chick Rearing	50	37	34
	Total	127	91	84

3.3.2 Analysis of GPS Data

Leach's Storm-Petrels are central-place foragers, returning to the colony after foraging before departing on a subsequent foraging trip. I analysed the GPS data for the number of foraging trips in each track, the cumulative travel distance (km) and duration (hours) of each trip, and the at-sea behaviour exhibited by each individual at each point. I then examined differences in foraging trip structure (duration, distance, core area use as measured by Kernel Home Range Analysis – see below) and the location of different at-sea behaviours (see below for behavioural states: transit, intensive search, extensive search) relative to oil platforms between chick-rearing and incubation and among years.

3.3.2.1 Trip Classifications

All analyses were performed in R Studio version 1.4.1103 (R Core Team 2019). I recorded multiple trips for some individuals in all years. Trips were classified using the "track2KBA" package (Beal et al. 2020) based on the proximity of the bird to the colony. A 'trip' had a minimum distance of 68km and a minimum duration of 8 hours. These values were chosen based on manual examination of a sample of GPS tracks. The trip durations (time elapsed between departing and returning to the colony) and total trip distances (the sum of the linear distance between each consecutive GPS point in a trip) were calculated using the function "tripSummary" from this package (Beal et al. 2020). To ensure that I did not underestimate these two metrics, I forced each complete trip to start and end at the colony for these calculations. I assigned the trip start as one hour before the first point and trip end was one hour after the last trip point, as this was half of the sampling interval of the GPS.

The 10-12 second search window results in a slight offset of the timing that each point is taken. Trip data were regularized so that the time interval between each point of each trip was exactly 2:00:00 (or 3:00:00 for 2019 trips). I approximated the longitude and latitude of each point at these regularized times. This is necessary to estimate points that the GPS device failed to record and to ensure proper behavioural classification by Hidden Markov Models (see below). For this reason, I did not include the points I added to force each complete trip to start and end at the colony in these analyses. The "spDistsN1" function of the R package "sp" (Pebesma and Bivand 2005, Bivand et al. 2013) was used to calculate the proximity of each trip path to an oil platform for the regularized data. These regularized data were used for all statistics, except for the calculations of total trip distance and trip duration, as the raw data give a more accurate estimation of these values

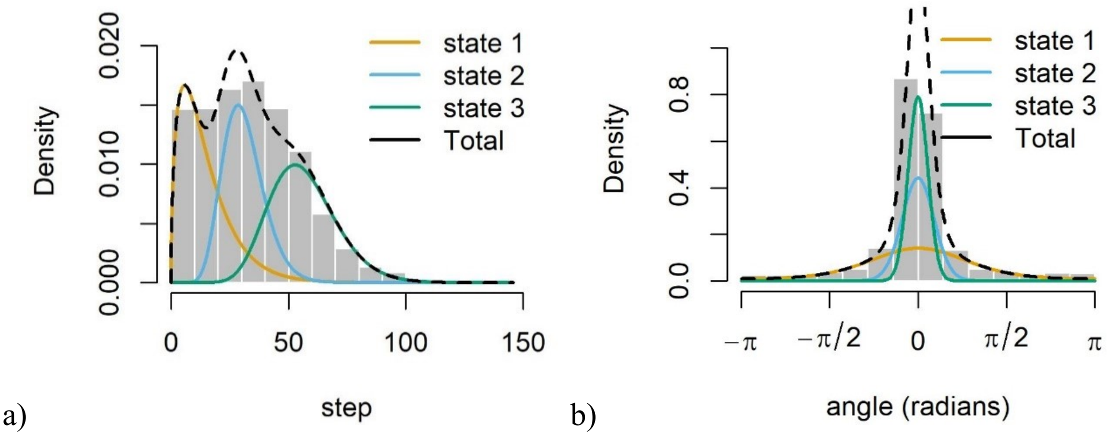
3.3.2.2 Behavioural Classifications

I assessed the behaviour of each bird at each point in a trip to explore differences in behaviour within and among years, and because the behaviour in an area may be able to inform the level of risk to the birds. For example, birds spend considerably more time in areas where they are resting or feeding than in areas through which they transit, so they will have a longer exposure time to any risk that is concentrated within a foraging ground than one that is contained within an area through which they typically transit.

Hidden Markov Models (HMMs) are commonly used to determine the behavioural state of an individual at each GPS point (Boyd et al. 2014, McClintock and Michelot 2018, Bennison et al. 2018). This method first calculates the step length (distance in km) and turning angle between each point. The mean step lengths and turning angles are then calculated for groups within the data, the number of which is predetermined. Each group represents a distinct behaviour known as a ‘behavioural state’. The chosen number of groups is the number of behaviours that the researchers expect to observe, and this can be chosen based on previous studies, and/or by running the model several times with a different number of groups and comparing these models using AIC. I constructed all HMMs using the “*momentuHMM*” package in R (McClintock and Michelot 2018). This package allows the addition of covariates in the model to account for variations in turning angle within a behavioural state, and for variations in the probability of transitioning between states. I chose to classify the data into three states to align with the methods of previous and ongoing seabird foraging behaviour studies (e.g. (Boyd et al. 2014, Torres et al. 2017, Bennison et al. 2018), and because a three-state model was better fitting than a two-state model according to AIC. I attempted models with different combinations of the variables *Hour* and *Bathymetry* to covary with these characteristics. Bathymetric data were obtained from the package "*marmap*" (Pante and Simon-Bouhet 2013). The HMM with both transition probabilities and turning angle varying with hour was the best model for the main dataset. For the 2019 dataset, the HMM with hour covarying with transition probabilities was the best model, though it was only marginally better than the same model used for the larger dataset. So, the same model was used for both datasets to ensure consistency. These models showed little deviation from the assumptions involved (no obvious patterns in the pseudoresiduals, no skewness in the normal q-q plot, and no evidence of autocorrelation).

Figure S 8 shows how the transition probabilities from state to state vary with hour of the day and Figure S 9 shows how the turning angle of each state varies with hour of the day. Figure 3.2 shows the distribution of step lengths and turning angles associated with each behavioural state. State 1 is characterized by short step lengths and tighter turning angles. State 2 has intermediate step lengths and wider turning angles than state 1. State 3 is characterized by much longer step lengths and turning angles closer to zero, meaning that the bird was travelling over long distances in a relatively straight path. I therefore consider state 3 as "Transiting". States 1 and 2 are likely representations of food searching and rest behaviour because the birds remain in the same general area over time.

Because state 1 shows birds spending the most time in a concentrated area, the birds may be resting or they may be actively feeding on a located food source. It is impossible to differentiate between these two behaviours with the two-hour time interval between each GPS point, but the continued improvement of battery life and memory in these miniature GPS devices is promising for future improvements in data and behavioural resolution. Although I cannot determine the specific behaviour of the birds when in state 1, I will refer to this state as “Intensive Search”. State 2 will be referred to as “Extensive Search”, because the birds have slowed their movement compared to transiting, likely in response to location of a food source or recognition of a feeding area, but cover a wider area compared to intensive search. Because the fit of the model can be improved with covariates and because other studies have deemed the HMM one of the best methods for modelling behavioural states in foraging seabirds (Bennison et al. 2018), I use the states produced by the HMM in further analyses.



a) b)

Figure 3.2. Distributions of step lengths and turning angles for each behavioural state. Within each behavioural state, there is a range of step lengths and turning angles that can be associated with each point

where the mean is the highest point of the smooth curve in both plots. Plot a) shows that the step lengths associated with state 1 are, on average, the shortest and the step lengths associated with state 3 are, on average, the longest. Step lengths associated with state 2 are usually between those of states 1 and 3. In b), the distributions of turning angles is shown for each state. Although the mean turning angle for all states was around 0, the distribution curve for state 3 is much steeper and tighter around 0 than those of states 1 and 2, which means that the turning angles associated with each state 3 point are most likely to be close to 0. The much flatter curve of state 1 means that sharper turning angles are more likely in this state. Again, the distribution of state 2 is between that of states 1 and 3.

3.3.3 Kernel Home Range Analysis

Kernel Home Range analysis uses GPS points to determine the general area that the birds are most likely to be found. This is based on the density of GPS points in a specific area (Worton, 1989).

Kernel Home Range analyses were conducted using “adehabitatHR” (Calenge, 2006). I utilized the reference bandwidth smoothing parameter (Worton, 1989), as the bandwidth that minimizes the least square cross validation score can result in highly fragmented and undersmoothed utilization distributions for large datasets with frequent (multiple per day) points (Kie, 2013). The 50%, 60%, and 95% Utilization Distributions (UDs) were constructed for the entire dataset. The 50% UDs were constructed for each year, for all chick-rearing and incubation trips, for the behavioural states, and for individuals to determine consistency in area use (Worton, 1989; Fieberg and Kochanny, 2005; Oppel et al., 2018).

3.3.3.1 Range Overlap

Range overlap analyses were conducted using the “kerneloverlaphr” function of the “adehabitatHR” package in R (Calenge 2006). Because some individuals were only tracked for a single trip whereas others had up to nine total trips, I compared only the ranges of individuals from their first trip, ensuring that there is no behavioural bias from acclimation to wearing the GPS device. In addition, I compared individuals within the same year and breeding phase, as I am also interested in the differences in area use among and within years. I compared area use among years within each breeding phase, and I compared breeding phased only within 2016, 2020, and 2021 as I did not have chick rearing data for 2018 and 2019. As recommended by Fieberg and Kochanny (2005) I used the Bhattacharyya Affinity Index (BAI) to measure similarity between UDs. The BAI ranges from 0 (no similarity) to 1 (completely similar). I also report the average percent overlap as these values compliment the presented maps of the UDs. The difference between chick-rearing and incubation in the proportion of time spent in each behavioural state was calculated with a test of equality of proportions.

3.3.4 Statistical Models

I interrogated the GPS data for general associations of trip distance and duration with breeding phase and year. I also assessed associations of the proximity (the minimum distance that a bird was from an oil platform on each trip) of a bird to an oil platform with year, breeding phase, behaviour, and trip characteristics, allowing determination of sources of variation in proximity to a risk.

The distances to oil platforms were calculated using the “spDistsN1” function of the R package “sp” (Pebesma and Bivand 2005, Bivand et al. 2013). I then calculated the proximity to any oil platform for each trip using the “summaryBy” function from the R package “doby” (Højsgaard and Halekoh 2020) and determined the time and behavioural state associated with that point. I calculated the number of birds that flew within the annual average and maximum light catch basins (average distance of attraction to illuminated platform based on a light radiance cut-off value of 0.75 nW·cm-2·sr-1, as determined from the maximum light radiance in areas far from any light source and thus considered dark) determined by Gjerdrum et al. (2021) .

To determine the overlap with and potential risk of light attraction for foraging parental Leach's Storm-Petrels and oil platforms, the average proximity to a platform and the proportion of trips in which an individual flew within the light catch-basin were calculated. For each trip, sunrise and sunset times for the date on which the bird was closest to an oil platform were obtained with the R package "suncalc" (Thieurmel and Elmarhraoui 2019), allowing the identification of the proportion of trips in which individuals passed closest by the oil platforms at night when the risk of light attraction is highest. The proportion of trips in which individuals were transiting when closest to an oil platform was also calculated.

I ran three models using the package "glmmTMB" (Brooks et al. 2017) to examine the sources of variation in total trip distance, trip duration, and proximity to an oil platform. All regression models were created and assessed following the steps of (Zuur and Ieno 2016) and all assumptions were checked according to (Zuur et al. 2010) using the R package "DHARMa" (Hartig 2020). For all models, the trip, not the individual, was the unit of replication.

Because I want to determine whether foraging trip metrics for adult Leach's Storm-Petrels were similar between breeding stages and among years, I looked at the variation of trip distance, trip duration, and proximity from an oil platform with Year and Breeding Phase and included the individual bird ID as a random variable. The models of trip distance and trip duration did not violate the assumptions of Gaussian distributed data. For the model of proximity to an oil platform, I also included the behavioural state of the bird at the minimum distance from an oil platform, the total trip distance, and whether the bird was closest to the platform during the day or at night to compare differences in proximity with behaviour and trip characteristics. Trip duration was not included due to high collinearity between trip duration and trip distance ($\rho = 0.878$). These data were highly right skewed, and a lognormal distribution was the best fitting distribution (dispersion = 1.016). The residual plot of trip distance revealed a potential logarithmic relationship with the log of proximity to an oil platform, and the log transformation of trip distance improved the fit of the model. The final models are shown in Equations 3.1-3.3.

$$Total\ Trip\ Distance_i \sim N(\mu_i, \sigma^2)$$

$$E(Total\ Trip\ Distance_i | ID) = \mu_i \quad \text{and} \quad var(Total\ Trip\ Distance_i | ID) = \sigma^2$$

$$\mu_i = \alpha + \beta 1 \cdot Year + \beta 2 \cdot Breeding\ Phase + \beta 3 \cdot ID_i$$

$$ID_i \sim N(0, \sigma_{ID}^2)$$

Equation 3.1. The General Linear Mixed Model of total trip distance varying with all selected predictors, where Total Trip Distance$_i$ is the distance in km for the ith foraging trip, α is the intercept, βx are the computed regression coefficients, ID$_i$ is the random intercept of each individual trip, and $i = 1,\ldots,130$.

$$Total\ Trip\ Duration_i \sim N(\mu_i, \sigma^2)$$

$$E(Total\ Trip\ Duration_i | ID) = \mu_i \quad \text{and} \quad var(Total\ Trip\ Duration_i | ID) = \sigma^2$$

$$\mu_i = \alpha + \beta 1 \cdot Year + \beta 2 \cdot Breeding\ Phase + \beta 3 \cdot ID_i$$

$$ID_i \sim N(0, \sigma_{ID}^2)$$

Equation 3.2. The general linear mixed model of total trip distance varying with all selected predictors, where Total Trip Duration$_i$ is the distance in km for the ith foraging trip, α is the intercept, βx are the computed regression coefficients, ID$_i$ is the random intercept of each individual trip, and i = 1,…,130..

$$log\ (Minimum\ Distance\ from\ Oil\ Platform_i) \sim N(\mu_i, \sigma^2)$$

$$E(log\ (Minimum\ Distance\ from\ Oil\ Platform_i) | ID) = \mu_i \quad \text{and}$$
$$var(log\ (Minimum\ Distance\ from\ Oil\ Platform_i) | ID) = \sigma^2$$

$$\mu_i = \alpha + \beta 1 \cdot Year + \beta 2 \cdot Breeding\ Phase + \beta 3 \cdot Behavioural\ State + \beta 4 \cdot \log(Total\ Trip\ Distance) + \beta 5 \cdot Day\ or\ Night + \beta 6 \cdot ID_i$$

$$ID_i \sim N(0, \sigma_{ID}^2)$$

Equation 3.3. The general log-linear mixed model of total trip distance varying lognormally with all selected predictors, where Minimum Distance from Oil Platform$_i$ is the closest proximity in km of a bird to an oil platform for the ith foraging trip, α is the intercept, βx are the computed regression coefficients, ID$_i$ is the random intercept of each individual trip, and i = 1,…,130.

3.4 RESULTS

Over 5 years, I captured the foraging tracks of 85 individual Leach's Storm-Petrels from Gull Island, Newfoundland and Labrador, Canada, resulting in 212 total trips and 182 complete trips.

Leach's Storm-Petrels breeding at Gull Island were mostly consistent in their foraging trip duration, cumulative distance, foraging locations, and locations of intensive and extensive search and transit behaviours during the study period. All tracks with point colours indicating behaviour are shown in Figure 3.3, and Figure 3.4 shows the UDs of the entire sample. Parental storm-petrels tended to forage over deeper waters off the Grand Bank. Some individuals also tended to forage closer to Gull Island, either after returning from a longer trip on which they foraged off the Grand Bank, or on a shorter trip where they exclusively foraged nearer to the colony (Figure 3.5). Individual storm-petrels performed both short and long trips, but there was no obvious pattern such as alternating between short and long trips (Table S 4).

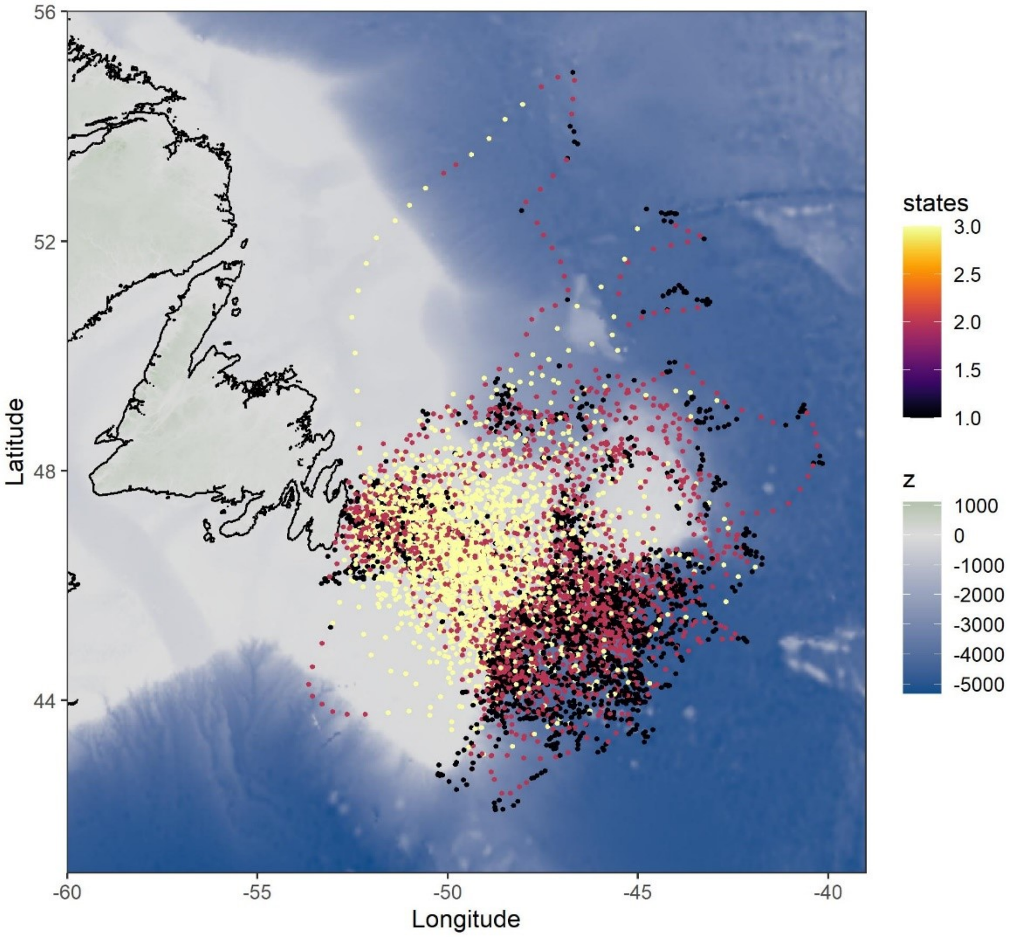


Figure 3.3. All tracking points coloured by behaviour for 84 Leach's Storm-Petrels from Gull Island, Witless Bay, Newfoundland, Canada from 2016 to 2021.

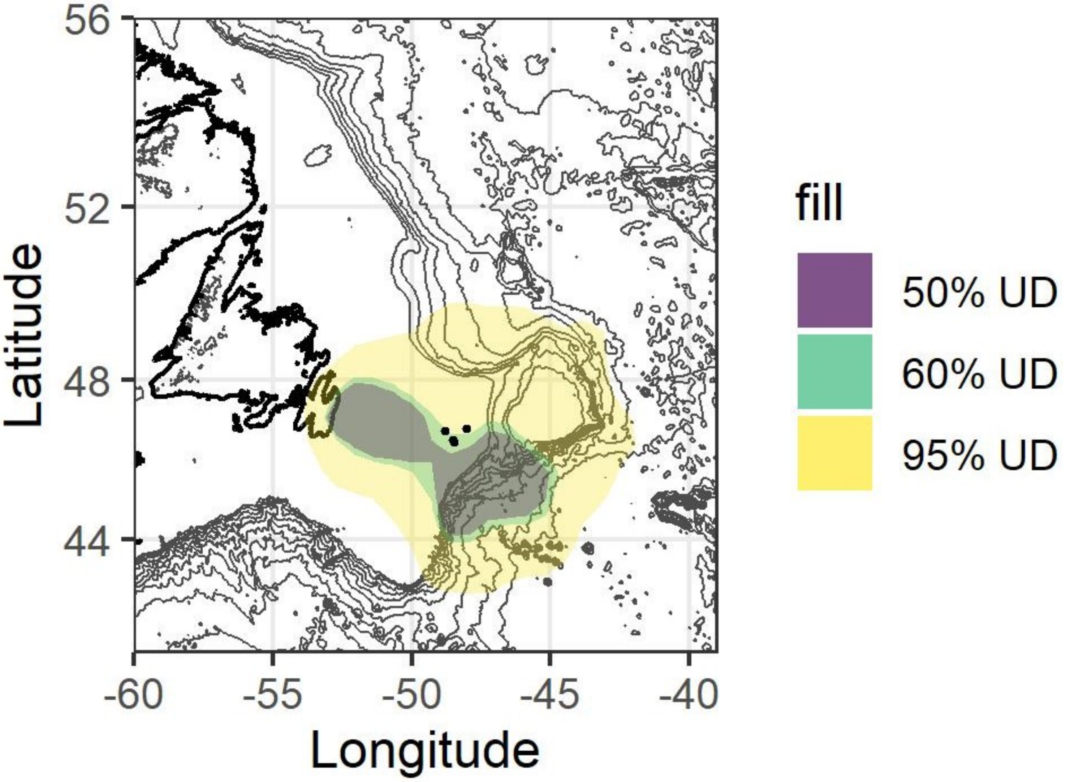


Figure 3.4. The Utilization Distributions for Leach’s Storm-Petrels breeding on Gull Island, Witless Bay, NL, Canada from 2016 to 2020. The black dots represent the locations of four oil production platforms on the Grand Bank of Newfoundland. Note that the 60% UD includes the oil platforms.

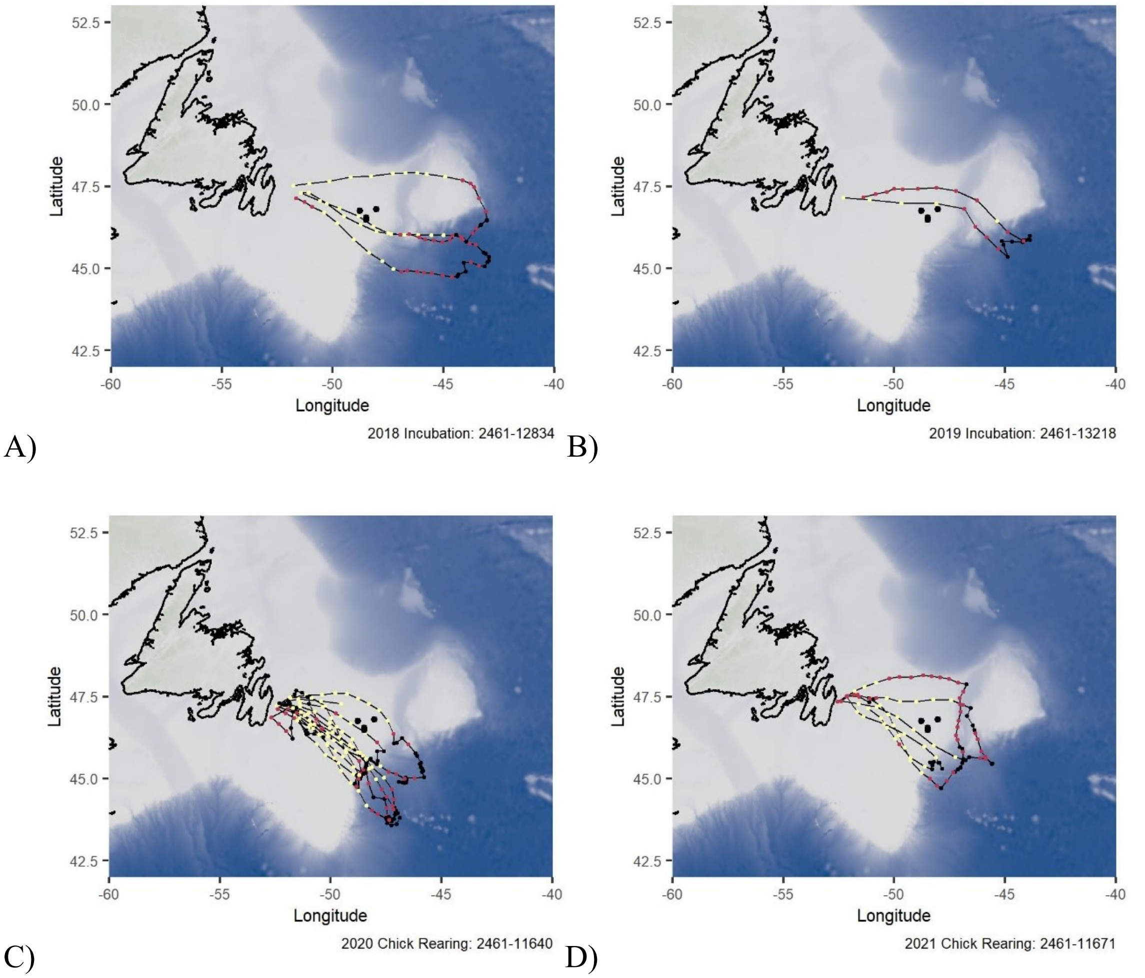


Figure 3.5. A selection of tracks from individual Leach's Storm-Petrels in the study sample from incubation in A) 2018, B) 2019, and from chick rearing in C) 2020, and D) 2021. Black points represent intensive search, pink points represent extensive search, and yellow points represent transiting. The larger, unconnected black dots represent the oil platforms. The bathymetry is represented where darker blue indicates deeper water.

Table S 5 shows the BAI and percent overlap for all groups of individuals, years, breeding phases, and behavioural states. Here, I report averages. There was high similarity between the UDs for intensive and extensive search behavioural states (BAI = 0.959, % overlap = 0.752). The UDs for transit and the foraging behaviours were more dissimilar (transit – intensive: BAI = 0.726, % overlap = 0; transit-extensive: BAI =

0.859, % overlap = 0.358; Figure S 10). Because birds tended not to transit and forage in the same locations, I investigated the overlap of foraging areas and transiting areas separately to better understand consistency in the areas used by Leach's Storm-Petrels.

The average similarity between the UD of all individuals (as measured by the average of each calculated BAI or % overlap for every possible pair of individuals) was higher for transiting locations (BAI = 0.747, % overlap = 0.435) than for foraging locations (BAI = 0.364, % overlap = 0.180). To examine area use overlap between years, I calculated the annual UD from all points within a breeding phase in each year. The average similarity in foraging areas between years was BAI = 0.866, % overlap = 0.644 for years with incubation tracks and BAI = 0.928, % overlap = 0.769 for years with chick rearing tracks (Figure S 11). The average similarity in transiting areas between years was BAI = 0.946, % overlap = 0.820 for years with incubation tracks and BAI = 0.965, % overlap = 0.844 for years with chick rearing tracks (Figure S 11). I also calculated the UD from all tracks collected during chick rearing, and the UD from all incubation tracks. The average similarity in UD between breeding phases was BAI = 0.947, % overlap = 0.759 for transiting areas, and BAI = 0.872, % overlap = 0.668 for foraging areas (Figure S 12). Overall, the area used to transit was more consistent (higher overlap among individuals, years, and breeding phases) than the area used to forage (Figure S 12).

Birds did not vary between chick rearing and incubation in the proportion of time spent in each behavioural state (Intensive: $\text{prop}_{\text{egg}} = 0.390$, $\text{prop}_{\text{chick}} = 0.329$, $\chi^2 = 0.405$, df = 1, p-value = 0.525; Extensive: $\text{prop}_{\text{egg}} = 0.323$, $\text{prop}_{\text{chick}} = 0.298$, $\chi^2 = 0.026$, df = 1, p-value = 0.871; Transit: $\text{prop}_{\text{egg}} = 0.287$, $\text{prop}_{\text{chick}} = 0.373$, $\chi^2 = 0.926$, df = 1, p-value =

0.336). Total trip distance and trip duration did not vary among years (distance: χ^2 = 6.704, p = 0.152; duration: χ^2 = 4.535, p = 0.338; Table S 6 and Table S 7), but trips during chick rearing were significantly shorter in both total distance and duration (distance: mean difference = 78.22 km, χ^2 = 4.495, p = 0.0340; duration: mean difference = 8.187 h, χ^2 = 6.115, p = 0.0134; Table S 6 and Table S 7).

The average minimum distance of a trip point to an oil platform was 68.87 km (range: 2.02 km – 411.46 km). A bird flew within the average light catch basin of an oil platform in 2.75% of trips and flew within the maximum average catch basin in 10.40% of trips. Leach's Storm-Petrels passed closest by the oil platforms during the daylight hours in 85.16% of trips. In 71.43% of trips, the birds were transiting when they flew closest to the oil platforms. Of birds that flew within the maximum light catch basin of the platforms, 89.47% flew past during the day, and 68.42% were transiting.

The proximity to an oil platform did not vary with breeding phase (χ^2 = 0.255, p = 0.614), or among years (χ^2 = 4.883, p = 0.300) (Table 3.2, Figure S 13a-b). Three of the four Grand Bank oil production platforms overlapped with the 50% UD of incubating birds, whereas none of the oil platforms were overlapped by the 50% UD of chick-rearing birds (Figure S 12). There was no significant relationship between the behavioural state of a storm-petrel at its closest point to an oil platform and the proximity to that platform (χ^2 = 1.116, p = 0.573), however, three of the four Grand Bank platforms overlapped with the 50% UD for transiting, and none overlapped with the 50% UD for foraging (Figure S 10). Total trip distance was negatively associated with proximity to an oil platform (χ^2 = 40.092, p < 0.001)(Figure S 13d). Time of day (day vs. night) did not affect the proximity of foraging storm-petrels to oil platforms ($\chi^2 = 2.550$, p = 0.110) (Table 3.2, Figure S 13e).

Table 3.2. Type III ANOVA table and random effects of the general linear mixed model for the minimum distance during a foraging trip traveled by Leach's Storm-Petrels past an oil production platform during the breeding season on Gull Island, Witless Bay, Newfoundland and Labrador, Canada.

Variable	**Chi squared**	**df**	**p value**
Intercept	112.4	1	< 0.001
Year	4.883	4	0.300
Breeding Phase	0.255	1	0.614
oilmin States	1.116	2	0.573
log(Distance)	40.092	1	< 0.001
Day or Night	2.550	1	0.110

	Groups	**Name**	**Variance**	**Standard Deviation**
Random Effects	*ID*	(Intercept)	0.253	0.503
	Residual		0.466	0.682

3.5 DISCUSSION

Individual Leach's Storm-Petrels exhibited similar foraging trip structure and behaviour across years. Individuals used very similar areas at sea (as measured by the 50% Utilization Distribution), and the population exhibited generally similar at-sea area use among years and between incubation and chick-rearing, although incubating birds tended to forage farther off the bank than chick-rearing birds (Figure S 12). The areas used for transiting were more consistent than areas used for foraging. Birds tended to transit along the Grand Bank, and intensively and extensively searched beyond the edge of the Grand Bank near the Flemish Cap, and at times near the colony (Figure 3.3, Figure S 10). Similar area use at sea among individuals has previously been observed in Leach's Storm-Petrels (Hedd et al. 2018), and in European Storm-Petrels (*Hydrobates pelagicus*) (Bolton 2021). More specifically, the utilization distributions observed in this study are consistent geographically with previous tracking of Leach's Storm-Petrels from this colony (Hedd et al. 2018). Similar at-sea area use was also found for this colony between 1966-1990 and 1998-1999 using transect observations (Hedd et al. 2009). Myctophids dominated the diets of the birds in these past studies, suggesting that they concentrate their foraging effort in deep waters off the Grand Bank (Hedd et al. 2009), as I observed in this study. There was considerable overlap in the areas in which birds intensively and extensively searched, but lower overlap among foraging areas and transit areas (Figure S 10). This suggests that, at the population level, storm-petrels breeding on Gull Island likely do not forage extensively over the Grand Bank, between these two main foraging areas.

Neither trip distance nor duration varied significantly among years. Within years, however, trips during chick rearing tended to have shorter duration and shorter total distance. This is consistent with my prediction and aligns with findings for other Procellariforms (Weimerskirch et al. 1993, Hedd et al. 2014, Bolton 2021, De Pascalis et al. 2021). Figure S 12 shows that birds tended to forage along the shelf of the Grand Bank, whereas birds tended to venture further into and around the Flemish Pass during incubation. The occurrence of short trips cannot explain this, as individual storm-petrels tended to take both short and long trips in no obvious pattern, and short trips were equally likely to occur in either chick-rearing or incubation (Table S 4). This observation is likely because of the increase in energetic demands once the chick has hatched (Ricklefs et al. 1980). Parents likely need to make more frequent foraging trips to accommodate these needs. Although birds reduced their foraging trips when they had chicks, incubating and chick-rearing adults spent proportionally similar amounts of time foraging versus transiting on their trips. Overall, these birds spent about a third of their time in each behavioural state, regardless of breeding stage. Because Leach's Storm-Petrels are central place foragers, they must optimize energy expenditure when foraging (Burke and Montevecchi 2009, Elliott et al. 2009). They are only able to fly so fast, and they must spend enough time foraging to make such a long trip worthwhile. Digestion, which likely occurs when storm-petrels are in behavioural state 1 (intensive search), is mutually exclusive from active foraging (Rosen et al. 2007). Digestion is also an important and time consuming component of the storm-petrel's foraging trip, as they reduce the food volume by concentrating it as high-energy oils which are used by the adult or fed to chicks (Place et al. 1989). Rather than changing the proportion of time spent doing specific behaviours, Leach's Storm-Petrels appear to compensate for the increased energy expenditure in different ways. For example, body mass loss during early chick rearing has been found to increase flight efficiency by 14% (Niizuma et al. 2001). While previous research has identified population-level consistency in the foraging locations of Leach's Storm-Petrels across years and throughout different stages of incubation (Hedd et al. 2009, 2018, Pollet et al. 2014b), this is, to my knowledge, the first study to compare foraging locations and behaviour between incubation and chick rearing.

As found previously (Hedd et al. 2018), the home range of Leach's Storm-Petrels (60% UD) overlapped with oil and gas production platforms (Figure 3.4). The average proximity to an oil platform throughout the sample was 68.87 km (range: 2.02 km – 411.46 km) , and birds flew within the maximum light catch basin in 10.40% of trips. The precision of these values is limited by the precision of the device itself (10-20 m), and by the large time interval between points. It is assumed that storm-petrels fly in a relatively straight line between captured GPS points, so the actual proximity to an oil platform is likely less than the presented value. It is also important to note that I used a value of 10.705 km for the maximum light catch basin, and that the catch basin of gas flares can be much greater than the values found by Gjerdrum et al. (2021). A 2002 gas flaring event in Alaska was reported to be seen more than 1000 km away (Day et al. 2015). I also used the average value, when it is known that the size of the catch basin can vary within the year (Gjerdrum et al. 2021). Additionally, I recaptured an average of 70% of deployed GPS devices. The birds that did not return may have abandoned the nest or died, so it is important to note that I am only able to document the behaviour of birds that survived and returned to the burrow. Hence, it is likely that the percentage of storm-petrels from Gull Island that fly within the light catch basin of oil platforms is higher than 10%.

In 71.43% of trips, storm-petrels were transiting when closest to an oil platform. Generally, birds that were transiting tended to be closer to oil platforms than birds who were intensively or extensively searching at that point of the trip (Table S 4, Figure S 13c). In addition, the oil platforms overlapped the 50% UD of all transiting points, but did not overlap with the foraging 50% UD (Figure S 10). This indicates that, even though some individuals were closest to an oil platform while foraging during their trip, these birds were distant from the platform and well outside that catch basin of the light. The negative association between trip distance and proximity to an oil platform is consistent with this foraging pattern (Table 3.2). Because the oil platforms are close to the shelf-edge of the Grand Bank, individuals heading to deep water and the Flemish Cap to forage fly past the platforms to get there. It appears that the time that Leach's Storm-Petrels are exposed to oil platforms is minimal, given that the birds are usually flying to or from the foraging area when they pass them. This is especially important given that the size of the light catch basin can vary with time of day, date, and weather (Gjerdrum et al. 2021), because longer duration in proximity to a platform increases the possibility of being caught within the light catch-basin.

Although there was no statistical difference in the proximity to an oil platform between chick-rearing and incubation birds, the 50% UD of incubating birds overlapped with oil platforms, whereas that of chick-rearing birds does not (Figure S 12). This could mean that incubating birds are more exposed to the risk of anthropogenically lit oil platforms than chick-rearing birds. In contrast, 75% of the birds that flew within the maximum light catch basin of an oil platform were rearing chicks at the time. This slight difference in area use could reflect changes in weather, individual differences, shifts in diet/prey distribution, and other factors that I did not measure in this study (e.g. Garthe et al. 2009, Hedd et al. 2009, Bonnet-Lebrun et al. 2018). Continued long-term monitoring of foraging patterns in chick-rearing and incubating birds in conjunction with studies of prey distribution and weather changes will help to understand the mechanism behind the observed shift in area use.

Leach's Storm-Petrels flew closest to an oil platform during the day in 85% of all trips. Proximity to the oil platforms was similar during the day and at night (Table 3.2). While attraction to artificial light during the day has been demonstrated for some animals (Baik et al. 2020), the light from oil platforms would be overwhelmed by sunlight on bright days, thus reducing the distance at which birds can see the artificial light source and limiting exposure of storm-petrels to the risk of attraction. Still, studies of light attraction in different environmental lighting conditions should be conducted to better understand the risk of to seabirds. This is particularly important in Newfoundland where foggy conditions are common (Isaac et al. 2020), as light may dissipate differently in fog and potentially influence the size of the light catch basin.

3.6 CONCLUSIONS AND FUTURE DIRECTIONS

In this study, I sought to quantify the exposure of breeding Leach's Storm-Petrels from Gull Island to brilliantly lit oil platforms on the Grand Bank of Newfoundland. Because breeding Leach's Storm-Petrels at Gull Island usually moved quickly past oil platforms during the day, it appears that the risk posed by light attraction is generally low for this segment of the population during the breeding season. Specifically, Leach's Storm-Petrels breeding on Gull Island flew within the light catch basin of oil platforms at night in 1.1% of trips, and they flew within the light catch basin during the day in 9.3% of trips.

Considerable effort is being invested into risk assessment for Leach's Storm-Petrels across Atlantic Canada with a focus on breeding adults, but the risk posed by light attraction to this group may be minimal. This is not to say that light attraction is not contributing to population declines. Recent evidence indicates that storm-petrels do strand on oil platforms during the breeding season, but in much smaller numbers than during the fall (Gjerdrum et al. 2021). This raises the concern of risk posed by light attraction during the remainder of the year. Light pollution poses a major risk to seabirds globally, especially tube-nosed seabirds (Reed et al. 1985, Wiese et al. 2001, Montevecchi 2006, Poot et al. 2008, Burke et al. 2012, Day et al. 2015, Rodríguez et al. 2017a, Rebke et al. 2019). Based on the expansive area covered by Leach's Storm-Petrels during the non-breeding period (Pollet et al. 2014a, 2019), individuals from this and other populations will be exposed to oceanic sources of anthropogenic light such as boats, oil platforms, and drill rigs. The age of the birds also needs to be considered. Very little is known about juvenile survival, but the majority of the seabirds that have been recovered from light-polluted areas are juveniles (Rodríguez et al. 2017b, Atchoi et al. 2020). One study found that the visual system of Leach's Storm-Petrel chicks develops very slowly, and eyes may not be fully developed until after fledging (Mitkus et al. 2018). (Atchoi et al. 2020) proposed a connection between the slow development of the visual system in juveniles and their increased level of attraction to light. Hence, adults and juveniles likely differ in their level of vulnerability to light attraction, owing to differences in eye structure (Mitkus et al. 2018), which may determine the wavelengths to which they are most attracted. It will be extremely important to identify light risk exposure for juveniles but I am limited by access to technology that allows remote download of tracking devices, which are not yet available for birds as small as petrels.

Mitigation efforts have been investigated regarding the light source itself. Changing the colour of the lights on the platforms may be effective, as certain wavelengths of light may differ in their level of attractiveness (Montevecchi 2006). There is, however, disagreement in the literature over the most attractive wavelengths to birds. Some studies have found that white and red light are the most attractive (Poot et al. 2008), whereas others have found that white, green and blue light attract more migrating birds (Rebke et al. 2019, Syposz et al. 2021). Shielding of light from unnecessary skyward projection (Reed et al. 1985) and changing the type of light source (i.e. LED versus high-pressure sodium; (Rodríguez et al. 2017a) have a range of efficacy that depends upon the species and, likely, the weather (Wilhelm et al. 2013).

Continued research on the risks of light attraction to Leach’s Storm-Petrels is needed but should be broadened to include vessel and coastal lighting, to assess the risks at different times of the year, and to assess the risks for individuals of different age groups. Further research on the visual system of Leach’s Storm-Petrels will be useful for informing best practices moving forward. Researchers and governments should work with corporations that produce oceanic light pollution to develop and implement mitigation strategies that will be effective for both adults and juveniles.

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CHAPTER 4:SUMMARY, SYNTHESIS, AND FUTURE DIRECTIONS

Leach's Storm-Petrels (*Hydrobates leucorhous*) have been listed as globally 'Vulnerable' on the IUCN Red List and the Atlantic population was assessed as 'Threatened' by COSEWIC as a result of their precipitous population declines (BirdLife International 2017, COSEWIC 2020). Five non-independent factors are thought to contribute to the decline, and I investigated the two of these that are most evident during the breeding season: predation and fatal attraction to anthropogenic light.

4.1 TERRESTRIAL RISKS DURING THE BREEDING SEASON

Herring Gulls (*Larus argentatus*) are the dominant predator of Leach's Storm-Petrels (*Hydrobates leucorhous*) on Gull Island, Witless Bay Ecological Reserve, Newfoundland, Canada. Predation of storm-petrels at these colonies is significant; at Great Island, annual predation (1976 and 1997) by gulls is estimated at 9% (Pierotti 1982, Stenhouse et al. 2000), and an estimated 110 000 storm-petrels were killed by gulls at Gull Island in 2012 (Bond unpubl. data).

Herring Gulls and Leach's Storm-Petrels are primarily active at opposite times of the day. Some Herring Gulls, however, specialize on preying on Leach's Storm-Petrels at night, and some individuals may be more nocturnally active than others for reasons unrelated to storm-petrel predation (i.e. individual variation). Nocturnal levels of Herring Gull colony activity vary with weather conditions that influence environmental light and maneuverability (Watanuki 1986, Pierotti and Annett 1991, Burger and Staine 1993, Gilchrist et al. 1998).

Spatial and temporal overlap in colony activity of Leach’s Storm-Petrels and Herring Gulls implies a greater level of predation risk. Leach’s Storm-Petrels usually vocalize outside the burrow where they are vulnerable to predators (Gladwell et al. 2019). Herring Gulls, the main predator of Leach’s Storm-Petrels, vocalize when defending a feeding territory, and generally vocalize frequently when awake (Weseloh et al. 2020). Because they are opportunistic predators (Ingraham et al. 2020), any awake/vocalizing Herring Gull is a potential danger to a Leach’s Storm-Petrel that is outside the burrow. Therefore, the overlap in vocal activity of these two species could inform the level of predation risk to Leach’s Storm-Petrels.

Leach’s Storm-Petrels are nocturnal, burrow-nesting seabirds, that are difficult to observe or monitor using traditional techniques. I employed sound recording techniques to assess the level of colony activity for both Leach’s Storm-Petrels and Herring Gulls. Calls were counted from recordings, and a model approach was used to examine temporal and environmental relationships between the activity levels of co-habiting gulls and storm-petrels.

The activity of each species varied with time. I found a strong, negative relationship between Leach’s Storm-Petrel and Herring Gull activity. Herring Gull activity was the most important predictor of variation of storm-petrel activity which was also associated with time and habitat, and weakly associated with cloud cover. Herring Gull activity was associated with date, and gulls tended to be more nocturnally active when the moon was more full.

Although Leach's Storm-Petrels are nocturnal at the colony regardless of the presence of gulls, it is possible that they modify their behaviour in response to the activity of their dominant predator. Moonlight and cloud cover had weak relationships with Herring Gull and Leach's Storm-Petrel activity; these factors both affect the amount of nocturnal light, so light may be another factor by which storm-petrels mediate their activity at the colony.

There are numerous constraints to Leach's Storm-Petrel activity at the colony which influence when adults return and depart. Because there is a short time window when adults will be relatively safe to return to and leave the burrow, the temporal structure of foraging trips, and therefore the timing of exposure to certain marine risks, will also be constrained. In Chapter 3, I examined and discussed the temporal, spatial, and behavioural structure of foraging trips throughout the breeding season to assess the level of risk posed by anthropogenic light emitted by offshore oil production platforms.

4.2 MARINE RISKS DURING THE BREEDING SEASON

Oil and gas production platforms on the Grand Banks of Newfoundland are located within the core foraging area of Leach's Storm-Petrels breeding on Gull Island in the Witless Bay Ecological Reserve (Hedd et al. 2018; and this thesis). The level of exposure to these platforms during the chick-rearing stage, when foraging trip structure may be modified to meet the increased energy demands of the chick, has been unknown until this study.

Spatial data were obtained from 84 GPS devices deployed on adult breeding Leach's Storm-Petrels between 2016 and 2021. These tracks were analysed using Hidden

Markov Models to determine locations and times that adults were foraging and transiting. Utilization distributions were created to identify the core foraging ranges of these birds, and to determine the level of overlap in foraging range between years, between chick-rearing and incubation, and between regions of foraging and transiting behaviours. I used a model-based approach to examine the sources of variation in trip duration, trip distance, and proximity to an oil platform during a trip.

Breeding adult Leach's Storm-Petrels were highly consistent in their foraging locations, trip distance and durations, and behaviour among years. Between incubation and chick-rearing, parental storm-petrels tended to reduce their foraging trip duration and total distance. The birds foraged near the colony and near the Flemish Cap over deep waters. Proximity to an oil platform did not vary between chick-rearing and incubation. Three oil platforms were within the 60% UD of the Leach's Storm-Petrels, and the average proximity to an oil platform throughout the study period was 68.87km. Birds transited past the platform on 71.43% of all trips, and the 50% UD for transiting behaviour contained the oil platforms, whereas the 50% UD for foraging areas did not. Birds also flew closer to platforms on longer trips, and even though some individuals were foraging when they were closest to a platform, this usually occurred on a short trip where they primarily foraged close to the colony. The birds were unlikely to forage near oil platforms. Storm-petrels flew closest to oil platforms during the day in 85.16% of all trips. Birds transiting past platforms thus had minimal exposure time to platforms and were passing by during the day when light attraction is minimized. Leach's Storm-Petrels were exposed to the light catch-basin of oil platforms at night in 1.1% of trips, and were exposed during the day in 9.3% of trips. Therefore, the overall risk from anthropogenically lit oil production platforms to adult Leach's Storm-Petrels breeding on Gull Island is low.

4.3 SYNTHESIS

While predation levels of Leach's Storm-Petrels have been found to be significant in the past (e.g. Stenhouse et al. 2000, Miles 2010, Hey et al. 2019, Bond 2012 unpubl. data), very few gulls nest on Baccalieu Island, the site of the world's largest colony that is also experiencing the most dramatic decline (Wilhelm et al. 2020). It appears, then, that predation is not a major driver of the declines in all colonies and cannot be considered the 'smoking gun' responsible for global declines. The strong negative association between storm-petrel and gull activity that could not exclusively be explained by time of day suggests that the storm-petrels use avoidance techniques to reduce predation. Many of the carcass remains found in previous studies may have included a disproportionate number of non-breeding individuals (Morse and Buchheister 1977, Stenhouse et al. 2000, Pollet et al. 2020), so adult breeders may predicate their behaviour on that of their predator, bolstering their survival.

These constraints likely also influence temporal and structural foraging patterns of breeding adults. This has important implications for risk exposure at sea, as the timing of exposure to certain risks may be constrained. I found that the relative risk posed by brilliantly illuminated oil platforms appears to be low due to the temporal patterning and behaviour of foraging parental storm-petrels.

While I found that Leach's Storm-Petrels breeding on Gull Island have behavioural patterns that likely reduce risks from predation and attraction to oil platforms, this does not mean that these factors do not pose risk here or in other colonies or locations, for other life stages, or at other times of the year. In addition, other risks such as pollution, changes in food availability, and the complex impacts of climate change require further investigation. It is clear that risk exposure across the full annual cycle of Leach's Storm-Petrels must be better understood to facilitate effective conservation.

Historically, Leach's Storm-Petrel populations have fluctuated (Duda et al. 2020a, 2020b). On Grand Columbier Island in Saint Pierre and Miquelon, and on Baccalieu Island, populations were generally increasing before European settlement (Duda et al. 2020a). On Grand Colombier Island, paleo-environmental data indicates that increases followed by decreases in population happened over the course of about 1500 years, and the magnitude of these decreases was about half of what has been observed in the past 800 years (Duda et al. 2020a). Following European settlement, the storm-petrel population on Baccalieu Island was increasing to a size far exceeding population estimates from the last 1700 years, however, since the population peaked in 1984, the population size has decreased at the fastest historic rate for this colony (Duda et al. 2020b). These modern decreases are worrying, because they are much more severe and rapid than any fluctuations in population size in these two colonies in millennia. These historic trends emphasize the need for immediate conservation measures, especially considering that populations nearing the 'tipping point' for collapse become even more sensitive to disturbance and may take longer to recover (Dai et al. 2012, 2013).

The concerning decline of Leach's Storm-Petrels is echoed in many other seabird species. 43% of all seabird species are classified as Near Threatened or worse, and nearly 50% of these species received this classification due to rapid declines (Croxall et al. 2012, Dias et al. 2019). In addition, 70% of all seabird species face multiple risk factors, including both terrestrial and marine threats, emphasizing the need for broad-scale studies and mitigation actions (Dias et al. 2019).

4.4 FUTURE RESEARCH

Currently, significant research efforts are being made in the Northwest Atlantic to understand the risks that breeding Leach's Storm-Petrels face. Risks to adults during the breeding season may not fully explain the observed population declines, and more research attention needs to be directed toward different times of the year and to different age groups of storm-petrels.

An update to the 2012 and 1997 estimates of predation rates of Leach's Storm-Petrels by gulls is needed for colonies in Witless Bay. Gull populations continue to decline (Bond et al. 2016), forage fish populations have not recovered (Buren et al. 2019), and fishing offal and discards have been severely reduced since the early 1990s (Regular et al. 2013), so predation rates may have changed.

More studies need to investigate the visual system of Leach's Storm-Petrels, and the species and age-specific response of these birds to different light sources. There is disagreement in the literature surrounding the optimal wavelength or type of light to minimize light attraction (Montevecchi 2006, Poot et al. 2008, Rodríguez et al. 2017a, Rebke et al. 2019). Light attraction may also differ with age in Leach's Storm-Petrels, owing to slow development of the visual system (Mitkus et al. 2018, Atchoi et al. 2020).

Fledgling risk exposure and survival should be monitored. Although fledging success tends to be high in the largest colonies in Newfoundland (Pollet et al. 2020), very little is known about juvenile survival. Juveniles are common in storm-petrel wrecks, in coastal towns, and on boats and oil platforms, suggesting that they are at greater risk than adults to light pollution (Rodríguez et al. 2017b, Atchoi et al. 2020, Gjerdrum et al. 2021). Research ability to monitor juvenile survival is currently limited by available technology, so technological development and use should be a priority to facilitate such studies.

One way that researchers could currently study the risk posed by oil platforms on juveniles is through systematic surveys conducted by trained on-board seabird observers on current platforms, exploration projects, and future developments. This suggestion has been included as part of the regulations on exploratory drilling on the Grand Banks of Newfoundland (Montevecchi et al. 2020, Regional Assessment Committee 2020), however, it is important that these data be rigorously collected and shared to build upon the knowledge base that exists.

Long-term studies should be implemented and continued so that researchers can better understand the effects of slow acting or gradually changing risk factors such as climate change and global changes in fish stocks, pollution, and changes in marine and terrestrial habitat. Promising research is already being conducted in many of these areas and will be vitally important for consideration by policy makers in the development of mitigation strategies.

Most importantly, future research should concentrate on the risk exposure and susceptibility of adult breeding Leach’s Storm-Petrels during migration and the non-breeding period. These birds migrate over ocean basin scales (Pollet et al. 2014a, 2019, Hedd et al. unpubl. data), and they are likely affected by global environmental changes and anthropogenic risks.

While much is now known about the risks to which Leach’s Storm-Petrels are exposed during the breeding season, more research needs to be conducted throughout the life cycle of these birds, allowing us to better understand the complex source of this global decline. Researchers also need to work with policy makers to develop best-practice, scientifically based mitigation strategies to slow this decline and aid in the Leach’s Storm-Petrel’s recovery (e.g. Beale et al. 2021).

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APPENDIX A: ETHICS STATEMENT

I have completed the Canadian Council on Animal Care (CCAC) National Institutional Animal User Training Core Modules. All procedures and handling of animals follow the guidelines set by the Memorial University of Newfoundland Committee on Animal Care (permit number 19-01-WM) and by Environment Canada (banding permit number 10332K).

APPENDIX B: CHAPTER 2 SUPPLEMENTARY MATERIALS

Supplementary Figures

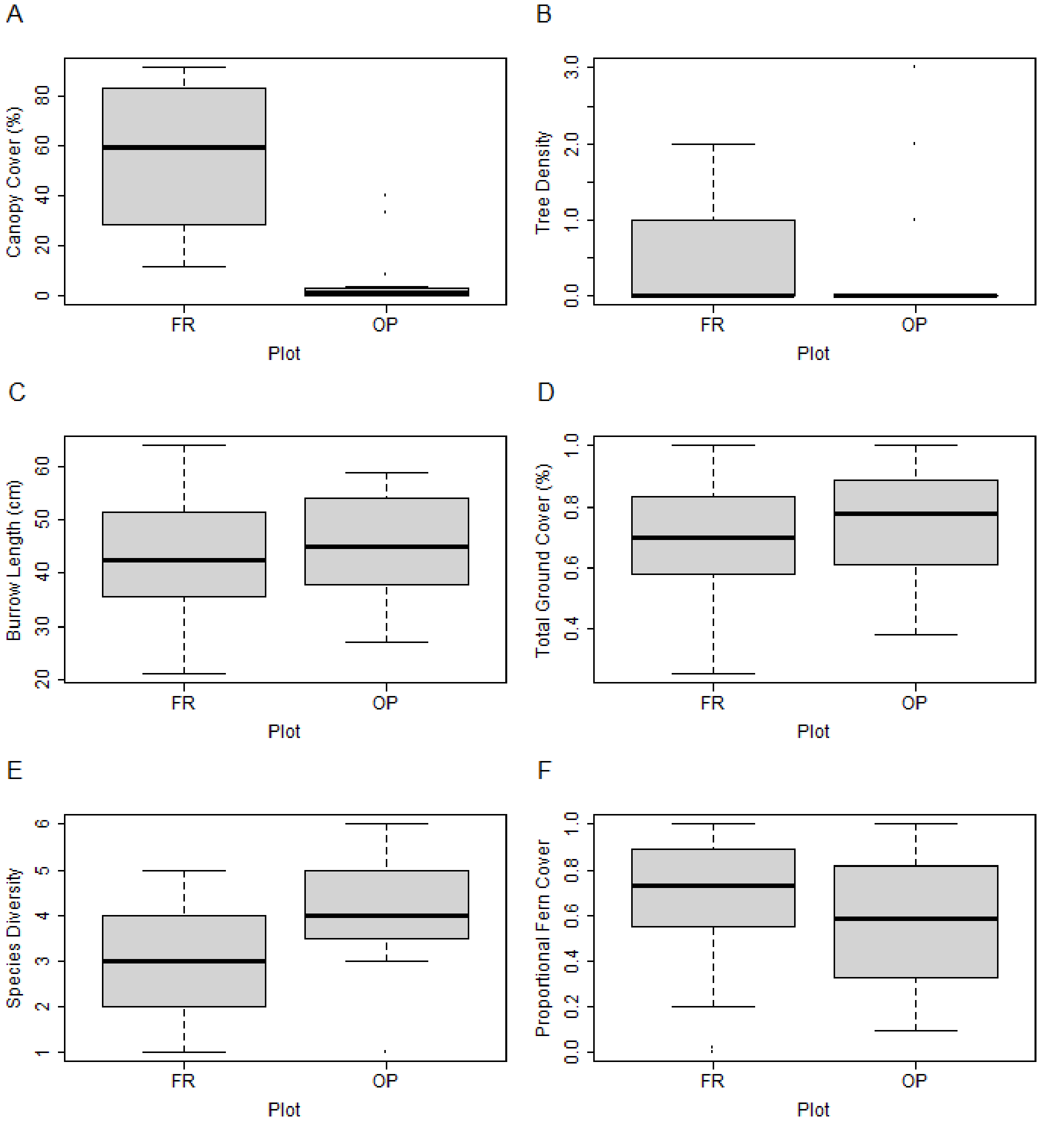


Figure S 1. Boxplots showing the difference between plots for A) canopy cover, B) tree density, C) burrow length, D) total ground cover, E) plant species diversity, and F) proportional fern cover.

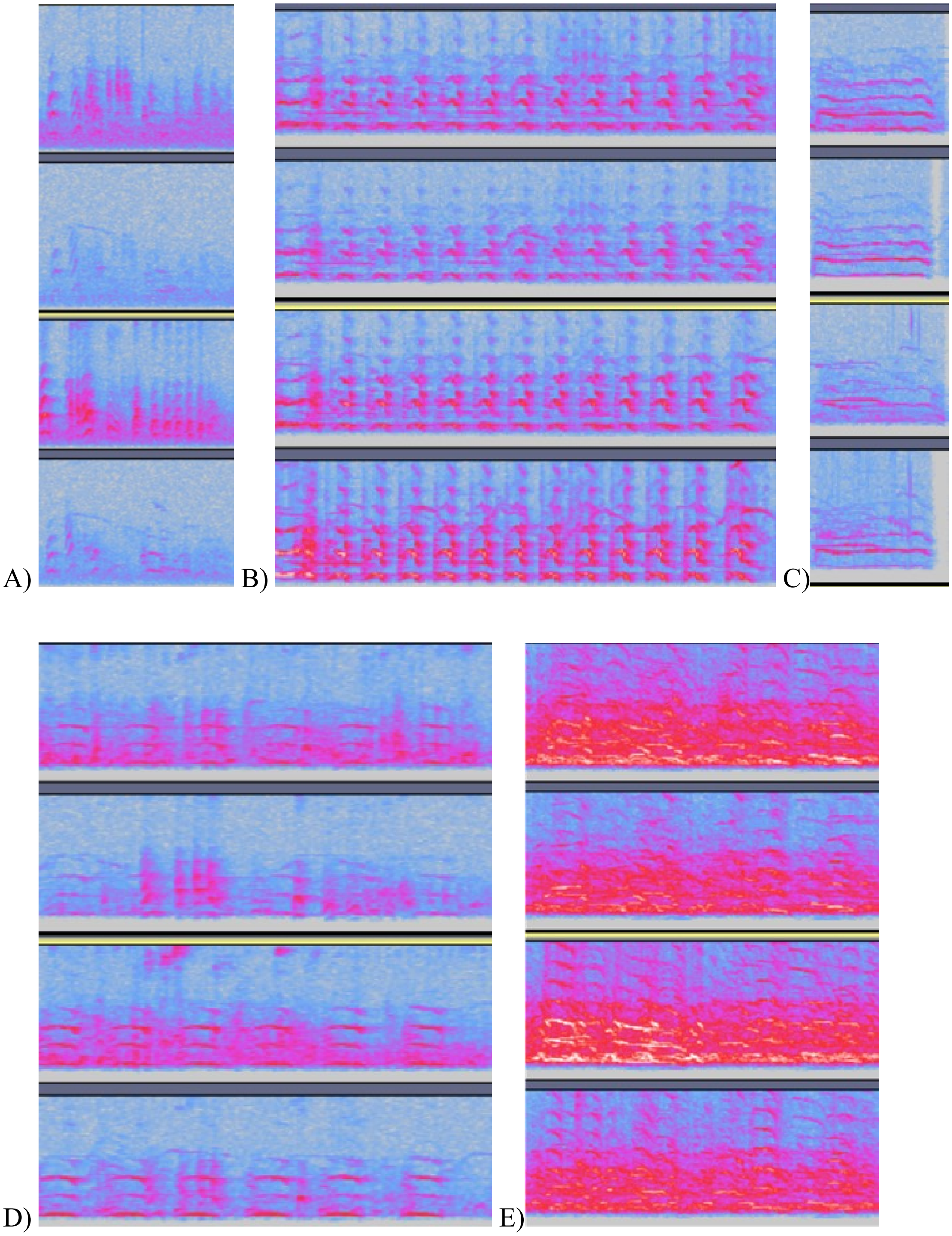
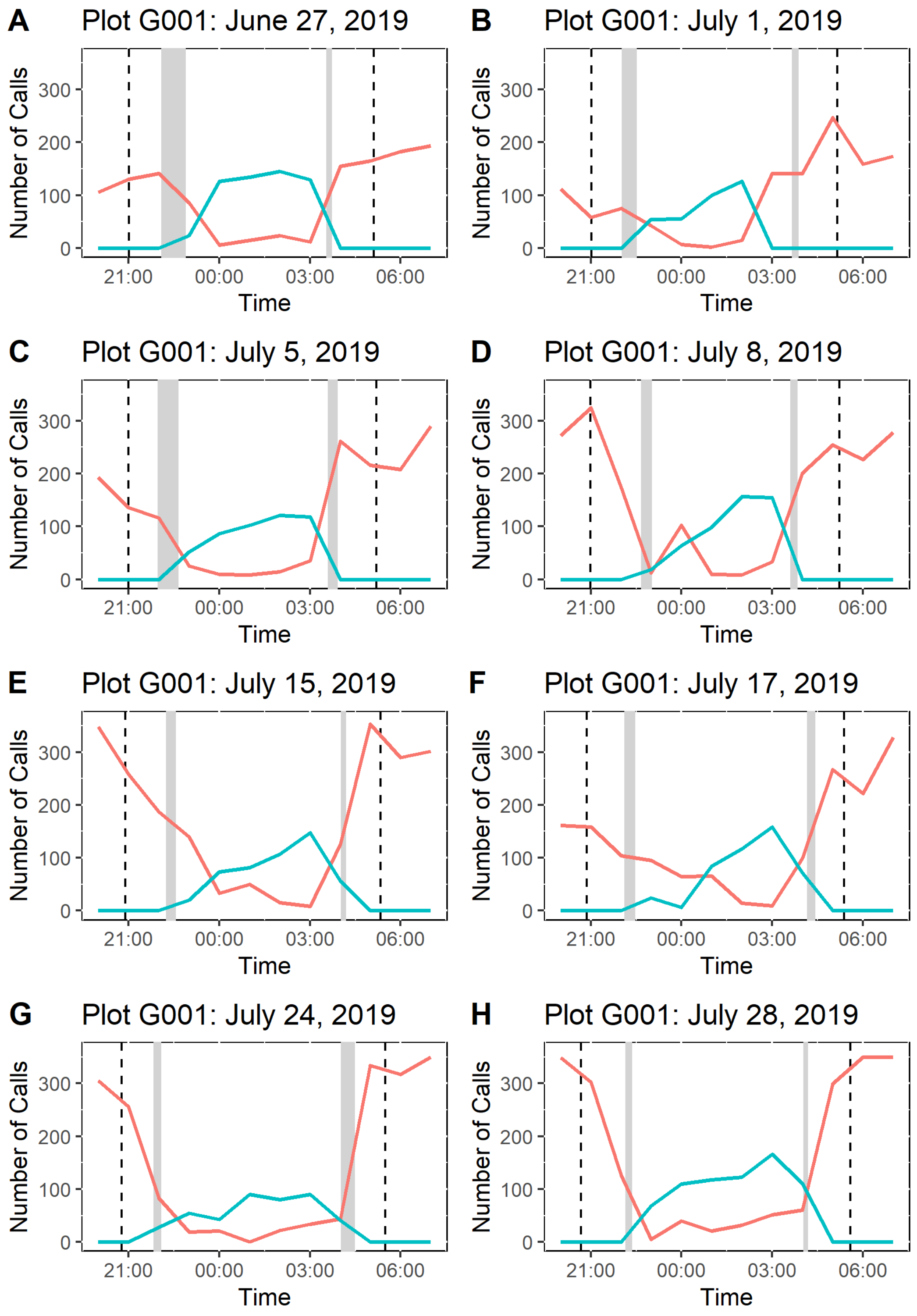


Figure S 2. Spectrograms of a) Leach's Storm-Petrel chatter call, b) Herring Gull long call, and c) Herring Gull mew call. Both species would often call simultaneously, and here I show examples of when individual calls were d) discernible to a trained researcher and e) indiscernible.


A
Plot G001: June 27, 2019
B
Plot G001: July 1, 2019
C
Plot G001: July 5, 2019
D
Plot G001: July 8, 2019
E
Plot G001: July 15, 2019
F
Plot G001: July 17, 2019
G
Plot G001: July 24, 2019
H
Plot G001: July 28, 2019
Number of Calls
0
100
200
300
Time
21:00
00:00
03:00
06:00

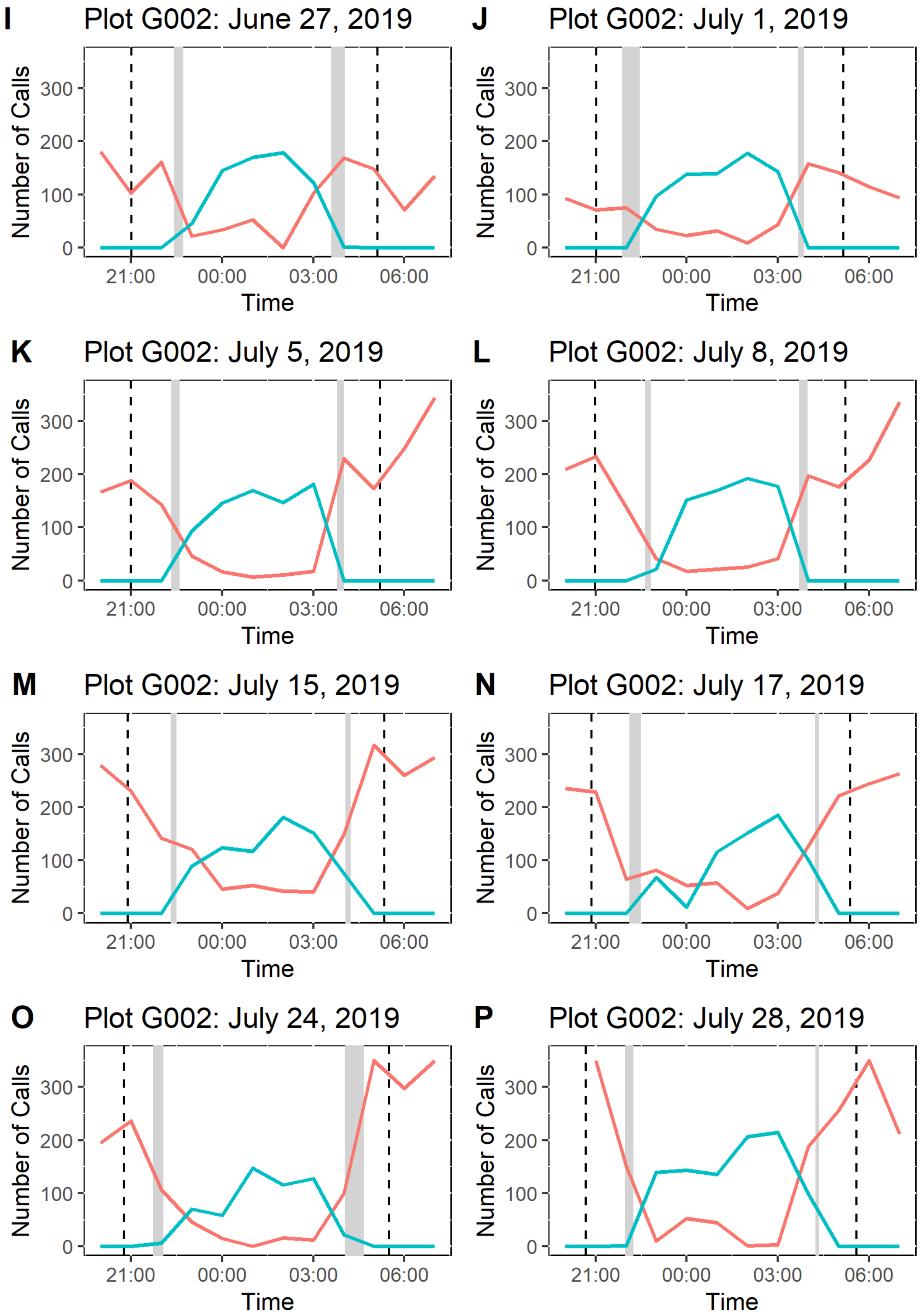


Figure S 3. Line graphs showing the relationship between call frequency of Leach's Storm-Petrels (blue) and Herring Gulls (orange). Grey bars represent the times of the first and last 30 calls for each day in each plot. Dotted lines represent the times of sunrise and sunset.

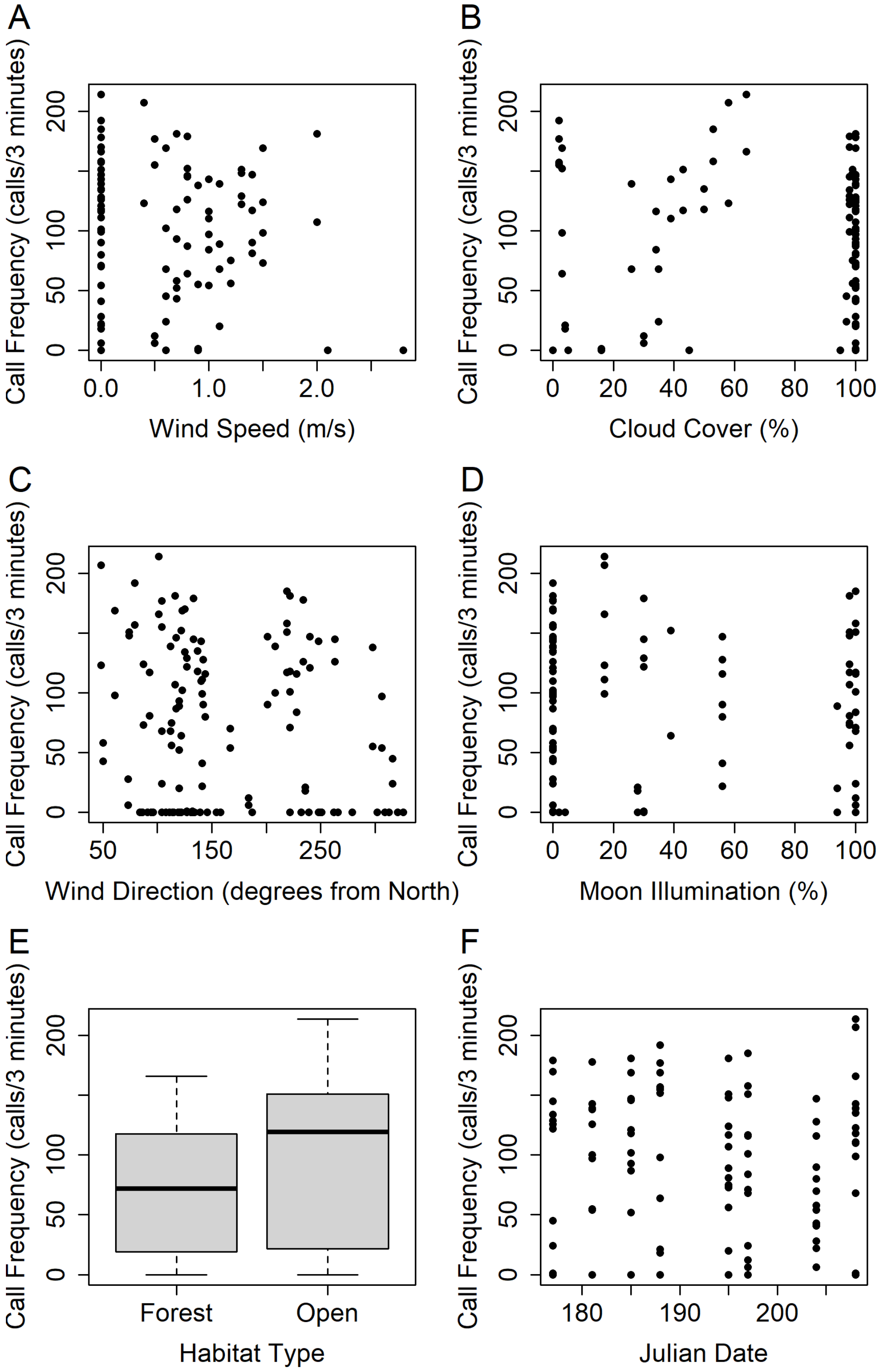


Figure S 4. Plots of untransformed variables associated with the call frequency of Leach's Storm-Petrels.

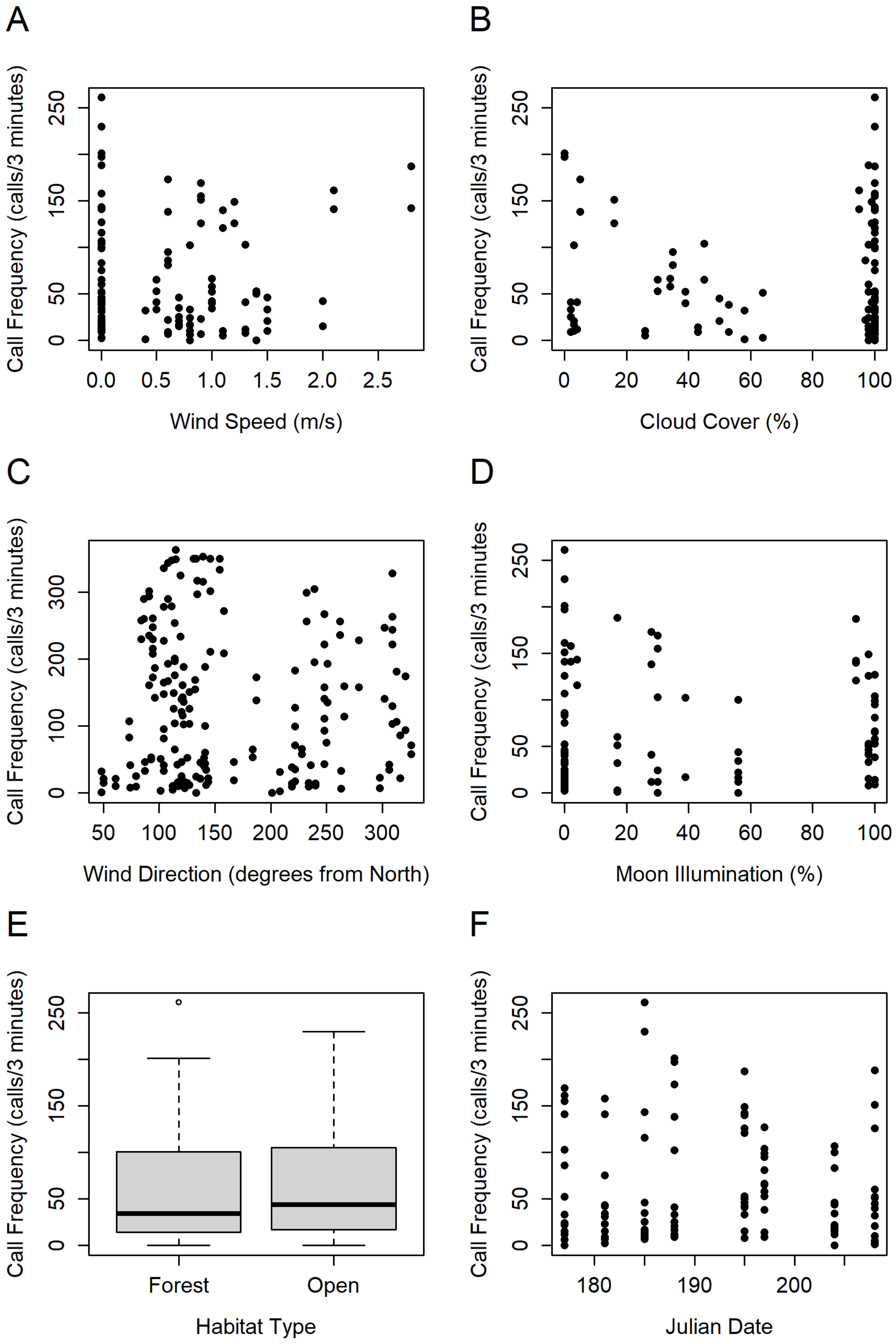


Figure S 5. Plots of untransformed variables with the call frequency of Herring Gulls.

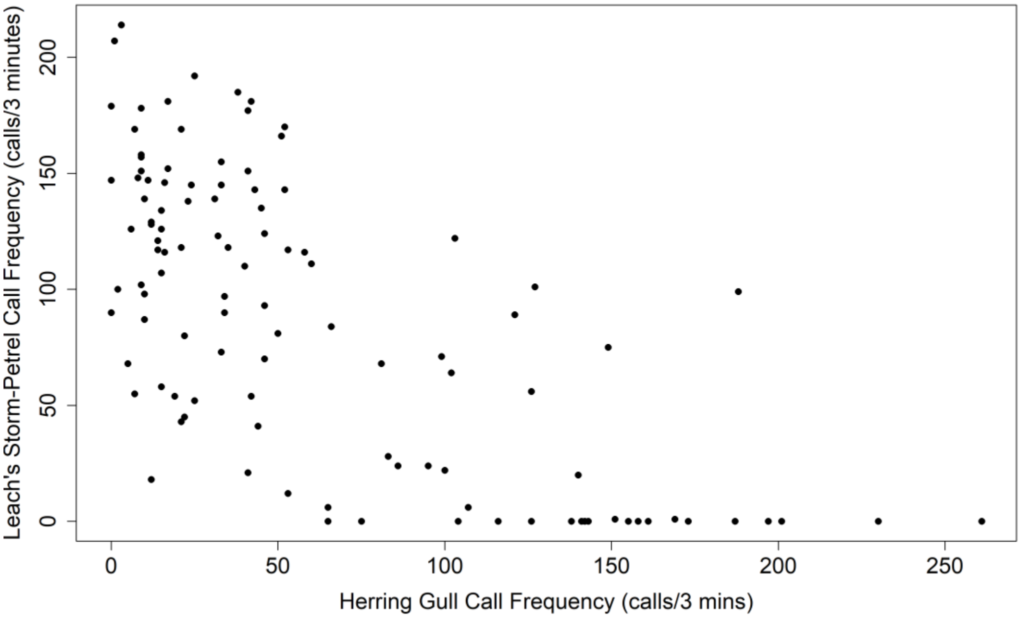


Figure S 6. Relationship between Leach's Storm-Petrel and Herring Gull call frequencies (calls/3 mins).

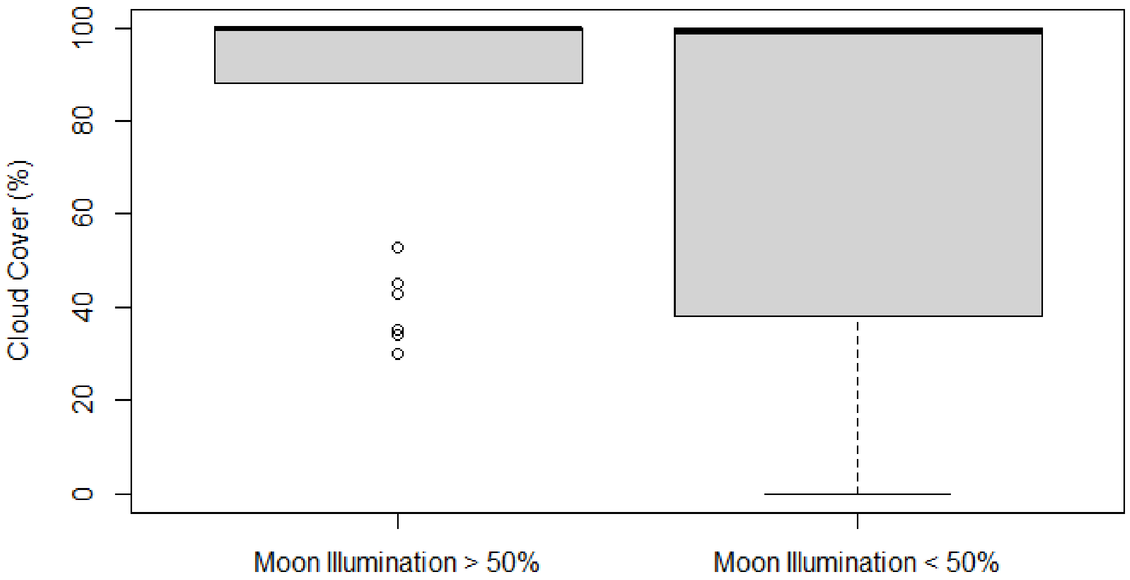


Figure S 7. Difference in percent cloud cover at times when the moon was greater than 50% full and less than 50% full. This figure demonstrates the by-chance association between cloud cover and moon phase in this study period that likely accounted for the lack of significant relationship between moon phase and the activity of Leach's Storm-Petrels and Herring Gulls.

Supplementary Tables

Table S 1. Different calls and their functions for adult Herring Gulls (based on Weseloh et al. 2020).

Call Type	Call Description	Call Function
Long Call	Variable series of high pitched notes which vary in length	Food competition Mate attraction Territorial defence
Long Call Note	Single note produced similar to the long call	Predator defence Individual identification
Mew	Long single note that wavers in pitch	Courtship Parent-offspring interactions Territorial defence Nest changeovers
Alarm	Long note that does not vary in pitch. Birds may shift from this call into another more intense call type if provoked	Predator defence
Choking Call	Low, strangled sounding staccato notes produced in quick succession, usually with 3-5 notes produced	Territorial defence Courtship Nest changeovers

Table S 2. Different calls and their functions for adult Leach's Storm-Petrels (Pollet et al. 2020).

Call Type	**Call Description**	**Call Function**
Chatter	Numerous (~10/ burst) short notes of descending pitch with a longer note in the middle	Mate attraction Mate recognition Nest defence Intra-sex competition
Purr	Very long call consisting of a series of repeated short notes, terminating in a trill of increasing frequency	Mate attraction Pair-bond maintenance
Screech	Abrasive, repeated with a large pitch range	Response to disturbance/ unwanted contact
Chip	Short clicking calls	Response to disturbance/ unwanted contact
Rhythmic	Series of fast, short notes	Female food begging (courtship)

Table S 3. Results of the linear regression models for the change in timing of onset and terminal calls with date. Numbers in bold represent significant relationships.

Model	**Parameter**	**Estimate**	**Standard Error**	**z value**	**p value**
Onset from 20:00	**Intercept**	**343.884**	**48.985**	**7.020**	**<0.001**
	Date	**-1.019**	**0.255**	**-4.004**	**<0.001**
	Plot	-3.620	5.232	-0.692	0.489
Onset from Sunset	**Intercept**	**162.966**	**47.030**	**3.465**	**0.001**
	Date	-0.359	0.244	-1.470	0.142
	Plot	-3.620	5.023	-0.721	0.471
Terminal from 20:00	**Intercept**	**234.367**	**28.702**	**8.166**	**<0.001**
	Date	**1.247**	**0.149**	**8.357**	**<0.001**
	Plot	5.744	3.066	1.873	0.061
Terminal before Sunrise	**Intercept**	**149.199**	**30.302**	**4.924**	**<0.001**
	Date	-0.333	0.158	-2.113	0.035
	Plot	-5.877	3.237	-1.816	0.070

APPENDIX C: CHAPTER 3 SUPPLEMENTARY MATERIALS

Supplementary Figures

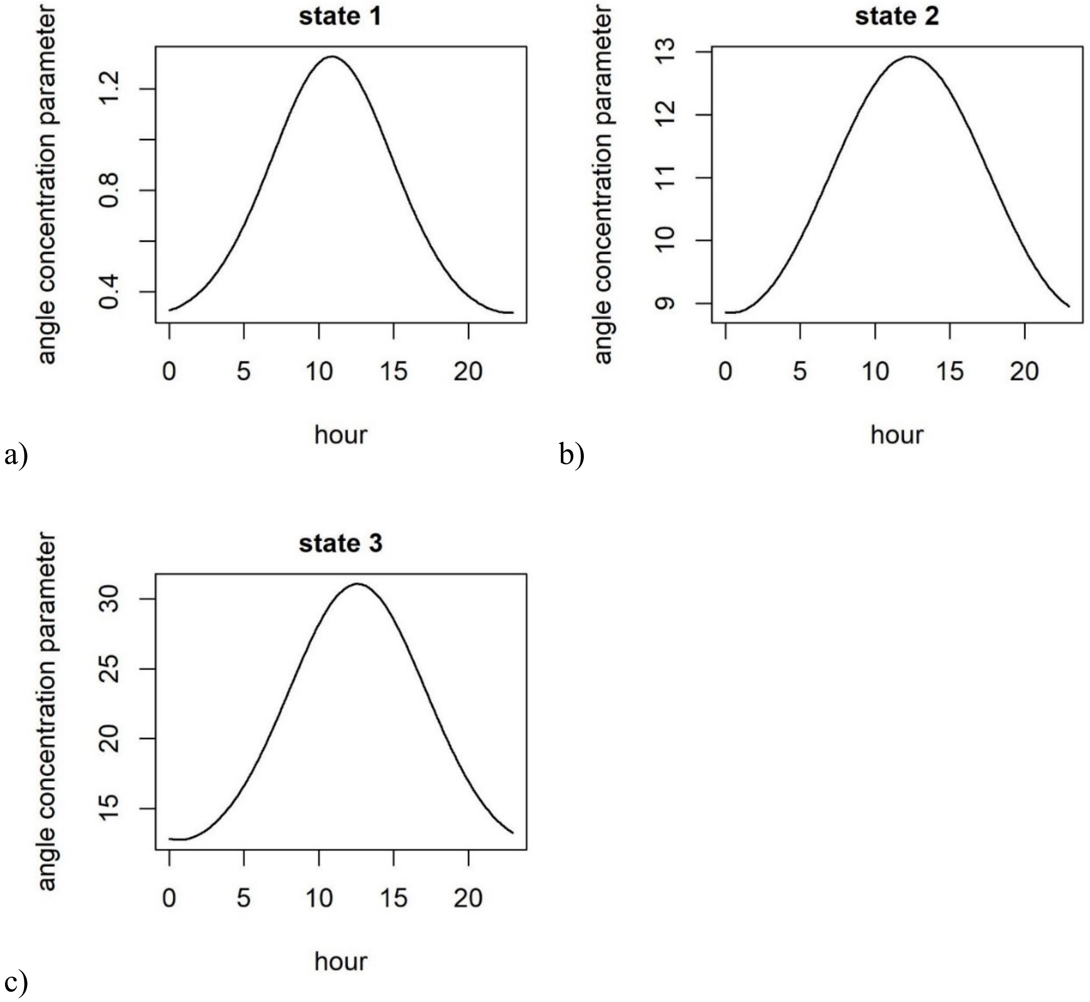


Figure S 8. The probability of transitioning between behavioural states for parental foraging Leach's Storm-Petrels with hour of the day. State 1 is intensive search, state 2 is extensive search, and state 3 is transiting.

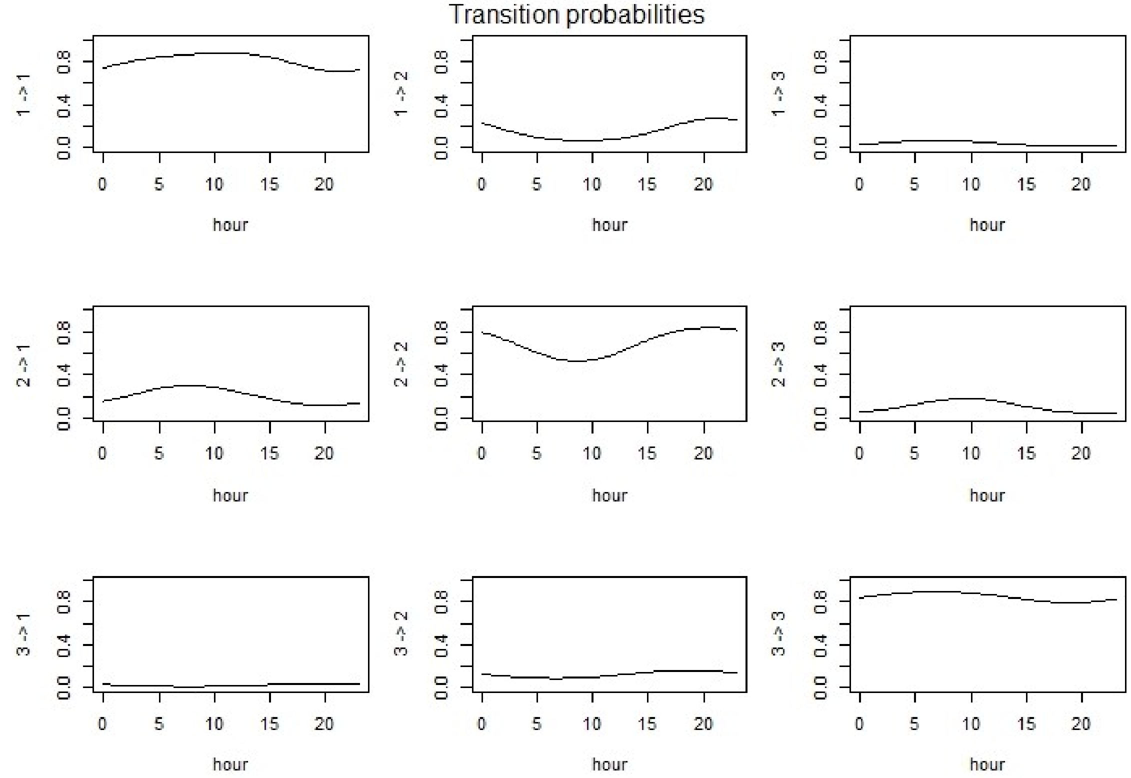


Figure S 9. Variation in the distribution of turning angle for each behavioural state with hour of day. a) State 1 - intensive search, b) state 2 - extensive search, and b) state 3 – transiting.

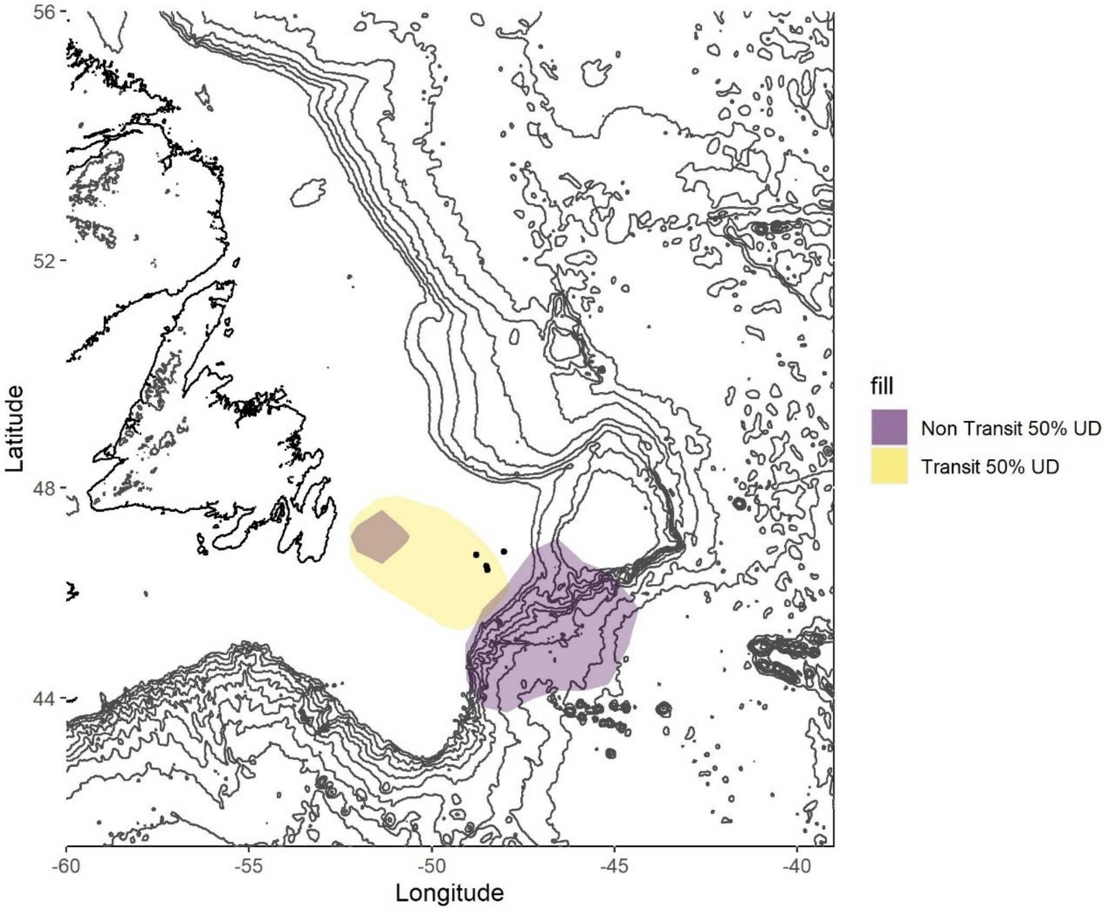


Figure S 10. 50% Utilization Distriution of the locations in which the Gull Island, Witless Bay, Newfoundland and Labrador, Canada population of Leach's Storm-Petrels exhibited behaviour associated with foraging (intensive and extensive searching) and transiting behaviour.

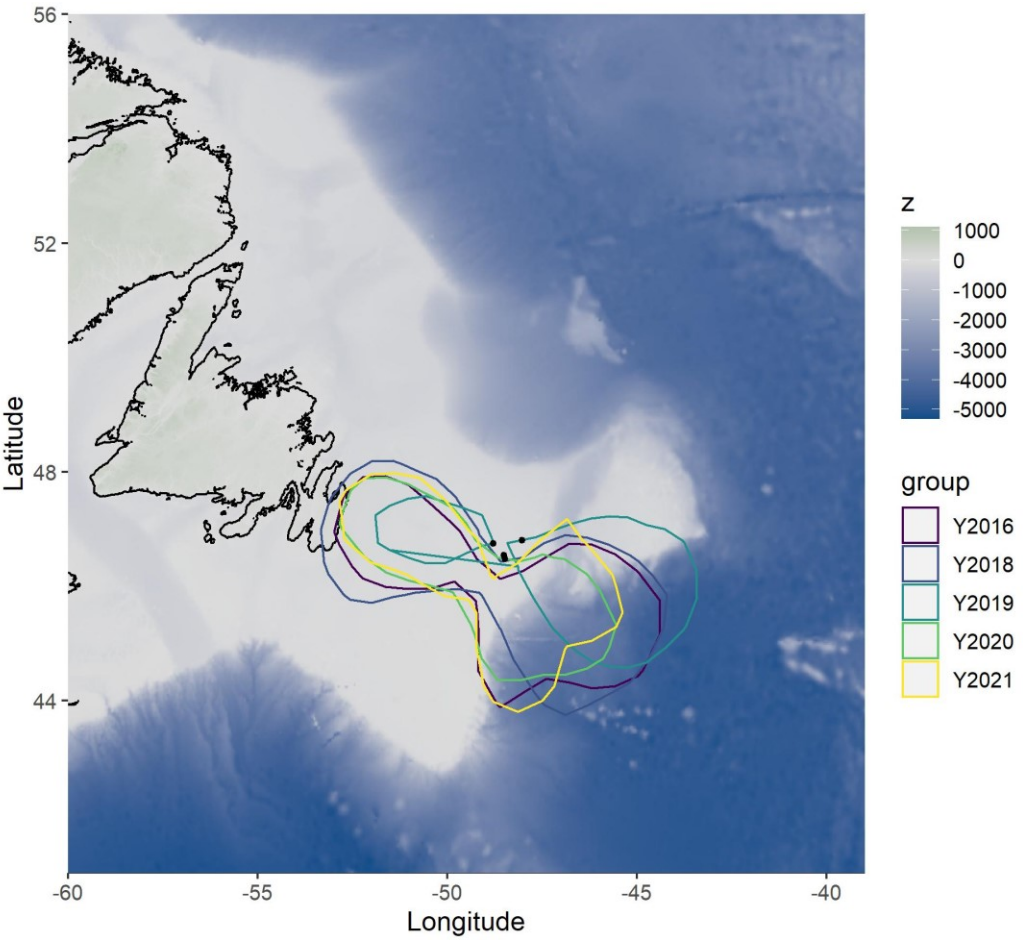


Figure S 11. 50% Utilization Distribution of the forage path locations of Leach's Storm-Petrels on Gull Island, Witless Bay, Newfoundland and Labrador, Canada, in each year of the study.

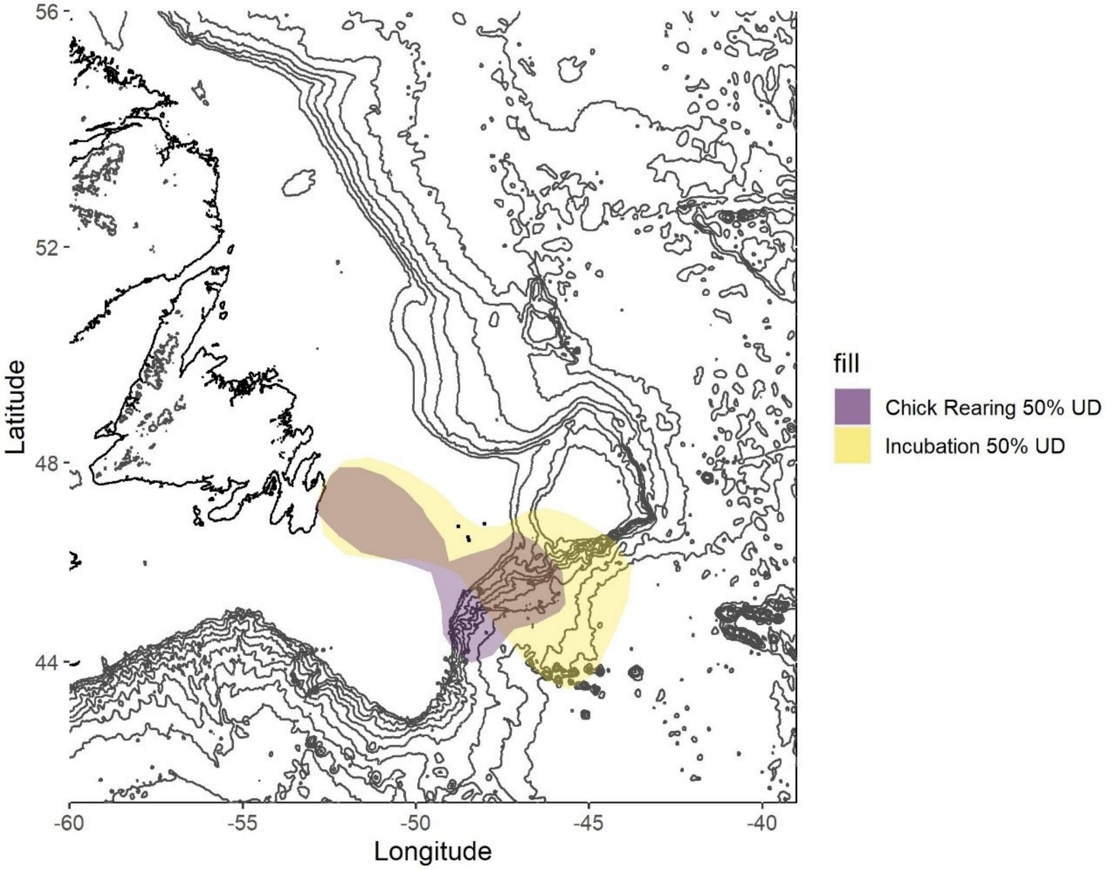


Figure S 12. 50% Utilization Distribution of the forage path locations of Leach's Storm-Petrels on Gull Island, Witless Bay, Newfoundland and Labrador, Canada, between incubation and chick rearing throughout the study

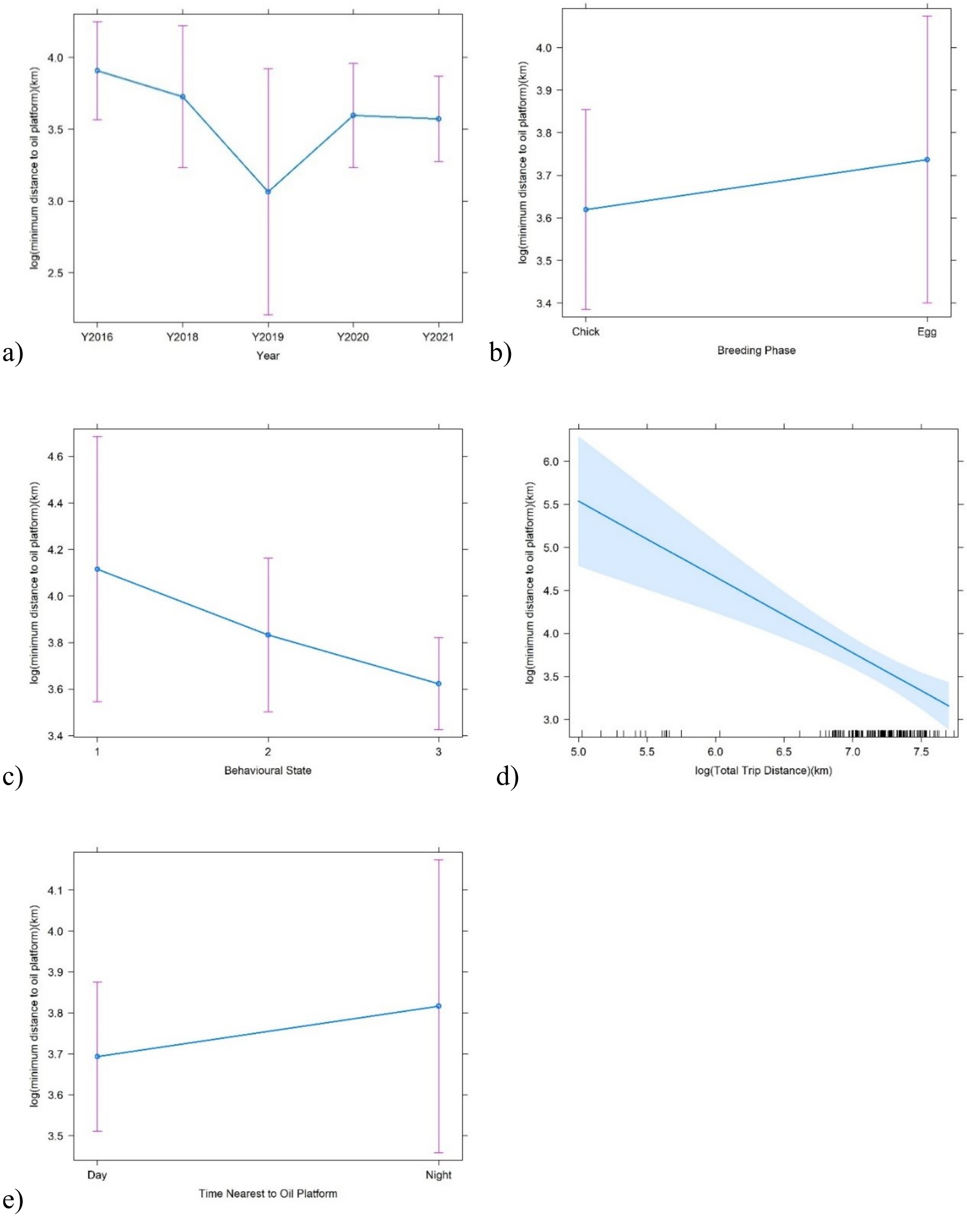


Figure S 13. Effect plots for the relationship between the proximity to an oil platform in a trip to a) year, b) breeding phase, c) behavioural state at the point closest to a platform, d) log of total trip distance, and e) whether the bird was closest to a platform during the day or at night.

Supplementary Tables

Table S 4. Summary information for all trips. Trips in which the bird flew within the maximum average light catch basin of Grand Bank oil production platforms are highlighted in yellow.

Bird ID	**Trip #**	**Trip Dur. (h)**	**Total Trip Dist. (km)**	**Max Dist. from Gull I. (km)**	**Year**	**Breeding Phase**	**Min Dist. to Oil Plat. (km)**	**Behav. State near Oil Plat.**	**Time Near Oil Plat.**
246102955	1	74.72	1523.87	694.60	2016	Egg	11.36	3	Day
246102956	1	74.65	1545.32	720.66	2016	Egg	82.03	3	Day
246102957	1	118.73	1649.88	685.24	2016	Egg	24.82	3	Day
246102960	1	94.37	1586.09	721.52	2016	Egg	29.09	3	Day
246102963	1	95.88	1529.54	633.82	2016	Egg	6.48	3	Day
246102964	2	92.51	1189.32	413.06	2016	Egg	93.68	2	Day
246102965	1	94.09	1566.48	662.19	2016	Egg	31.74	3	Day
246102998	1	78.30	1421.31	589.43	2016	Chick	55.38	3	Night
246102998	2	72.30	1568.84	467.10	2016	Chick	49.16	3	Day
246102998	3	42.15	987.48	461.42	2016	Chick	34.85	3	Day
246102998	4	50.22	1007.69	439.48	2016	Chick	65.93	2	Day
246102998	5	72.16	1354.28	595.90	2016	Chick	28.38	3	Day
246102999	1	98.30	1780.86	728.53	2016	Chick	76.35	3	Night
246102999	2	72.16	1486.13	591.90	2016	Chick	35.34	3	Day
246111609	1	72.00	1417.17	659.72	2020	Chick	17.38	3	Day
246111609	2	70.00	1298.34	581.79	2020	Chick	29.48	2	Day
246111611X	1	70.00	1920.33	823.04	2021	Egg	28.78	3	Day
246111611X	2	66.00	1545.81	624.45	2021	Chick	30.65	3	Night
246111611X	3	70.00	1532.19	708.90	2021	Chick	2.02	3	Day
246111634	1	74.00	1349.67	632.71	2020	Chick	23.16	3	Day
246111634	2	72.00	1475.07	600.23	2020	Chick	45.17	3	Night
246111634	3	118.00	1831.85	623.47	2020	Chick	14.15	2	Night
246111634	4	72.00	1155.45	469.16	2020	Chick	54.99	3	Night
246111635	1	74.00	1285.89	534.55	2020	Chick	41.42	2	Day
246111635	2	44.00	1149.43	504.82	2020	Chick	128.63	3	Day
246111635	3	52.00	1142.83	444.71	2020	Chick	49.47	3	Day
246111635	4	50.00	1096.15	429.56	2020	Chick	52.30	2	Day
246111635	5	48.00	995.04	439.62	2020	Chick	77.19	3	Day
246111635	6	48.00	1007.82	433.51	2020	Chick	121.27	2	Day
246111635	7	24.00	251.34	103.94	2020	Chick	311.61	1	Day
246111636	1	92.00	2266.83	867.50	2020	Chick	82.88	3	Day
246111636	2	70.00	1374.23	585.70	2020	Chick	65.09	3	Day
246111636	3	118.00	2256.58	953.04	2020	Chick	196.05	2	Night

246111636	4	52.00	1214.11	496.02	2020	Chick	24.98	3	Day
246111637	1	104.00	2052.92	762.44	2020	Chick	19.41	3	Night
246111637	2	62.00	1338.50	582.41	2020	Chick	81.61	3	Night
246111638	1	74.00	1558.11	665.38	2020	Chick	50.62	3	Day
246111638	2	72.00	1478.63	698.45	2020	Chick	19.23	3	Night
246111638	3	72.00	1162.07	478.98	2020	Chick	42.57	3	Day
246111638	4	70.00	1379.08	620.27	2020	Chick	10.66	2	Day
246111638	5	68.00	1379.04	605.48	2020	Chick	13.94	2	Day
246111640	1	96.00	1502.18	591.55	2020	Chick	31.40	3	Day
246111640	2	48.00	937.03	403.65	2020	Chick	73.59	2	Day
246111640	3	74.00	1521.48	604.52	2020	Chick	49.49	3	Day
246111640	4	48.00	935.76	416.37	2020	Chick	60.94	3	Day
246111640	5	68.00	1440.39	585.22	2020	Chick	57.19	3	Day
246111640	6	28.00	453.81	215.67	2020	Chick	177.08	1	Day
246111640	7	50.00	1034.37	426.61	2020	Chick	6.78	3	Day
246111641	1	96.00	1655.43	552.89	2020	Chick	124.57	2	Day
246111641	2	44.00	1022.74	458.45	2020	Chick	59.41	3	Day
246111641	3	54.00	1362.28	504.72	2020	Chick	124.27	3	Day
246111642	1	98.00	1986.60	846.78	2020	Chick	4.62	3	Day
246111642	2	68.00	1058.56	456.44	2020	Chick	16.21	2	Night
246111642	3	70.00	1203.56	521.38	2020	Chick	8.10	3	Night
246111647	1	92.00	1442.59	591.93	2021	Egg	20.18	3	Night
246111647	2	116.00	1658.42	752.77	2021	Egg	23.74	2	Night
246111648	1	100.00	2394.50	951.01	2021	Egg	41.59	3	Day
246111648	2	14.00	264.15	86.55	2021	Egg	319.92	1	Day
246111653	1	116.00	1960.08	764.16	2021	Egg	45.92	3	Day
246111654	1	72.00	1469.63	679.24	2021	Egg	26.17	3	Day
246111654	2	94.00	1714.17	668.99	2021	Egg	66.06	3	Day
246111657	1	54.00	1193.01	531.80	2021	Chick	78.04	3	Day
246111657	2	68.00	1242.24	538.38	2021	Chick	28.31	3	Day
246111657	3	74.00	1271.42	554.50	2021	Chick	146.31	3	Day
246111657	4	48.00	1046.48	461.47	2021	Chick	81.35	3	Day
246111657	5	72.00	1494.00	590.56	2021	Chick	74.10	3	Day
246111657	6	72.00	1287.78	493.27	2021	Chick	103.46	2	Day
246111657	7	76.00	1134.67	490.58	2021	Chick	128.54	2	Day
246111657	8	62.00	1140.35	488.77	2021	Chick	93.17	3	Day
246111657	9	74.00	1097.05	471.27	2021	Chick	95.71	2	Day
246111659	1	66.00	1158.55	500.25	2021	Chick	59.32	3	Day
246111659	2	74.00	1192.78	506.46	2021	Chick	80.50	3	Day
246111659	3	74.00	1091.23	506.36	2021	Chick	125.15	3	Day
246111660	1	72.00	1623.49	654.27	2021	Chick	56.11	3	Day

246111660	2	100.00	1614.65	718.12	2021	Chick	13.52	3	Day
246111660	3	48.00	1072.75	496.37	2021	Chick	17.12	3	Day
246111661	1	46.00	1353.72	580.47	2021	Chick	29.71	3	Day
246111661	2	76.00	1243.85	472.60	2021	Chick	4.80	3	Day
246111661	3	72.00	1225.37	479.31	2021	Chick	4.90	3	Day
246111661	4	46.00	1099.74	462.34	2021	Chick	10.17	3	Day
246111663	1	74.00	1456.60	629.89	2021	Chick	17.43	2	Day
246111663	2	72.00	1128.46	464.47	2021	Chick	37.05	3	Day
246111663	3	48.00	1016.62	437.31	2021	Chick	33.17	2	Day
246111663	4	46.00	1173.12	513.48	2021	Chick	19.13	3	Day
246111665	1	74.00	1387.02	622.12	2021	Chick	7.51	2	Day
246111665	2	76.00	1344.85	533.16	2021	Chick	38.25	3	Day
246111665	3	94.00	1586.87	609.28	2021	Chick	24.13	3	Day
246111666	1	100.00	1423.69	598.67	2021	Chick	9.99	2	Day
246111666	2	94.00	1406.21	606.27	2021	Chick	9.05	2	Night
246111668	1	98.00	1728.00	666.16	2021	Chick	14.02	3	Day
246111668	2	94.00	1656.51	657.22	2021	Chick	39.32	3	Day
246111671	1	74.00	1347.14	587.72	2021	Chick	41.84	3	Day
246111671	2	96.00	1465.35	492.40	2021	Chick	95.61	2	Day
246111671	3	46.00	1007.72	436.87	2021	Chick	41.47	3	Day
246111672	1	96.00	1778.13	726.06	2021	Chick	77.10	3	Night
246111672	2	70.00	1304.35	437.19	2021	Chick	19.21	1	Day
246111672	3	118.00	1646.04	526.83	2021	Chick	19.01	3	Night
246111672	4	42.00	1079.46	464.36	2021	Chick	21.09	3	Day
246111672	5	122.00	2120.24	476.09	2021	Chick	4.45	1	Day
246111672	6	68.00	1292.36	484.24	2021	Chick	45.29	3	Night
246111672	7	70.00	1339.46	541.50	2021	Chick	66.80	3	Night
246111673	1	102.00	1641.88	585.67	2021	Chick	69.56	3	Day
246111673	2	18.00	220.33	87.20	2021	Chick	332.85	1	Day
246111673	3	52.00	1226.76	493.16	2021	Chick	78.08	3	Day
246111674	1	72.00	1353.69	531.99	2021	Chick	26.68	3	Day
246111674	2	68.00	1189.26	485.02	2021	Chick	28.59	3	Day
246111674	3	44.00	1150.67	523.92	2021	Chick	54.65	3	Day
246111675	1	74.00	1508.98	609.54	2021	Chick	17.86	3	Day
246111675	2	94.00	1712.83	680.48	2021	Chick	101.05	3	Day
246112812	1	72.00	1524.19	687.34	2018	Egg	23.40	3	Day
246112812	2	74.00	1363.67	638.47	2018	Egg	48.93	3	Day
246112815	1	72.00	1491.18	643.07	2018	Egg	26.58	3	Day
246112821	1	96.00	1817.87	811.06	2018	Egg	30.10	3	Day
246112824	1	140.00	1969.48	584.21	2018	Egg	126.29	3	Day
246112825	1	72.00	1514.75	705.25	2018	Egg	49.91	3	Day

246112826	1	96.00	1422.49	595.79	2018	Egg	7.04	3	Day
246112827	1	118.00	1913.72	792.36	2018	Egg	133.92	3	Day
246112827	2	78.00	1649.76	747.01	2018	Egg	99.51	3	Day
246112828	1	72.00	1654.73	735.83	2018	Egg	16.09	3	Day
246112828	2	20.00	349.32	135.68	2018	Egg	261.86	1	Day
246112828	3	70.00	1165.46	484.52	2018	Egg	12.44	3	Day
246112830	1	118.00	1922.14	857.60	2018	Egg	19.15	3	Day
246112831	1	22.00	219.56	94.51	2018	Egg	311.29	1	Day
246112831	2	70.00	1350.98	627.55	2018	Egg	8.12	3	Day
246112832	1	96.00	1503.71	694.90	2018	Egg	49.25	3	Night
246112832	2	94.00	1578.56	649.48	2018	Egg	141.79	3	Day
246112833	1	24.00	793.61	289.76	2018	Egg	38.98	1	Night
246112833	2	48.00	886.94	421.95	2018	Egg	111.34	2	Night
246112833	3	68.00	1313.42	547.54	2018	Egg	107.94	2	Day
246112834	1	76.00	1669.74	745.95	2018	Egg	30.56	3	Day
246112834	2	96.00	1766.21	789.05	2018	Egg	12.92	3	Day
246112836	1	70.58	1206.58	536.94	2018	Egg	8.65	3	Day
246112837	1	26.15	312.44	135.22	2018	Egg	376.22	2	Night
246112837	2	22.22	294.38	130.96	2018	Egg	367.46	1	Day
246112837	3	24.36	332.56	127.28	2018	Egg	375.11	1	Day
246112837	4	46.64	408.86	145.15	2018	Egg	411.46	1	Day
246112837	5	86.93	1368.27	604.67	2018	Egg	92.56	1	Day
246113218	1	92.00	1640.68	697.57	2019	Egg	16.06	3	Day
246113218X	1	118.00	1858.56	594.30	2021	Egg	12.96	2	Day
246113218X	2	92.00	1704.05	675.23	2021	Egg	36.12	3	Day
246113223	1	71.00	1586.67	678.42	2019	Egg	30.33	3	Day
246113223	2	92.00	1723.11	742.98	2019	Egg	33.59	2	Day
246113405	1	122.00	1927.76	697.31	2020	Chick	13.28	2	Night
246113405	2	72.00	1004.06	454.96	2020	Chick	66.87	2	Day
246113405	3	72.00	1199.90	525.42	2020	Chick	22.82	3	Night
246113405	4	96.00	1845.71	701.70	2020	Chick	35.41	3	Day
246113415	1	120.00	1645.32	676.55	2020	Egg	21.89	3	Day
790112070	1	74.30	1832.05	732.83	2016	Egg	12.13	3	Day
790112070	2	20.22	370.69	117.49	2016	Egg	362.81	2	Day
790112071	1	70.44	1407.96	542.78	2016	Egg	56.09	3	Day
790112072	1	76.51	1809.20	717.61	2016	Egg	22.78	3	Day
790112079	1	94.37	1712.25	746.58	2016	Egg	123.68	3	Day
790112087	1	76.00	1410.42	563.85	2020	Chick	10.09	3	Day
790112087	2	64.00	1188.88	485.95	2020	Chick	18.37	3	Day
790112087	3	50.00	1212.93	479.11	2020	Chick	11.39	3	Day
790112087	4	48.00	1104.42	405.20	2020	Chick	12.65	1	Day

790112087	5	46.00	1277.61	479.98	2020	Chick	29.30	3	Day
790112087	6	74.00	1394.83	557.96	2020	Chick	20.83	3	Day
790112088	1	74.44	1408.55	610.27	2016	Chick	10.55	3	Day
790112088	2	22.08	205.55	82.41	2016	Chick	327.23	1	Day
790112088	3	96.80	1902.46	703.19	2016	Chick	37.33	3	Day
790112088	4	22.07	289.66	131.92	2016	Chick	330.74	1	Day
790112091	1	92.51	1718.52	692.32	2016	Chick	45.69	3	Day
790112091	2	68.65	1601.70	660.96	2016	Chick	19.68	3	Day
790112093	1	98.66	1548.19	634.19	2016	Chick	49.86	3	Day
790112093	2	50.29	1319.04	600.77	2016	Chick	13.48	3	Day
790112093	3	88.16	1432.59	567.79	2016	Chick	188.77	2	Night
790112094	1	78.16	1416.51	527.51	2016	Chick	54.08	3	Day
790112094	2	64.30	1297.41	518.08	2016	Chick	40.36	3	Day
790112094	3	76.44	1247.46	478.41	2016	Chick	129.38	1	Day
790112095	1	117.09	2093.27	562.51	2016	Chick	60.61	3	Day
790112095	2	74.58	1194.82	519.56	2016	Chick	21.43	3	Day
790112096	1	74.09	1332.06	499.66	2016	Chick	75.75	3	Day
790112096	2	46.50	1028.21	463.49	2016	Chick	136.03	3	Night
790112096	3	92.51	1828.06	617.39	2016	Chick	75.24	3	Day
86107045	1	96.00	2077.69	810.88	2020	Chick	22.97	3	Day
86107045	2	72.00	1390.81	530.66	2020	Chick	50.80	3	Day
86107045	3	52.00	1100.37	487.80	2020	Chick	42.43	2	Day
86107045	4	20.00	349.10	123.01	2020	Chick	268.56	1	Day
86107045	5	76.00	1361.87	560.88	2020	Chick	27.02	3	Day
86107055	1	98.00	1725.85	709.96	2019	Egg	11.42	3	Day
86107093	1	98.00	1724.52	681.86	2019	Egg	8.87	2	Day

Table S 5. BAI and percent overlap for all groups of individuals, years, breeding phases, and behavioural states.

Transit or Forage	Comparison	Time	BAI	% Overlap
NA	States	Extensive to Transit	0.859	0.358
NA	States	Intensive to Extensive	0.959	0.752
NA	States	Intensive to Transit	0.726	0.000
Transit	Breeding Phase	2019-2021	0.947	0.759
Forage	Breeding Phase	2019-2021	0.872	0.668
Transit	Individuals	2016 Chick	0.834	0.555
Forage	Individuals	2016 Chick	0.554	0.332
Transit	Individuals	2016 Egg	0.628	0.352
Forage	Individuals	2016 Egg	0.222	0.085
Transit	Individuals	2018 Egg	0.806	0.426
Forage	Individuals	2018 Egg	0.249	0.148
Transit	Individuals	2019 Egg	0.899	0.657
Forage	Individuals	2019 Egg	0.843	0.531
Transit	Individuals	2020 Chick	0.762	0.479
Forage	Individuals	2020 Chick	0.425	0.170
Transit	Individuals	2020 Egg	0.847	0.527
Forage	Individuals	2020 Egg	0.393	0.108
Transit	Individuals	2021 Chick	0.767	0.449
Forage	Individuals	2021 Chick	0.421	0.199
Transit	Individuals	2021 Egg	0.679	0.398
Forage	Individuals	2021 Egg	0.399	0.176
Transit	Individuals	All Birds	0.747	0.435
Forage	Individuals	All Birds	0.364	0.180
Transit	Years	Chick Rearing	0.965	0.844
Forage	Years	Chick Rearing	0.928	0.769
Transit	Years	Incubation	0.946	0.820
Forage	Years	Incubation	0.866	0.644

Table S 6. Type III ANOVA table and random effects of the general linear mixed model for Leach's Storm-Petrel foraging trip distance during the breeding season on Gull Island, Witless Bay, Newfoundland and Labrador, Canada.

Variable	**Chi Squared**	**df**	**p value**
Intercept	255.4	1	<0.001
Year	6.704	4	0.152
Breeding Phase	4.495	1	0.034

Random Effects	**Groups**	**Name**	**Variance**	**Standard Deviation**
	ID	(Intercept)	19627	140.1
	Residual		145034	380.8

Table S 7. Type III ANOVA table and random effects of the general linear mixed model for Leach's Storm-Petrel foraging trip duration during the breeding season on Gull Island, Witless Bay, Newfoundland and Labrador, Canada.

Variable	**Chi Squared**	**df**	**p value**
Intercept	199.36	1	<0.001
Year	4.535	4	0.338
Breeding Phase	6.115	1	0.0134

Random Effects	**Groups**	**Name**	**Variance**	**Standard Deviation**
	ID	(Intercept)	85.25	9.233
	Residual		486.9	22.066