

Defining the phenology of early breeding behaviours of Leach's storm petrels in the  
northwest Atlantic (*Hydrobates leucorhous*)

by

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## Abstract

Laying date is one of the most important reproductive fitness metrics in birds, as timing it well optimizes food availability and ensures the best chance at reproductive success. This is especially pertinent for Leach's Storm Petrel, a declining seabird species in Atlantic Canada, as they have low reproductive capacity. At present, our understanding of the timing of early reproductive behaviours for Leach's Storm Petrels in the northwest Atlantic is minimal, limited to rough estimates of hatch date based on chick measurements.

This study's goal was to determine the timing of early breeding phenology for Storm Petrels from a dataset of geolocation sensor data (GLS) for six long-term study colonies: Kent, Bon Portage, Country, Middle Lawn, Gull, and Baccalieu islands. GLS data describes location and activity of tagged individuals through recording environmental light levels; as Storm Petrels are burrow nesting seabirds, GLS light data can determine when they occupy their burrow during the day. I aimed to characterize the timing of first burrow re-occupancy, differences in pre-laying activity between the sexes, and the lay-dates or start of incubation behaviour across the study colonies.

Linear and generalized linear mixed models were run to determine if sex, colony, or year had a significant effect on breeding phenology. We found that colony significantly impacted the timing of first burrow re-occupancy and lay-date/start of incubation, with Kent Island, New Brunswick, having the earliest first burrow arrival and lay-date, and Middle Lawn, Newfoundland, having the latest of both phenologies. Year significantly impacted the timing of first burrow re-occupancy, as 2015 had the earliest arrival date. These findings indicate that when Storm Petrels return to their breeding colony, they may be influenced by global ocean climatic conditions (annual differences), but that lay-date/start of incubation is mainly influenced by localized conditions at the colony. Sex significantly impacted pre-laying burrow activity, with males visiting the burrow considerably more often and for longer periods than females, but females had a longer pre-laying exodus. Our findings may aid future research on Leach's Storm-Petrel reproductive success by informing conservation management regarding the timing of key breeding activities.

**Keywords:** Pre-laying exodus, timing of breeding, Procellariiforms, reproductive strategies, geolocator, light sensor

## List of Abbreviations

|         |  |
|---------|--|
| COSEWIC | Committee on the Status of Endangered Wildlife in Canada |
| DFO     | Department of Fisheries and Oceans Canada                |
| ECCC    | Environment and Climate Change Canada                    |
| GLS     | Geolocator Sensor  |
| IUCN    | International Union for the Conservation of Nature       |
| NAOI    | North Atlantic Oscillation Index                         |
| NOAA    | National Oceanic and Atmospheric Administration          |

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## **Chapter 1: Introduction**

Seabirds face multiple threats from anthropogenic sources and have declined globally (Croxall et al 2012, Phillips et al 2023). Human activities impacting seabirds includes coastal development, introduction of invasive species, offshore energy production, fisheries, pollution, and climate change. Assessing the impacts of human-caused threats on seabirds is difficult because of the remoteness of their breeding sites and the difficulty with observing them over the ocean during the non-breeding season (Pollet et al 2023); hence, for many species there is a lack of data on their foraging, reproductive, and migratory behaviours.

One such seabird in decline is the Leach's Storm Petrel (*Hydrobates leucorhous*). Leach's Storm Petrels are a federally threatened species that nests on roughly 80 island colonies throughout Atlantic Canada (COSEWIC 2020). The International Union for Conservation of Nature (IUCN) recognizes the global population as vulnerable (Pollet et al 2021) due to a 54% decline in the Atlantic population in the past 40 years (COSEWIC 2020). Roughly 91% of the global population is found breeding off Canada's eastern and western coastlines, highlighting a need for research and conservation efforts in Canada to help restore this species to its former population level of 10 million birds (ECCC and Birds Canada 2024). The reasons for this large population decline are not well understood, and with the advent of offshore wind development in Atlantic Canada, there is even greater need to understand reproductive behavior and potential environmental impacts to this species' ability to successfully reproduce.

### ***1.1: Background and context***

Leach's Storm Petrels belong to the order Procellariiforms, colloquially known as "petrels" or "tubenoses". Like most petrels, Leach's Storm Petrels have slow life histories; they live to roughly 30 years of age, reach sexual maturity at 6 or 7 years-old, and typically produce one egg per breeding season (COSEWIC 2020, Pollet et al 2021). Furthermore, Storm Petrels may choose to forego breeding for the year, potentially due to the female facing stressful overwintering conditions whilst at-sea. Stressors on females range from lack of food resources, exposure to pollutants or contaminants (e.g., mercury, plastics),

storms, predation risks, and competition with other petrels (intra-specific) or other seabirds (inter-specific). Preventing anthropogenic stresses to female storm-petrels is key for preventing disruption to their breeding cycle; however, there is a notable lack of data on many aspects of northwest Atlantic Leach's Storm Petrel's breeding cycles.

Breeding seasons for Storm Petrels, and most other Procellariiforms, is defined in the following key stages: arrival back to colony, nest preparation, re-establishment of pair bonds, pre-laying exodus, mating, egg laying, egg incubation, chick hatching, and chick fledging. Male storm-petrels arrive back at the colony before their partners, known as protandry, during which it is believed they spend time preparing the burrow in which the couple will nest (Pollet et al 2021). Storm Petrels are site philopatric, meaning they return to the same island and burrow to breed every year. It is believed that nest site fidelity helps reinforce the monogamous pair bond between male and female, as partners often separate during the migration and overwintering period (Bried et al 2003). Pairs reinforce their bonds either within their burrows or above ground on their colonies through vocalizations (Pollet et al 2021). Once the pair is reestablished and the burrow site is prepared for nesting, it is believed that the pair mates within their burrow multiple times (Mauck et al 1995). It is theorized the pair then leaves the colony for an intensive period of foraging at-sea known as the "pre-laying exodus" (Hatch 1983, Pollet et al 2021); however, Bond and Hobson (2015) claimed to find no evidence of an exodus in this species. Exoduses lasting from several days to multiple weeks have been found in multiple species of seabirds (Newton 2011), such as Sooty Shearwaters (*Puffinus griseus*; Hedd et al 2014). Upon returning, the egg is laid, and the pair take turns incubating it over shifts lasting multiple days, with the male taking on the brunt of egg care so that the female may regain the energy reserves used in creating the egg (Mauck et al 2011).

## *1.2: Summary of literature*

Egg lay-date phenology is a key metric of reproductive success in birds. Laying at a strategic time in the season determines the quality and quantity of resources the chick will have access to upon hatching based on environmental conditions at that time in the season (Sutton and Freeman 2023). Populations within a single species may differ in lay-date

depending on their geographic location to better match the timing of environmental factors that increases their reproductive success.

A lack of data on lay-dates and pre-laying behaviour has also meant few verifications that Leach's Storm Petrels follow the breeding phenology patterns seen with most Procellariiformes, including male pre-incubation behaviours and activity during, or existence of, the pre-laying exodus (Hedd et al 2014, Bond and Hobson 2015). While early breeding phenology is broadly defined for the global population (Pollet et al 2021), this remains as a coarse estimate and does not capture potential differences within and between colonies of the Northwest Atlantic.

Previous studies examining other aspects of breeding phenology and physiology of the populations breeding in the Northwest Atlantic have found differences within and between colonies. For example, Montevecchi et al (1992) found differences in metabolic rates of birds during their breeding seasons between and within colonies, suggesting that birds from different colonies rely on different foraging areas and prey sources. This may play into lay-date differences if birds are correlating their laying times with peak foraging opportunities, as suggested by Mauck et al (2018), who found that global mean temperatures were the greatest predictor for hatchling success in Leach's Storm Petrels due to temperature's influence on ocean surface prey communities that storm-petrels feed on. Other studies on longitudinal differences in lay-date within bird populations have supported that differences in breeding phenology reflect adjustment to regional environmental factors and the fitness of individual birds (VonBank et al 2024); hence, describing differences in Leach's Storm Petrel laying phenology at a finer scale in this study may contribute to an increased understanding of differences in fitness of individuals as well as breeding colonies.

Specific breeding metrics like pre-laying behavior and lay-date are difficult to determine in Storm Petrels due to the remoteness of their breeding colonies and difficulties with observing them within their burrows. Geolocation sensors (GLS) have been used in lieu of field observations to gather substantial data on Atlantic Leach's Storm Petrel activity for over a decade (Pollet et al 2019). GLS provide data on location and activity of tagged

individuals through recording environmental light levels; night and day length are used to estimate latitude, while deviations in the timing of daily light peaks from Greenwich Meridian Noon-Time are used to estimate longitude (Biotrack Ltd 2013, Lisovski et al 2020). As Storm Petrels are burrow-nesting seabirds, GLS data can be used to determine when they return to their respective burrows for their breeding season since days spent underground are clearly identifiable in the light level data. Extended periods of burrow re-occupancy can serve as a proxy for lay date and start of incubation behaviour, which are both important aspects of breeding phenology (Cross et al 2024).

### *1.3: Research Questions*

In this thesis, my aim is to address fundamental questions concerning the early breeding phenology (burrow use behaviour, lay date) of Leach's Storm Petrels from six different populations (colonies) breeding in Atlantic Canada. Using GLS light waveform data, I identify variation in the pre-laying behavioural patterns of Leach's Storm Petrels. I then examine whether there are: (1) sex-differences in first burrow re-occupancy at breeding colonies, as well as sex-differences in (2) the number of pre-laying burrow visits, and (3) the duration of time each spent in the burrow prior to laying; (4) sufficient evidence for a pre-laying exodus in this species; and (5) colony differences in estimated lay-dates for females and start of incubation behaviour of males (a proxy for lay date, see Methods section). Describing these five aspects of pre-incubation and laying behaviours will expand on our current understanding of the timing of key reproductive parameters and sex differences in reproductive effort. Results may also point to differences amongst colonies that could have implications for management.

### *1.4: Summary of approach*

I addressed these research questions by examining the early breeding phenology of six populations of Storm Petrels from three island colonies in Newfoundland (Baccalieu, Middle Lawn, Gull), two in Nova Scotia (Bon Portage, Country), and one in New Brunswick (Kent) from a GLS dataset collected from 2014 to 2023. Storm Petrels can be presumed as underground in their burrows via GLS detection of full darkness during daylight hours. Male and female birds have a biparental care system, hence swap places when present in the burrow (Pollet et al 2021). Using these GLS waveform patterns, I estimated timing of

first burrow visit, pre-lay visits, and lay-date or start of incubation. First arrival back to the burrow was derived from the first prolonged gap in light detection. It was expected that these patterns would be sporadic as males undergo activities to prepare their burrows for their mate's arrival; however, patterns become predictable after lay-date as males consistently swap incubation shifts with their partner, resulting in visits stretching over every 3-4 days (Tyson et al 2022). Differences in the length and number of light and dark detections between males and females assisted with determining differences in pre-lay activities. Finally, lay-date was derived from when females first had over two full days of darkness during daylight hours, as it is assumed that they are in the process of laying their egg (Cross et al 2024).

Similarly, male start of incubation was derived as the first darkness period over two full days of darkness during daylight hours as it is assumed they take the first incubation shift immediately after their mate lays (Mauck et al 2011). From this analysis, I compared our estimates from the light waveform data to the field notes taken by the biologists monitoring these colonies to confirm if birds were failed breeders, had an egg, or had a chick at time of GLS tag retrieval.

## **Chapter 2: Literature Review**

Leach's Storm Petrels are among the most well-researched storm-petrels in the world (Pollet et al 2023); however, the early stages of their breeding phenology remain poorly understood. The goal of this literature review is to assess existing research on the timing of early breeding phenology in seabirds, which includes pre-laying activity, laying and start of incubation. In doing so, this chapter will demonstrate the value of utilizing GLS methodology to determine breeding behaviours. Emphasis will be placed on the importance of understanding breeding phenology for conservation planning and management with marine birds.

### *2.1 Importance of timing for breeding birds*

The timing of breeding phenology is key to understanding the reproductive success in birds. Documenting breeding phenology allows for the detection of changes and predicting how a bird's breeding biology may be altered when faced with conservation challenges as, ultimately, it is reproductive strategies that define an animal's population levels and how they vary over time (Varpe 2017). Birds have greatest reproductive success when they match the timing of their breeding with local, seasonal conditions that provide best food availability for both parent and provisioning of offspring (Williams 2012). The window for this timing is narrow and its detection relies on a variety of environmental cues (Crossin et al 2022) that trigger the decision to breed. As breeding is a decision, some individuals within a population demonstrate a greater capacity to time their breeding for optimal reproductive success.

Cues for triggering breeding include changes in photoperiod (Helm and Visser 2010), temperature (Visser et al 2006), and habitat characteristics such as vegetation or prey species abundances (Madsen 2001). Williams (2012) argues that photoperiod and temperature act as the primary cues for migratory breeding birds, who then tailor the timing of reproduction to localized resource availability upon arrival to the breeding grounds. Male and female interpretation of cues may vary; however, reproductive success is ultimately reliant on proper timing to ensure offspring have the greatest chance of future survival and reproducing themselves (Varpe 2017).

For birds, two main hypotheses are thought to define the timing of breeding. First, the “date hypothesis”, dictates that birds attempt to breed within the time that allows for their most optimal environmental conditions, such as access to food resources and limited predation risks (Williams 2012); avoidance of nest parasitism from other bird species (Brown and Brown 1999); or best access to high quality habitat (Dzus and Clark 1998). Another hypothesis for timing breeding, the “quality hypothesis”, suggests that birds will minimize the overlap of energetically expensive life history processes like breeding and molting; and attempt to maximize the time for adults to recover from raising their offspring and increase their own energy stores for migration (Williams 2012). Ultimately, both a balance of optimizing available resources for offspring and for greatest parental survival play into the reproductive timing of birds.

Of all the early breeding stages, Williams (2012) argues that pre-laying is the most important as it defines the timing of behavioural and physiological changes that sets a bird into breeding. The outcomes of the pre-laying period influence all following stages of breeding, including nest site establishment, laying date, and incubation. Thus, the timing of breeding dictates how the rest of the breeding season will unfold. Although pre-laying timing is broadly defined by environmental conditions, there is high variability in how specific environmental factors impact the sexes, and how these impacts differ at population and individual levels in different bird species. Furthermore, understanding the timing of early breeding phenology may be key in assessing how breeding will be impacted by human-influenced environmental changes (Sutton and Freeman 2023), such as climate change or habitat alterations.

## *2.2 Leach’s Storm Petrel: A seabird under threat*

### 2.2.1 Population trends and reasons for declines

Seabirds, like Leach’s Storm Petrel, are on of the world’s most at-risk groups of vertebrates, with 56% of the 314 seabird species in decline (Phillips et al 2023). Within seabirds, the tubenoses are some of the most vulnerable to extinction. In Canada specifically, most monitored seabirds are in decline, including the Leach’s Storm Petrel (ECCC and Birds Canada 2024a). The Atlantic population of Leach’s Storm Petrels has declined by 54% in the

last 40 years due to a variety of threats at their breeding colonies and across their at-sea migratory range (COSEWIC 2020).

Paleolimnology research at two major Newfoundland colonies suggest much of this rapid decline is human-driven (Duda et al 2021). The major terrestrial threats to Atlantic Canadian Leach's Storm Petrels include avian predators such as gulls, skuas, corvids, and owls (Hey et al 2019, Hoeg et al 2021, Pollet et al 2021); mammalian predators such as rodents, mustelids, and foxes (Skelpkovich and Montevecchi 1996, Bicknell et al 2020, Hoeg et al 2021); and onshore light attraction from coastal communities (Pollet et al 2023). Major at-sea threats include spatial-temporal shifts in prey availability (Pollet et al 2023); bioaccumulation of toxins such as mercury (Pollet et al 2017); and offshore light pollution from resource activities such as oil and gas platforms and shipping vessels (Gjerdrum et al 2019, Collins et al 2022). These threats may vary across colonies due to differences in foraging areas (Pollet et al 2014b, Hedd et al 2018, Mauck et al 2022) and colony habitat conditions (COSEWIC 2020). For example, birds of Baccalieu face the unique threat of on-land burrow competition with Atlantic Puffins (COSEWIC 2020), whereas birds at Country Island have been depleted due to predation from an introduced vole species (Hoeg et al 2021).

Climate change represents a complex threat, as it acts synergistically on existing threats, but is believed to be one of the leading threats on reproductive success (Mauck et al 2017). Overall, this large variety of threats across great spatial and temporal ranges put the species at a great risk from cumulative impacts (Pollet et al 2023). Thus, there is ongoing need to characterize the timing of the species phenology in relation to perceived threats, especially considering that Canada is currently in the pursuit of developing offshore wind energy markets that is likely to increase the level of offshore industrial activity in core Leach's Storm Petrel foraging areas (Daborn et al 2025, McDonald et al 2025).

As 91% of the global population breeds off Canada's coastline (ECCC and Birds Canada 2024b), Leach's Storm Petrel is a significant conservation concern for Canadian scientists. This has resulted in long-term monitoring efforts yielding decades-worth of data from the Seabird Monitoring Program at several major breeding colonies (ECCC and Birds Canada

2024b). Evidence from monitoring efforts indicates a decline across the majority of the major breeding colonies (COSEWIC 2020), including at the world's largest breeding colony, Baccalieu Island, off the eastern coast of Newfoundland (Wilhelm et al 2019). Furthermore, the Canadian Atlantic population demonstrates a lower-than-expected adult survival rate of 79-86% (Fife et al 2015, COSEWIC 2020), which is likely a contributor to their steep decline. As such a well-monitored species, Leach's Storm Petrel represents an opportunity to determine drivers of seabird declines globally and act as a model for further conservation efforts, especially with concern to species occupying similar niches such as the globally endangered Ashy Storm Petrel (*Hydrobates homochroa*), the European Storm Petrel (*H. pelagicus*), the Fork-tailed Storm Petrel (*H. furcatus*), the Least Storm Petrel (*H. microsoma*), and the Black Storm Petrel (*H. melania*; Pollet et al 2023).

### 2.2.2 Concerns with breeding phenology

Thanks to rigorous monitoring of Atlantic Leach's Storm-Petrels, there exist a robust body of literature on various aspects of the bird's breeding and non-breeding phenology in terms of timing, location, and potential risk exposures during various life stages. Like many *Procellariiformes*, Leach's Storm Petrel balances the costs of annual reproductive efforts with self-maintenance (Tyson et al 2022, Haussmann et al 2024). Generally, there is a lower drive to reproduce because the species is long-lived with an average lifespan of 30 years (COSEWIC 2020). Female storm petrels likely evaluate the decision to breed against their own body condition, as the egg they lay is roughly 20-25% of their body weight (Bond and Hobson 2015), making reproduction an energetically expensive process for females to undertake. As such, the female may forgo the decision to breed if her body condition is poor from challenges encountered during her overwinter at-sea migration (e.g., storms, predation, lack of food resources; Elliot et al 2020, Haussmann et al 2024). This further contributes to the harsh decline of this seabird, as it is a slow reproducer by optionally laying one egg per year, and by taking 6-7 years to reach sexual maturity (COSEWIC 2020, Pollet et al 2021). Any risks to the species' reproductive biology need further research to ensure that populations can reverse the declining population trend seen across colonies.

Most activities at colonies during breeding have been extensively studied as this is the time of the year when birds are most accessible for observation via field excursions. Most

research has characterized the mid- to late-season breeding phenology, primarily incubation and chick-rearing (Zangmeister 2009, Mauck et al 2011, Pollet et al 2014b, 2017, Hedd et al 2018, Elliot et al 2020, Mauck et al 2022, Tyson et al 2022, Hausmann et al 2024); however, there remain knowledge gaps on patterns of early breeding phenology. For example, protandry lacks thorough study in Leach's Storm Petrel despite being a key assumption in Mauck et al.'s (2011) study on male-biased reproductive efforts. This lack of study on timing extends to other reproductive activities prior to laying, such as burrow preparation and re-establishment of pair bonds (Mauck et al 1995), and the potential for female pre-laying exodus. Pre-laying exodus is a behaviour used to build up energy stores after fertilization and prior to laying that is seen in many colonial seabirds (Hatch 1993, Pollet et al 2021), but its occurrence in Leach's Storm Petrel is contested (Newton 2012, Bond and Hobson 2015). Furthermore, well-studied breeding phenology such as laying, incubation, and chick-rearing has only been well-characterized for a few of the major breeding colonies using limited sample sizes, most often at Bon Portage (Fife et al 2015, Pollet et al 2014b, 2017, Tyson et al 2022), and Kent (Mauck et al 1995, Zangmeister et al 2009, , 2011, 2018, d'Entremont et al 2020, Elliot et al 2020, Hausmann et al 2024) islands; hence, it is unknown the extent of how the colonies across Atlantic Canada may differ in their strategy of timing for reproduction.

As previously mentioned, birds may differ in their timing of reproduction across differences in latitude and longitude to account for differences in environmental conditions, primarily food resource availability (Williams 2012). There is currently no literature examining cross-colony differences in the timing of reproduction in Leach's Storm Petrel; however, it is known that colonies forage over different areas of the Atlantic Ocean during the incubation and chick-rearing stages (Pollet et al 2014b, Hedd et al 2018, Mauck et al 2022). These areas encompass a vast scale of up to 500 km away from their respective colonies during foraging (Hedd et al 2018), with females ranging 160 km further than males (Mauck et al 2022). Hedd et al (2018) found that the colonies included in this study range over the following areas: Baccalieu birds forage over the northern Grand Bank and Flemish Cap, Orphan Basin, and western Labrador sea; Gull Island birds forage over the Grand Bank and Flemish Cap as well, and south into the Newfoundland Basin; Middle Lawn birds forage

near the Laurentian Fan and across the southwestern portion of the Grand Bank; Country Island birds forage across the Scotian Shelf, into the Laurentian Fan and to the southwest of the Grand Banks; Bon Portage, the most southernly colony, sees its birds forage east of George's Bank; and finally, Kent Island birds concentrate their foraging in the Gulf of Maine and over George's Bank. Besides Kent Island Storm Petrels, who forage in shallow neritic waters of 200 m depths, all colonies forage over deep oceanic waters of 1,950-meter depths (Hedd et al 2018).

Each foraging region experiences its own seasonal shifts in marine productivity that influences the availability of food due to a variety of oceanographic factors such as water column stratification, sea ice coverage, pH, and oceanic currents (Bernier et al 2023). Leach's Storm Petrel prey is reliant on highly seasonally variable plankton blooms (Hedd and Montevecchi 2006, Hedd et al 2009, Pollet et al 2021), so I expect that each colony may demonstrate differences in reproductive timing to match best prey availability in accordance with these blooms.

### *2.3 Studying the timing of seabird breeding phenology*

Although a knowledge gap in Leach's Storm Petrels, the timing of early breeding phenology has been described in several seabird species of similar life histories and varying conservation concern. Lay-date phenology has been described for Chatham Petrel (*Pterodroma axillaris*) using burrow monitoring and GLS data (Rayner et al 2012), Mediterranean Storm Petrel (*Hydrobates pelagicus melitensis*) using long-term field monitoring and environmental data (Ramírez et al 2016); terns (*Sterna spp.*), auks (family Alcidea), and Black-Legged Kittiwakes (*Rissa tridactyla*) using long-term field monitoring data in the North Sea (Wanless et al 2009); Common and Brünnich's Guillemots (*Uria aalge* and *Uria lomvia*, respectively) using light and salt water immersion GLS data (Merkel et al 2019); and Rhinoceros Auklets (*Cerorhinca monocerata*) using GLS data (Cross et al 2024). Several of these studies have identified major effects on early breeding phenology, including migration distance (Cross et al 2024); sea surface temperatures (Merkel et al 2019); latitude (Wanless et al 2009, Quillfeldt et al 2014, Cross et al 2024); longitude (Gaston et al 2017); colony nesting density (Merkel et al 2019); and local oceanographic conditions such as water stratification (Ramírez et al 2016). Overall, lay-date phenology has been a large area of

research for many seabird species, but there are few studies focusing on the initial phases of breeding despite its influence on the remainder of a bird's breeding season.

This literature review has outlined the importance of understanding specific timing of breeding bird biology in the context of Leach's Storm Petrels in Atlantic Canada and it has identified the need to characterize early aspects of breeding phenology to aid in conservation management of the species. The timing of breeding phenology will likely be altered by climate change, and may be influenced by increased anthropogenic activity from resource exploitation, pollution, and habitat alteration; highlighting the need for further research that is specific to North Atlantic seabirds. Despite the need to characterize breeding phenology to understand how it may be changing in seabirds, many species have only been studied thoroughly in recent years due to technological and logistical constraints. Furthermore, these studies vary in scale: some for single populations and some across multiple scattered breeding colonies. There is a need to investigate Leach's Storm Petrel's early breeding phenology at the regional scale where populations are declining in the northwest Atlantic, which in turn may help with future studies regarding population recruitment and reproductive success.

## **Chapter 3: Materials and Methods**

### *3.1 Study sites, years, and sample sizes*

Geocator (GLS) datasets overlapping the early breeding period for 292 Leach's storm petrels breeding in Atlantic Canada between 2012 and 2023 were provided by researchers from Environment and Climate Change Canada (ECCC), Bowdoin College, and Acadia University. Geolocators from Migrate Technology Ltd. (Cambridge, UK; Intigeo-W30A9-SEA) or Biotrack Ltd. (Dorest, UK; MK5740 or MK5040, 2012-2015 only) were typically deployed late in the breeding season (mid-August to late September) and retrieved after laying following year (late June to mid-July). Deployment occurred in New Brunswick on Kent Island (Bowdoin College); in Nova Scotia on Bon Portage (Acadia University) and Country islands (ECCC); and in Newfoundland and Labrador on Middle Lawn, Gull, and Baccalieu islands (ECCC; Fig. 1). At the time of tag retrieval, the nest contents (egg or chick) were recorded. These supplementary breeding data aided with the interpretations of light intensity patterns and identification of breeding behaviours. Sex was determined through genetic analysis of blood samples taken from birds the brachial vein at the time of GLS retrieval (Fridolfsson and Ellegren 1999). Birds for whom sex was indeterminate were excluded from the final dataset used for analysis (n = 15).

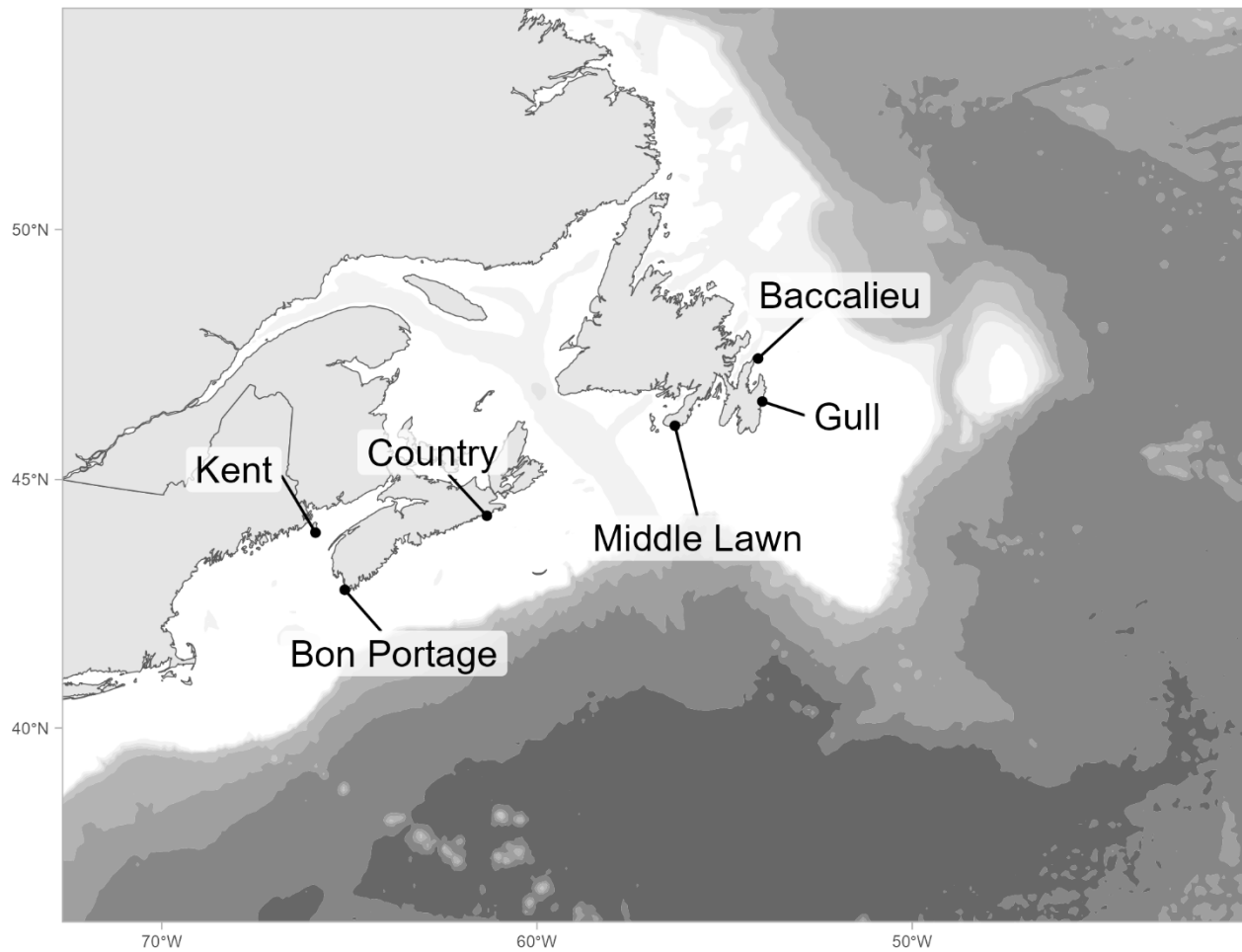


Figure 1: Map of Atlantic Canada with the six study colonies Kent in New Brunswick, Bon Portage and Country in Nova Scotia, and Middle Lawn, Gull, and Baccalieu in Newfoundland and Labrador.

### 3.2 Processing geolocator light intensity data

Protandry, pre-laying visits, pre-laying exodus, lay-date, and start of incubation burrow use patterns were derived from GLS light waveform data similar to Cross et al (2024). GLS waveform data was processed to select data within the spring migration and breeding season of Leach’s Storm Petrels from March to the end of tag deployment (Pollet et al 2021). Noise in light data during the night was removed using the *lightFilter* function in R package *GeoLight* with three iterations. We defined darkness as periods with light intensity values below 11 for Migrate Technology tags or below 1 Biotrack tags, which correspond to roughly equivalent light levels (Bråthen et al 2021). I then identified the date and time of each ‘event’ when conditions crossed from dark to light, or light to dark, and removed any periods of darkness < 4.5 hours to eliminated records likely caused by light interference (e.g., artificial

light sources), tag shading, or tag malfunction (Cross et al 2024). The duration of each 'dark' period was then calculated. Since the shortest night expected for the northernmost colony in this study was 8 hours, period of darkness > 16 hours (the longest day expected) were assumed to indicate burrow use during the day. The start date and time and the duration of each of these extended dark periods was recorded.

Waveform data were plotted using the R package *ggplot2* to visualize patterns in light vs. dark conditions. Where available, field notes on the birds breeding status at tag retrieval were compared with burrow use patterns to determine if breeding was successful, with the presence of an egg or chick demarking successful breeding as of the time of tag retrieval. First burrow usage was determined as the first extended dark period lasting > 16 hours, and typically  $\geq 24$  hours. Start of incubation (if male) or lay date (if female) was determined as the first extended dark period lasting  $\geq 48$  hours (2 days) which was followed  $\leq 7$  days later by another extended dark period lasting  $\geq 48$  hours (Appendices A1-A4). Seven days was used as an estimate of the maximum incubation shift duration by a birds' mate (Great Island, NL; Pollet et al 2021). Since many birds were retrieved and their tags removed soon after the start of incubation, we also allowed start of incubation/lay date to be identified where the first extended dark period was followed by the end of the dataset (retrieval) within 7 days. Failed breeders and birds without a clear shift to incubation behaviour in their light data, were discarded from the final dataset (n = 90, final dataset included 202 birds).

Potential pre-laying exoduses were identified by calculating the number of days between the start of incubation/lay date and the most recent prior incident of daytime burrow use (if present). Most birds (n = 148 or 73.3% of usable dataset) had potential pre-lay exoduses events. The number of daytime burrow occupancy events and the total duration of these events was also quantified for each bird.

The identified noticeable patterns of extended dark periods (daytime burrow use) were exported from RStudio to Microsoft Excel to allow for data compilation and cross-comparison within and between colonies. Dates for each breeding phenology variable were converted to Julian Day format to enable comparison across years.

### 3.3 Statistical analysis

I used linear models, linear mixed models and generalized linear mixed models (type III sum of squares) to test whether colonies displayed differences in their early breeding phenologies (R package *lme4*; Bates et al 2015). Linear mixed models are extensions of simple linear models to allow both fixed and random effects, and are particularly useful when there is non independence, such as that which arises from a hierarchical structure, in this case colony of origin (metapopulation of Leach's Storm Petrels, *sensu* Fox et al 2014). Generally, one can think of fixed effects as variables that explain variation within the response variable, and random effects as variables that structure the unexplained variation. Generalized linear mixed models are used when the residual structure of a linear model is not normally distributed.

To address the first question – whether there are sex differences in colony arrival timing, defined here as first daytime burrow occupancy date, I used a generalized mixed model (Equ. 1). Protandry, where the male is first to return to the breeding grounds, is common in seabird species, so I expected there to be sex differences in first burrow re-occupancy; however, I had no a priori prediction about the effects of colony of origin or year. Individual estimates of the first date of first burrow re-occupancy were tested against these described effects to determine if any of the predictor variables had a significant effect on the response variable (Equ. 1):

**Equation 1:** *Arrival timing* ~ *Year* + *Colony* + *Sex*

Here, there is no random effect because I was exploring whether there are annual, colony level, and/or sex effects; hence, all effects were classified as fixed.

For my second and third questions – whether there are sex differences in the number of total pre-laying burrow visits after arrival (Equ. 2) and the total duration of time spent in the burrow prior to laying (Equ. 3) – I used linear mixed models. I assumed that sexes would have differences in all pre-laying activities, and that these behaviours would be conserved across populations (Mauck et al 2011). As such, I did not expect pre-laying behaviour to vary amongst colonies (populations), and so colony of origin was included as a random effect. The response variables were log-transformed to meet model assumptions of normality:

**Equation 2:**  $\log(\text{Number of Pre – Laying Burrow Visits}) \sim \text{Year} + \text{Sex} + (1|\text{Colony})$

**Equation 3:**  $\log(\text{Total Duration of Pre – Laying Burrow Occupancy}) \sim \text{Year} + \text{Sex} + (1|\text{Colony})$

To test my fourth question concerning the duration of potential pre-laying exodus, I predicted a sex difference as the duration of the exodus as this period is central to a female's need to forage whilst undergoing rapid yolk synthesis and egg production (Equ. 4; Newton 2011, Bond and Hobson 2015). I predicted that males would have a shorter exodus as they are not undergoing the energetically expensive tasks of developing an egg and may have duties towards ensuring the nest is prepared for their mate's lay-date (Mauck et al 2011).

**Equation 4:**  $\log(\text{Duration of Pre – Laying Exodus}) \sim \text{Year} + \text{Sex} + (1|\text{Colony})$

Finally, to test my fifth and ultimate question, whether there are differences in lay date amongst the six colonies studied, I used a generalized linear mixed model to account for response variables with varying distributions (Equ. 5). Sex was included as a random effect to account for any indirect effects on lay date; given that males who don't lay at the start of incubation behaviour is assumed synonymous with lay date as male seabirds often the first incubation shift after the female has laid the egg (*sensu* Cross et al 2024). Including a random effect for sex will indicate whether this assumption of males taking first incubation shift after their partner lays is sound.

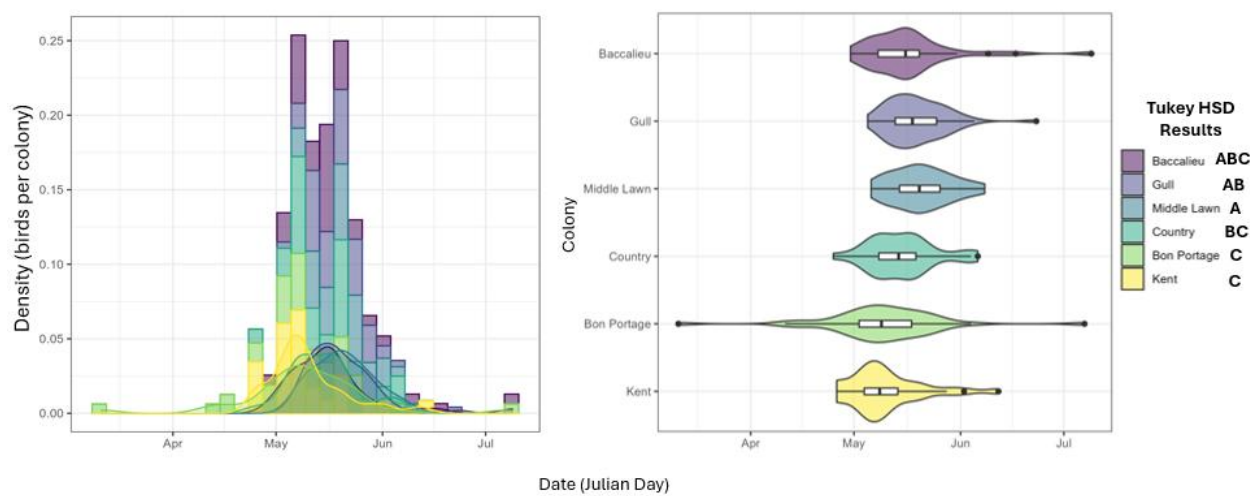
**Equation 5:**  $\text{Lay Date (or Start of Incubation Behaviour)} \sim \text{Year} + \text{Colony} + (1|\text{Sex})$

For all the equations described above, post-hoc comparisons were performed using either a Tukey's HSD test (comparison of means amongst groups with unequal sample sizes; Cabral 2008) or a student's t-test. The student's t-test was used for comparing the means of model results where sex was the only significant effect, as this effect has two groups with unequal sample sizes (Mishra et al 2019) in comparison to the multiple groups with unequal sample sizes seen with the year and colony effects.

## Chapter 4: Results

### *4.1 First arrival to burrow*

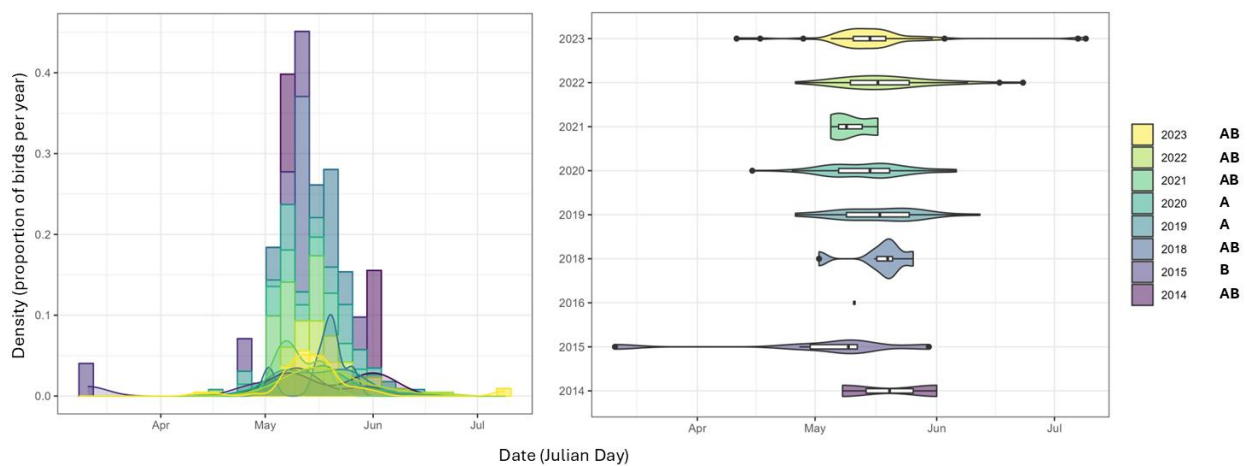
For first detected arrival to the burrow, I found that colony and year had a significant effect ( $\chi^2_{\text{colony}} < 0.0001$ ;  $\chi^2_{\text{year}} = 0.0071$ ; Figs. 2-5). In terms of colony, Storm Petrels from Kent and Bon Portage islands had the earliest first burrow visitations, with mean first day in-burrow being May 6<sup>th</sup>  $\pm$  3.11 days for Kent and May 9<sup>th</sup>  $\pm$  2.81 days for Bon Portage (Figs. 2 and 3). By contrast, Middle Lawn had the latest first day of detection with mean date of May 23  $\pm$  3.23 days (Figs. 2 and 3). Birds from Baccalieu, Gull, and Country were similar in first date of burrow usage: Baccalieu birds mean first date of burrow usage was May 19  $\pm$  2.6 days; Gull was May 15  $\pm$  2.83 days; and Country was May 12  $\pm$  2.97 days (Figs. 2 and 3). According to my post-hoc test, Kent and Bon Portage significantly differed from Gull and Middle Lawn but all other colony-comparisons were not significantly different (Figs. 2 and 3).



Figures 2 and 3: Stacked bar chart, density curves, and violin plots for date of first detected burrow visit (in Julian Day) of 202 Leach's Storm-Petrels, ordered most northern to southern, from Baccalieu, Gull, Middle Lawn, Bon Portage, Country, and Kent colonies throughout 2014-2023. Significance between colonies demonstrated by compact letter display, where shared letters indicate non-significant differences between colonies.

In terms of year, I found considerably fewer differences than with the effect of colony ( $\chi^2_{\text{year}} = 0.0071$ , Figs. 4 and 5). Birds from 2015 entered their burrow earliest at mean date

of April 30  $\pm$  4.56 days (Figs. 4 and 5). The remainder of the years were fairly similar in their first burrow arrival date ranged, and, as follows, are ranked from earliest to latest for first burrow entry: May 5  $\pm$  8.18 days in 2021, May 10  $\pm$  1.92 days in 2023, May 15  $\pm$  1.87 days in 2022, May 15  $\pm$  5.69 days in 2018, May 17  $\pm$  1.59 days in 2020, May 17  $\pm$  2.38 days in 2019, and June 3  $\pm$  12.76 days in 2014 (Figs. 4 and 5). The post-hoc test showed that all years were relatively statistically similar; however, 2015, 2019, and 2020 were the most different as they are the only years with single letter compact displays (Figs. 4 and 5).



Figures 4 and 5: Stacked bar chart, density curves, and violin plots for date of first detected burrow visit (in Julian Day) of 202 Leach’s Storm-Petrels throughout 2014-2023, ordered most northern to southern, from Baccalieu, Gull, Middle Lawn, Bon Portage, Country, and Kent colonies. Significance between years demonstrated by compact letter display, where shared letters indicate non-significant differences between years.

#### 4.2 Pre-laying activity: Burrow visits, time spent in burrow, and exodus

The analysis on the three pre-laying activities revealed that sex was the only model parameter to have a significant effect; specifically, the number of burrow visits prior to incubation was significantly higher in males than females ( $p = 0.0001$ , Fig. 6). Males visited the burrow an average of 0.87 more time than females, averaging  $4.21 \pm 0.35$  visits in total versus  $3.34 \pm 0.35$  visits (Fig. 6). Males had several outliers that visited the burrow nine to thirteen times, resulting in a long tail on their distribution (Fig. 6).

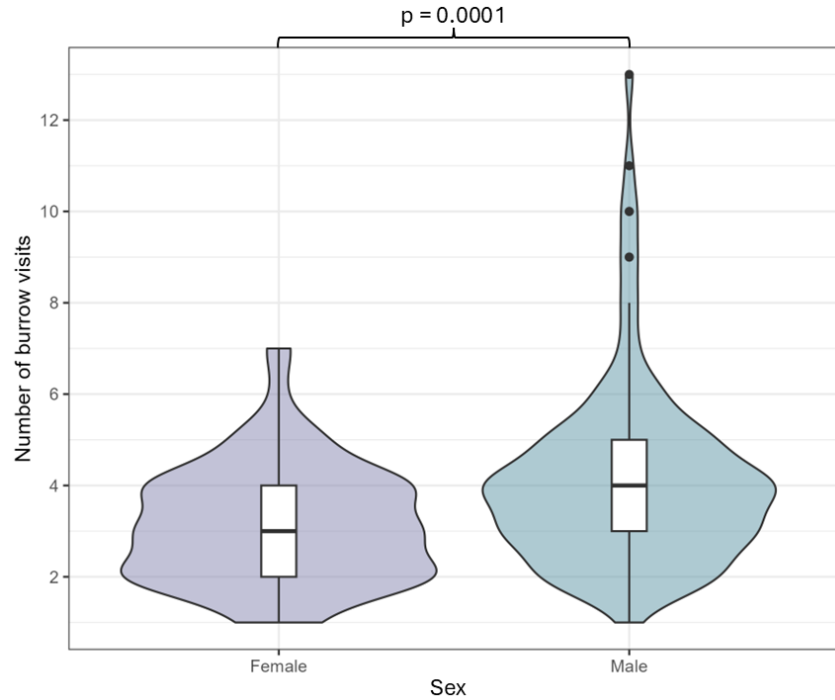


Figure 6: Violin plot of number of burrow visits for 79 female and 123 male Leach’s Storm-Petrels from, ordered most northern to southern, from Baccalieu, Gull, Middle Lawn, Bon Portage, Country, and Kent colonies from 2014-2023.

As with number of burrow visits, males also spent 25.44 more hours in the burrow than females ( $p = 0.0007$ , Fig. 7). Males spent a mean of 139.52 hours, or 5.81 days, in the burrow over multiple visits prior to start of incubation (Fig. 7). By contrast, females spent a mean of 114.08 hours, or 4.75 days, within the burrow prior to laying (Fig. 7).

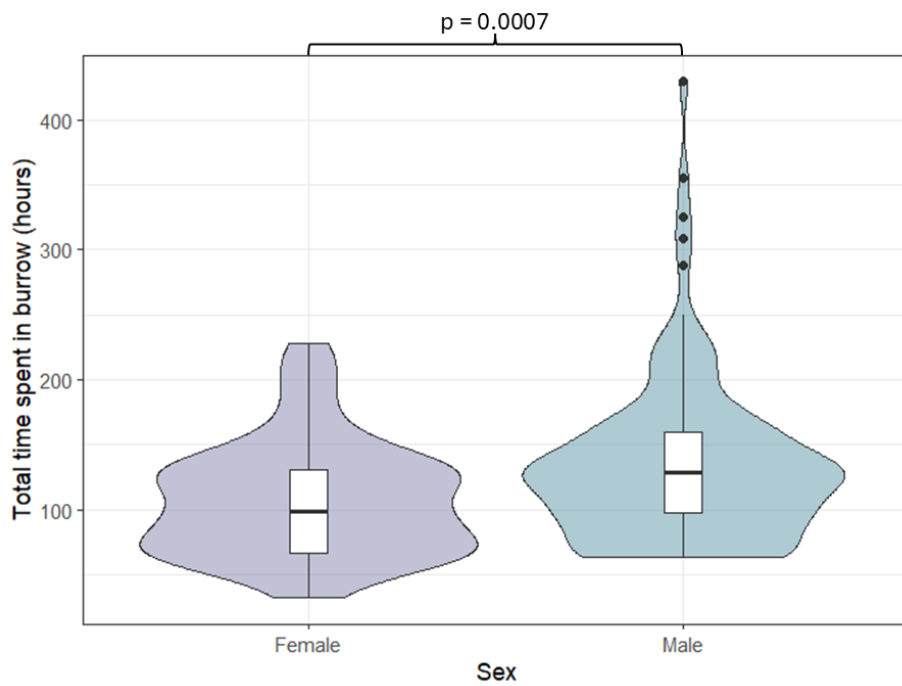


Figure 7: Violin plot of total time spent in the burrow prior to start of incubation for 79 female and 123 male Leach's Storm-Petrels from, ordered most northern to southern, from Baccalieu, Gull, Middle Lawn, Bon Portage, Country, and Kent colonies from 2014-2023.

Finally, females had a longer period without any daytime burrow use between the last pre-lay visit and lay date compared to males ( $p < 0.0001$ ; Fig. 8). On average, females were gone from the burrow for  $15.05 \pm 1.07$  days, whilst males were gone for an average of  $10.66 \pm 1.06$  days (Fig. 8).

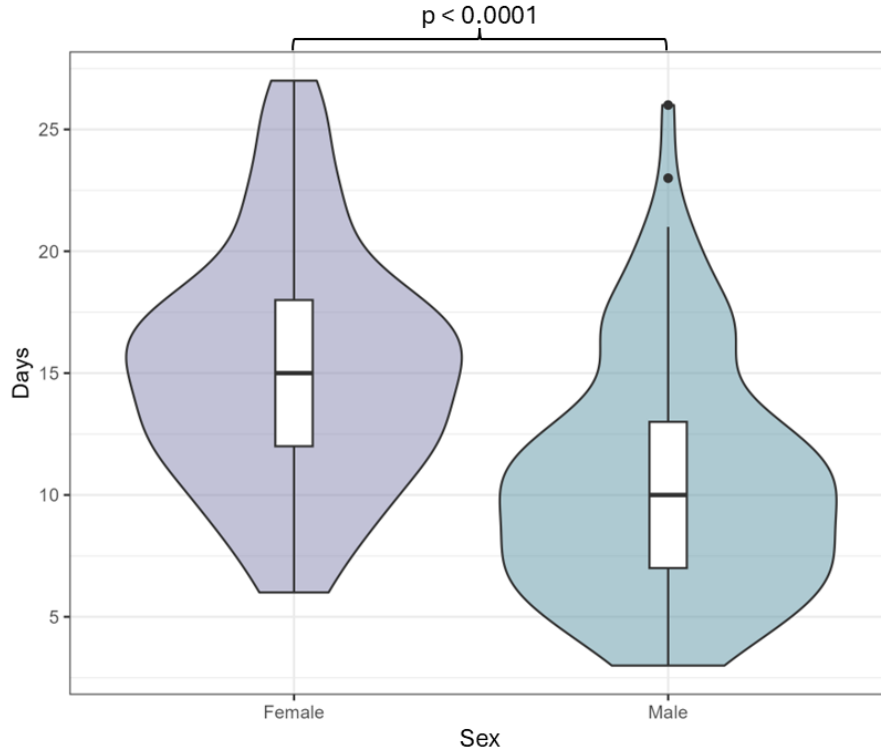
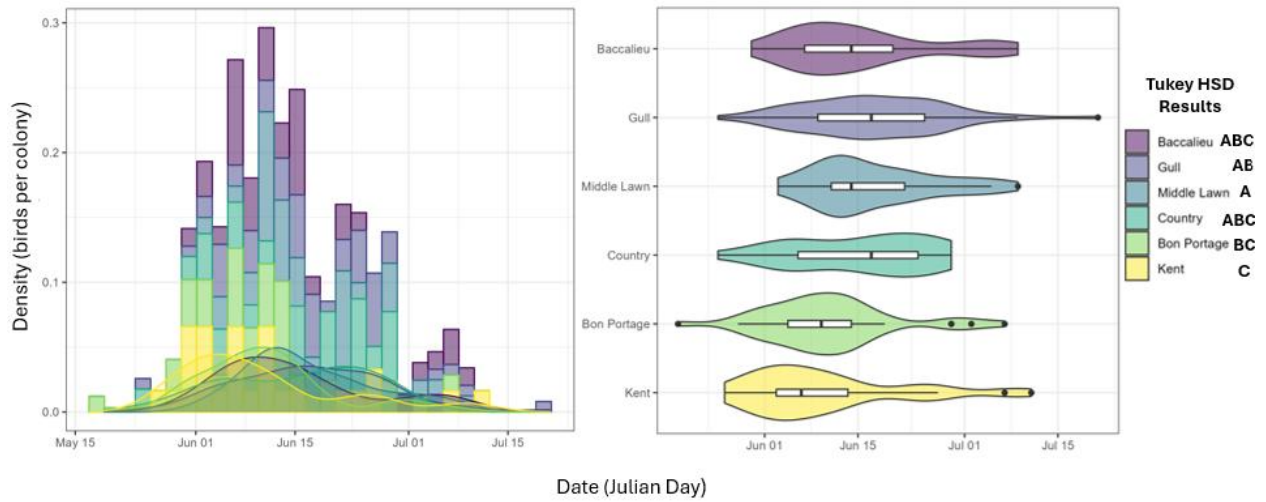


Figure 8: Violin plot of length of exodus (in days) prior to start of incubation for 79 female and 123 male Leach's Storm-Petrels from, ordered most northern to southern, from Baccalieu, Gull, Middle Lawn, Bon Portage, Country, and Kent colonies from 2014-2023.

### 4.3 Lay date/start of incubation

Finally, for the ultimate question regarding the timing of lay-date and onset of incubation behaviour, I found that the only significant effect was colony ( $\chi^2 = 0.0014$ ; Figs. 9 and 10). Kent island birds had the earliest mean lay date/start of incubation of June 7  $\pm$  4.21 days; whilst Middle Lawn birds had the latest mean date of June 22  $\pm$  4.20 days (Figs. 9 and 10). All remaining colonies did not differ significantly from one another in mean lay date/start of incubation: Bon Portage had a mean date of June 11  $\pm$  3.81 days, Country a mean date of June 14  $\pm$  4.00 days, Baccalieu a mean date of June 19  $\pm$  3.88 days, and Gull a similar mean date of June 19  $\pm$  3.64 days (Figs. 9 and 10). My post-hoc analysis suggested that Middle Lawn and Kent were the most significantly different colonies (Figs. 9 and 10).



Figures 9 and 10: Stacked bar chart, density curves, and violin plots for lay date or start of incubation (in Julian Day) of 202 Leach’s Storm-Petrels from, ordered most northern to southern, from Baccalieu, Gull, Middle Lawn, Bon Portage, Country, and Kent colonies from 2013-2024. Significance between colonies demonstrated by compact letter display, where shared letters indicate non-significant differences between colonies.

## **Chapter 5: Discussion**

This study used geolocation sensors to derive precise estimates of phenology and pre-breeding behaviour in Leach's storm-petrels. The return from overwinter migrations at sea, or 'arrival timing', was estimated from burrow re-occupancy. Via the analysis of burrow entry and departures, I also estimated pre-laying behaviour, as well as and lay date, which is synonymous with the start of incubation behaviour. My aim was to determine if six longitudinally different colonies possessed differences in early breeding phenology and if breeding phenology varied by sex. Colony of origin and year were found to be significant factors affecting first date of burrow re-occupancy (Figs. 2-5); this may indicate that, regardless of overlapping overwintering foraging locations (Bicknell 2011, Pollet et al 2014a, 2021, Potvin et al pers comm), individuals may be able to recognize environmental cues that indicate when it is most optimal to return to their respective breeding colonies. Differences in years may indicate that annual climatic factors can lead to some variation in return timing (Figs. 4 and 5). I also found evidence for sex differences in pre-breeding behaviours; males spent significantly more time at the burrow and visited it more frequently, potentially indicating sex-biased roles in burrow preparation (Figs. 6 and 7). There was also evidence that this species likely undergoes a pre-laying exodus, and that this may be pertinent to the female's ability to accrue energy reserves needed for egg formation considering she was gone from the colony an average of five more days than her male counterparts (Fig. 8). Finally, I found that colony also significantly affected lay-date and start of incubation, with differences between colonies following a similar trend to that of first burrow re-occupancy (Figs. 9 and 10). These findings indicate that Leach's Storm Petrels are variable in migratory behaviours for timing their return to the breeding colony. Whether this variation is advantageous is subject for further research. I also demonstrated that local conditions at the colony should be further explored in future work as they potentially correlate and drive returning timing and subsequent breeding phenology.

### *5.1 Patterns in first arrival to burrow*

Colony of origin and year had a significant effect on first burrow re-occupancy, but not sex. Patterns of first burrow re-occupancy roughly matched the latitudinal and longitudinal gradients at which the colonies are located and forage; with the most

southwestern colonies Kent and Bon Portage having the earliest burrow re-occupancy dates and other colonies, besides Middle Lawn, not differing substantially among this gradient (Figs. 2 and 3). Middle Lawn had the latest first arrival to burrow despite not being the most extreme colony in terms of latitude and longitude. Surprisingly, our northernmost colony, Baccalieu, was most alike to all other colonies located along the latitude-longitude gradient. These findings suggest that birds may possess some internal mechanisms for detecting when is optimal for timing arrival back to the colony, as they share common feeding grounds across the Atlantic Ocean during the winter (Bicknell 2011, Pollet et al 2014a, 2021, Potvin et al per comm). Year influencing burrow re-occupancy dates was also expected as this factor captured potential annual climatic differences that Storm Petrels experienced at-sea, and has been previously found to have a significant impact on defining the colony arrival within regions roughly 86 km apart in other seabird species (Wanless et al 2009). Considering the study colonies are separated by greater distances and have distinct foraging areas that range in 500 km radiuses, it fits these findings that there would be yearly differences in arrival date. Sex defied our expectations, as we expected evidence of protandry but found none.

Looking deeper into the differences between colonies, Kent Island likely had the earliest mean burrow re-occupancy date as it is the only colony that feeds over the shallow neritic waters of the Gulf of Maine during the breeding season (Hedd et al 2018). Considering that the Gulf of Maine is located at the mouth of the Bay of Fundy, it experiences lower temperatures than other Atlantic Leach's Storm Petrel centralized feeding areas (Hedd et al 2018) and has a highly productive ecosystem so may have greater early foraging opportunities (Archambault et al 2010). The shallowest feeding habitat having the earliest burrow re-occupancy also agrees with the findings of Ronconi et al (2022), who found that bathymetry was the greatest predictor of differences in Leach's Storm-Petrel foraging areas. Bon Portage, as the southernmost colony and feeding over George's Bank, farther off the Gulf of Maine, that is considerably deeper than the foraging area of Kent Island (Hedd et al 2018), also agrees with these findings by having the second earliest burrow re-occupancy date (Figs. 2 and 3).

That Middle Lawn had the latest burrow re-occupancy date did not meet our predictions (Figs. 2 and 3), as it is not the colony with the most northern latitude. Furthermore, Middle Lawn was dissimilar in burrow re-occupancy date to Gull Island, despite having similar latitudes of 46.87 ° versus 47.26 °, respectively. This finding may reflect microclimatic differences where Middle Lawn is more affected by freshwater discharge from the St. Lawrence River system due to being located closer to the Laurentien current than the other Newfoundland colonies (Gaston et al 2009). Previous studies found that Leach's Storm-Petrels from a colony neighbouring Middle Lawn, called Green Island, fed primarily on Horned Lantern Fish (*Centrophryne spinulosala*), other mesopelagic lanternfish (Myctophidae), and crustaceans from the Laurentian Channel approximately 125 km from the colony; whilst birds from Gull and Baccalieu fed primarily on Arctic Telescope (*Protomyctophum arcticum*) found directly offshore (Hedd et al 2009). A decline in crustacean species from the Laurentian Channel in the early 2000s may have contributed to birds readjusting the timing of breeding to better suit prey availability (Gaston et al 2009). Hedd et al (2018) found that Middle Lawn shares little foraging area overlap with Gull and none whatsoever with Baccalieu, which further suggests that the timing of this colony's first burrow re-occupancy may be different from other Newfoundland colonies because of its reliance on differing foraging conditions.

It is also possible that on-land characteristics of the colonies could influence differences between first burrow re-occupancy date. For example, predation risks or habitat conditions could limit when would be ideal for a Storm Petrel to return to its burrow. It is possible that birds from Middle Lawn do not face the same level of predation or inter-species competition as birds from Gull and Baccalieu. The gull colonies that prey on Middle Lawn birds have increased in number considerably in recent decades (Gaston et al 2009), and there is also suspicion that these birds may suffer from predation by American mink (*Mustela vison*; Fraser et al 2013); hence, birds may be able to re-occupy their burrows later to avoid predation risks. Further investigation is needed into how gull predation impacts Leach's Storm Petrel breeding phenology, as this has also been identified as an issue on Gull Island (Bond et al 2023).

Middle Lawn also lacks substantial forested habitat and has the most prolonged history of grazing compared to the other Newfoundland colonies (Fraser et al 2013, Government of Newfoundland 2015). This lack of forested areas may influence the breeding success of Leach's Storm Petrels, as Stenhouse and Montevecchi (2000) found that Leach's Storm Petrels demonstrated a preference for looser, deeper peat soil types found in the forested regions of Great Island, a seabird colony in the same ecological reserve as Gull Island. This is further supported by Duda et al (2020), who found that the growth of a Leach's Storm Petrel colony can eventually alter an island's vegetation community to favour preferred burrowing vegetation types via fertilization from bird droppings. As Gull Island's Storm Petrel population has increased only briefly in recent decades (Gaston et al 2009), it is possible that vegetation alterations that promote ideal burrowing conditions are not fully developed yet.

It is also possible that soil moisture conditions on Middle Lawn are not ideal for nesting until later in the season, as this was found to be a significant factor in deciding burrow choice by Storm Petrels from Kent Island (Fricke et al 2015). It is uncertain how Middle Lawn may be different in these conditions from Gull and Baccalieu, as they share the same ecoregion so could be expected to have similar weather exposure patterns (Government of Newfoundland 2015). I suggest that future research should further investigate the importance of long-term trends in habitat characteristics, predation rates, and prey availability on early breeding phenology to further determine why this difference between Middle Lawn and the other higher latitudinal-longitudinal colonies exist, as issues with habitat shifts from forested to open and Storm Petrel breeding success have also been identified at Kent Island (d'Entremont et al 2020).

In terms of year's impact on first burrow re-occupancy, the findings of this study finding agree with Merkel et al (2019), who found that guillemots' (*Uria spp.*) arrival to colony, but no other aspect of breeding, shifted with warming ocean temperatures. Indeed, in 2015, which was the earliest for burrow re-occupancy (Figs. 4 and 5), there were abnormally warmer sea surface temperatures because this was an unusually high positive North Atlantic Oscillation Index (NOAI; NOAA 2025). The NOAI was also unusually high positive in 2020; however, this year experienced the third latest mean arrival date of May

17 ± 1.59 days, so the NOAI does not seem to be the only explanation for annual climatic factors altering burrow re-occupancy date. Further research is needed to determine potential impacts of other broad-scale Atlantic Ocean climate factors that may influence this phenology in Leach's Storm Petrel.

## *5.2 Protandry*

There was no significant difference between sexes for first burrow usage, which is counter to prediction and what we know generally about Procellariiform seabirds (Newton 2012). This may indicate that first burrow usage was not an effective metric for detecting protandry in Leach's Storm Petrels, and so it is possible that protandry exists in this species, but that some other measure is needed to detect it. It is possible that males could be arriving at offshore foraging areas near the colony prior to females, but delaying burrow re-occupancy until the female's arrival. I am hesitant to dismiss protandry as it is a common phenology for many other colonial seabird species (Desprez et al 2018, Ismar-Rebitz et al 2020, Snell et al 2021); however, there is little confirmation of protandry in Leach's Storm Petrels (Mauck et al 2011, Bond and Hammond 2015, Pollet et al 2021).

Pavesky (2021) argues that protandry is mainly for competitive reasons between males, allowing earlier arriving males to have the best access to resources to attract mates. For a long-lived monogamous seabird like Leach's Storm Petrels, such competition may be unnecessary for returning breeders such as the ones used in this study, which could explain why it was not detected. I suggest that protandry may be a behaviour detectable in prospecting male Leach's Storm Petrels who do not yet have a burrow or mate. As these males are in competition to establish their reproductive success, they may demonstrate protandry compared to first breeding females. This has been found for similar species such as the European Storm Petrel, where prospecting males arrived earlier than females to establish themselves before potential breeding competition and successfully find a mate (Medeiros et al 2012). Furthermore, both sexes re-occupying the burrow site at similar times may reflect that burrow philopatry plays a more important role in first reuniting the couple than it does for reinforcing pair bonds (Bried et al 2003), as this would explain why both sexes arrive in the same period. I suggest that future work should expand on the differences in established and prospecting breeders for Leach's Storm Petrels.

### 5.3 Patterns in pre-laying burrow preparation

Our findings support that burrow preparation may be undertaken after mate pairs are reunited through first burrow re-occupancy. I found that males take on the brunt of burrow preparatory duties (Figs. 6 and 7), which agrees with Tyson et al (2022) and Zangmeister et al (2009), who found that males exhibit greater levels of burrow attendance and take longer to abandon burrows if they fail to breed. Quillfeldt et al (2014) found similar phenological patterns for Thin-billed Prions (*P. belcheri*), where males spent longer on land to defend their burrows. My findings suggest that male-biased parental care is sustained throughout the entire breeding period (Mauck et al 2011). This agrees with my predictions that the female has less of a role in burrow and nest preparations because of the energetic demands of yolk deposition and egg creation.

### 5.4 Pre-laying exodus

I also found that the sexes differed with time spent away from the burrow prior to lay date and start of incubation, with females being away longer than males (Fig. 7). This would agree with the definition of a pre-lay exodus, that being an “[extended] leave [of their] breeding areas for periods of days or weeks” after the return to the colony, re-occupation of the nest site, and re-establishment of pair bonds (Newton 2011); thus, disagreeing with Bond and Hobson (2015) that a pre-laying exodus is generally not present in this species. Our findings do agree with Bond and Hobson’s (2015) assumptions (as derived from Astheimer and Grau’s 1990 model for Procellariiformes) that it takes 15-16 days for the female to form an egg, as we observed the mean exodus length time in females to be  $15.05 \pm 1.07$  days (Fig. 8). This would follow the definition of an exodus as supported by Newton’s (2011) review, where exoduses were found to vary in length of 14 to 22 days dependent on species. In his review, Newton (2011) noted an exodus of a similar length to that of our studies Leach’s Storm Petrels was present in a similar far-ranging pelagic petrel species, the White-chinned Petrel (*Procellaria aequinoctialis*).

Furthermore, evidence suggesting that female Leach’s Storm Petrels can store sperm and control when their egg is fertilized further support our estimates for exodus length, as this would explain why females can depart for longer than it takes for a fertilized egg to form after copulation in the burrow (Hatch 1983). This may also facilitate their longer

foraging ranges near the colony, as Mauck et al (2022) noted females' range on average 160 km farther than males during the incubation stage of breeding. Males having a shorter exodus also fits with evidence that males play a greater role in burrow and nest maintenance (Mauck 2011, Pollet et al 2021), as they may be cutting their exodus short to ensure the nest is ready for their mates. The idea that males cut their exodus shorter for increased burrow attendance is also supported by our findings for increase male burrow visits and longer visits prior to laying, and further supported by Quillfeldt et al (2017) with Thin-billed Prions.

### *5.5 Lay date and start of incubation*

For the ultimate question on the timing of lay date and start of incubation, I found that the only significant impact was from colony (Figs. 9 and 10). The pattern of lay date and start of incubation between the colonies roughly followed the same pattern as first burrow re-occupancy (Figs. 9 and 10), which may further support that the mechanism for deciding when to lay/start incubation across populations is well-conserved. That I detected no differences between sexes suggest our assumption that males take the first incubation shift, as is common in other seabird species (Cross et al 2024), is likely correct. I expected some noticeable difference between the sexes if females were more likely to take the first incubation shift, but my results suggest she leaves shortly after laying. Year having no significant effect also agrees with previous studies that first date on nesting grounds is altered by climatic factors, but does not affect subsequent breeding phenology (Merkel et al 2019). This may suggest that the environmental cues that Leach's Storm Petrels utilize to time laying may be more relaxed than cues that influence return to the colony.

Lay-date occurred over a much shorter time range than first burrow re-occupancy (Figs. 8 and 9). My estimates of lay date and start of incubation closely matched previous estimates for Bon Portage at June 10-20 between 2011-2015, with the overall mean being June  $15 \pm 5$  days (Pollet et al 2017), as my estimate was June  $11 \pm 3.81$  days from 2014 to 2023. However, my estimate of June  $7 \pm 4.21$  days was considerably earlier than previous lay-date predictions for Kent Island, where mean lay date was previously found to be June  $19 \pm 13$  days (Pollet et al 2021). As the earliest arriving birds, Kent Island was also the earliest to lay and start incubation and, similarly, Middle Lawn birds were the latest to

arrive and latest lay and start incubation (Figs. 9 and 10). This further reflects Merkel et al's (2019) findings that breeding phenology following arrival to the nesting colony is not impacted by climatic conditions, but disagrees with Pollet et al (2017) who found that year played a significant role in determining lay date for birds of Bon Portage. However, my results are supported by other seabird studies on regional variations on start of incubation. For example, Ancient Murrelets in the Pacific were found to vary in lay date following an east to west gradient (Gaston et al 2017), which was also found in this study with Leach's Storm Petrels.

Ultimately, these findings suggest that lay date is variable amongst the colonies but does not vary yearly. I suggest that future research focus on better understanding what colony-specific factors influence lay date and breeding success. It may also be valuable to investigate potential carry-over effects on females for determining annual breeding success, as my study did not examine any individuals between years.

### *5.6 Potential limitations and sources of errors*

The main limitation of this study was a lack of alternate metrics to corroborate GLS estimates of breeding events. Most GLS studies to-date recommend a secondary variable to assist with confirming inferred behaviours (Perez et al 2014, Gowe 2015, Gowe et al 2016, Anders et al 2017). This can also be valuable for eliminating the uncertainty of brief, nighttime visits to the burrow, which are undetectable with the methodology used in this study. With seabirds, saltwater immersion data is a common secondary variable; however, this was not included in this study as there are limited published works utilizing salt-water immersion data with Leach's Storm-Petrels (Mauck et al 2022). Hence, there are few sources for aiding with recognizing patterns of saltwater immersion in this species and correlating this with burrow usage. Furthermore, Leach's Storm-Petrels do not consistently feed via fully emerging their legs in the water, instead often skimming or plucking their prey from the ocean's surface (Pollet et al 2021). This would make saltwater immersion unreliable for inferring activity as the level of immersion detection would not necessarily correlate with foraging intensity or length, unlike with Rhinoceros Auklets in Cross et al (2024). Finally, light form data has been reliably used in several studies to determine early breeding phenology in other bird species (Rayner et al 2012, Guilford et al 2012, Perez et al

2014, Quillfeldt et al 2014, Gaston et al 2017, Merkel et al 2022, Cross et al 2024), so overall is a reliable and well-used method for determining these behaviours in burrow-nesting birds.

There is the potential source of error with noise in waveform data; however, most of this was eliminated during the early processing stages. The reliability of our assumptions for eliminating noisy and unclear data was reliable, as the final cleaned dataset was 202 birds, a reduction of 90 birds from the initial historical GLS tagging dataset. Considering that most colonies are not near significant sources of light pollution (Gjerdrum et al 2021), we were correct in assuming that this source of error will have minimal impact on the final sample size of 202 birds utilized in our models.

## **Chapter 6: Conclusion**

This study aimed to define the timing of the following early breeding phenology in six longitudinally different Atlantic Leach's Storm Petrels colonies: first instance of burrow re-occupancy, pre-laying visits to burrow, pre-laying exodus, and lay date or start of incubation. The study demonstrated that first burrow re-occupancy differs between colonies and year, suggesting that localized and pelagic ocean conditions determine when birds migrate back for the breeding season. In terms of pre-laying activity, the study found that the sexes differed in the amount of time spent visiting the burrow and away for the pre-lay exodus. Males visited and spent longer at the burrow than females, whilst females had a longer pre-laying exodus. These differences between the sexes for pre-laying activities further confirms that this species has sex-biased parental care systems. Finally, I found that lay-date or start of incubation differed between the colonies, indicating that localized conditions may be more important for defining lay-date than the at-sea conditions experienced during the winter migratory months.

I suggest that future research focus on quantifying what specific conditions at each colony influence lay-date, as the high variability between colonies makes it difficult to determine what specific conditions influence breeding phenology. The findings of this study may also aid in future research on Leach's Storm Petrel breeding success by establishing a baseline timing for the earliest sequences of breeding phenology, as this study utilized nearly a decade's worth of data. This study has also demonstrated the value of long-term GLS records, as we were able to answer multiple questions regarding breeding phenology from a single historical dataset.

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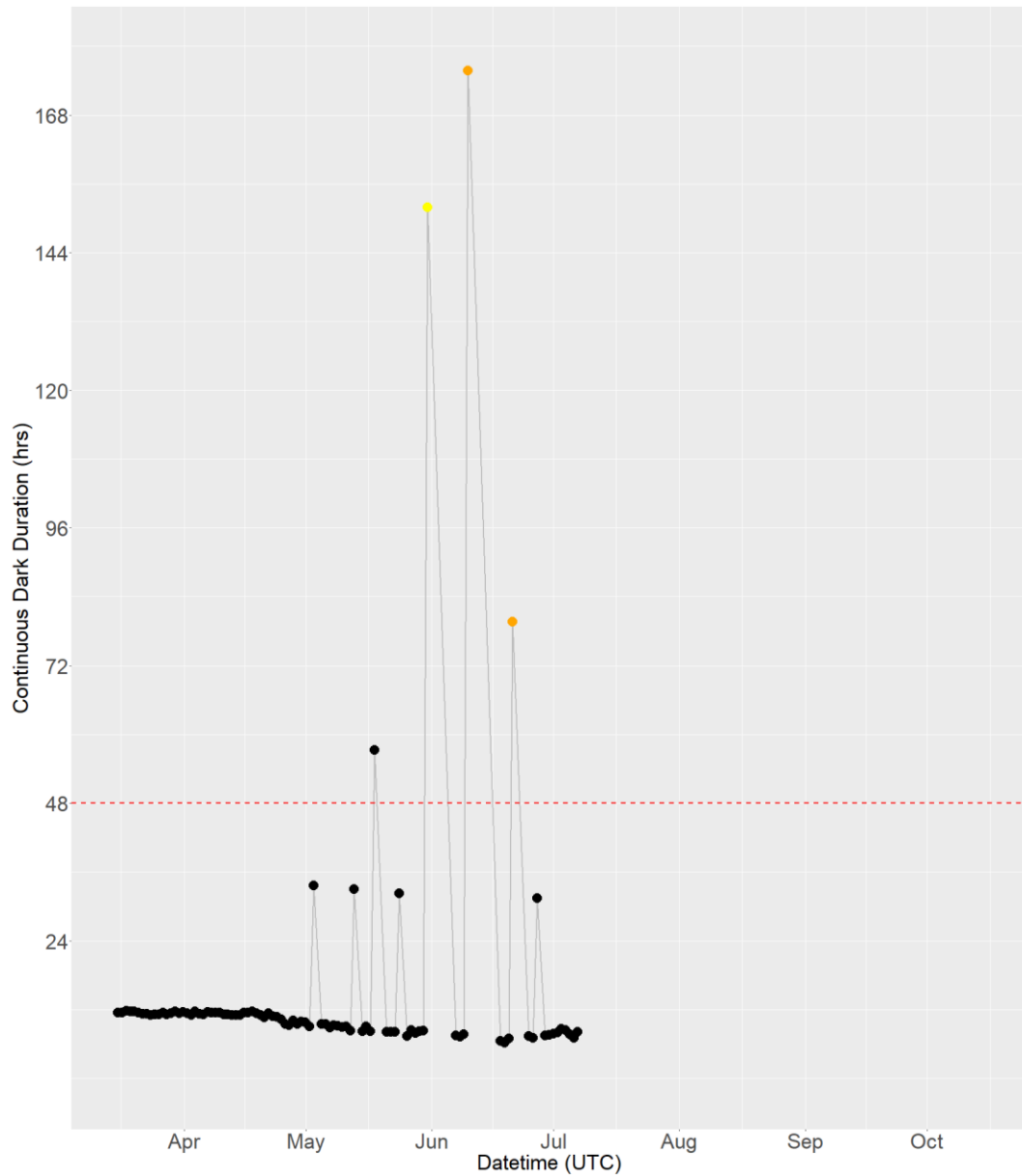
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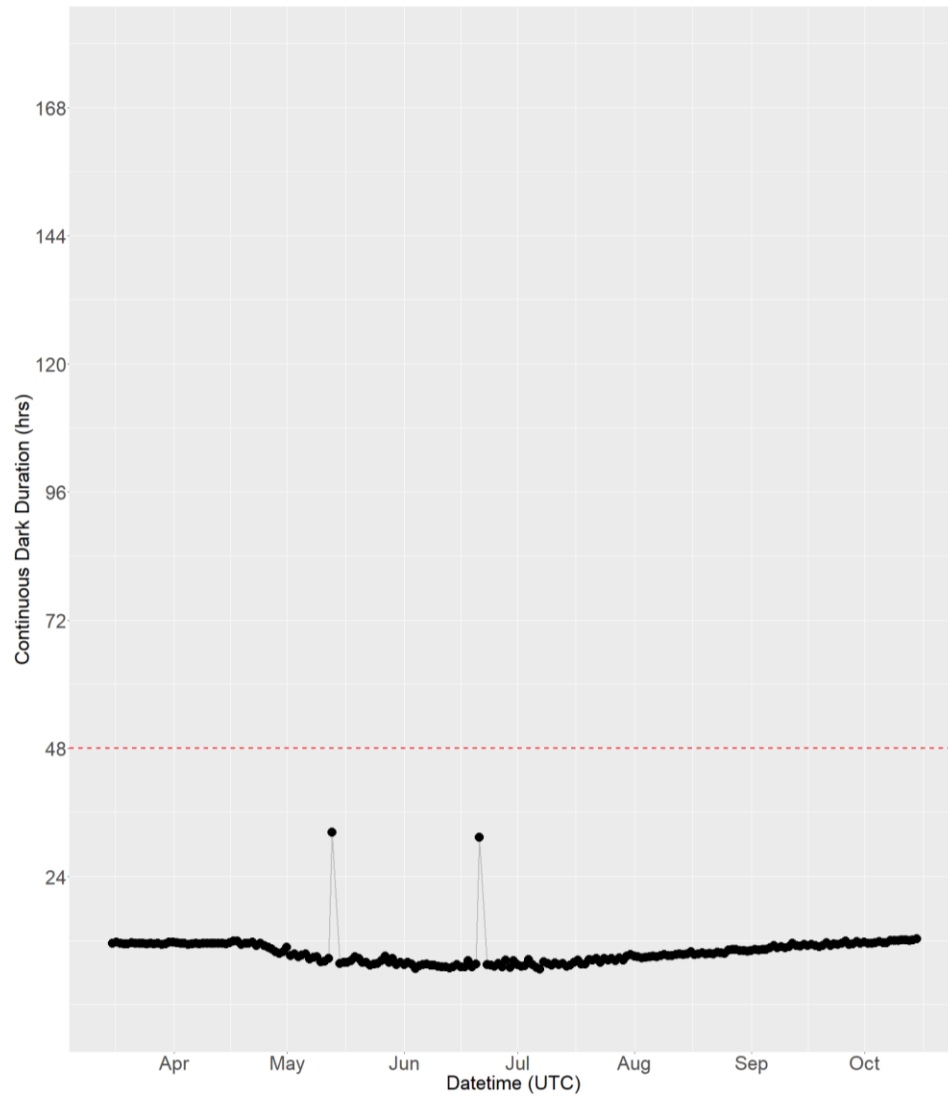
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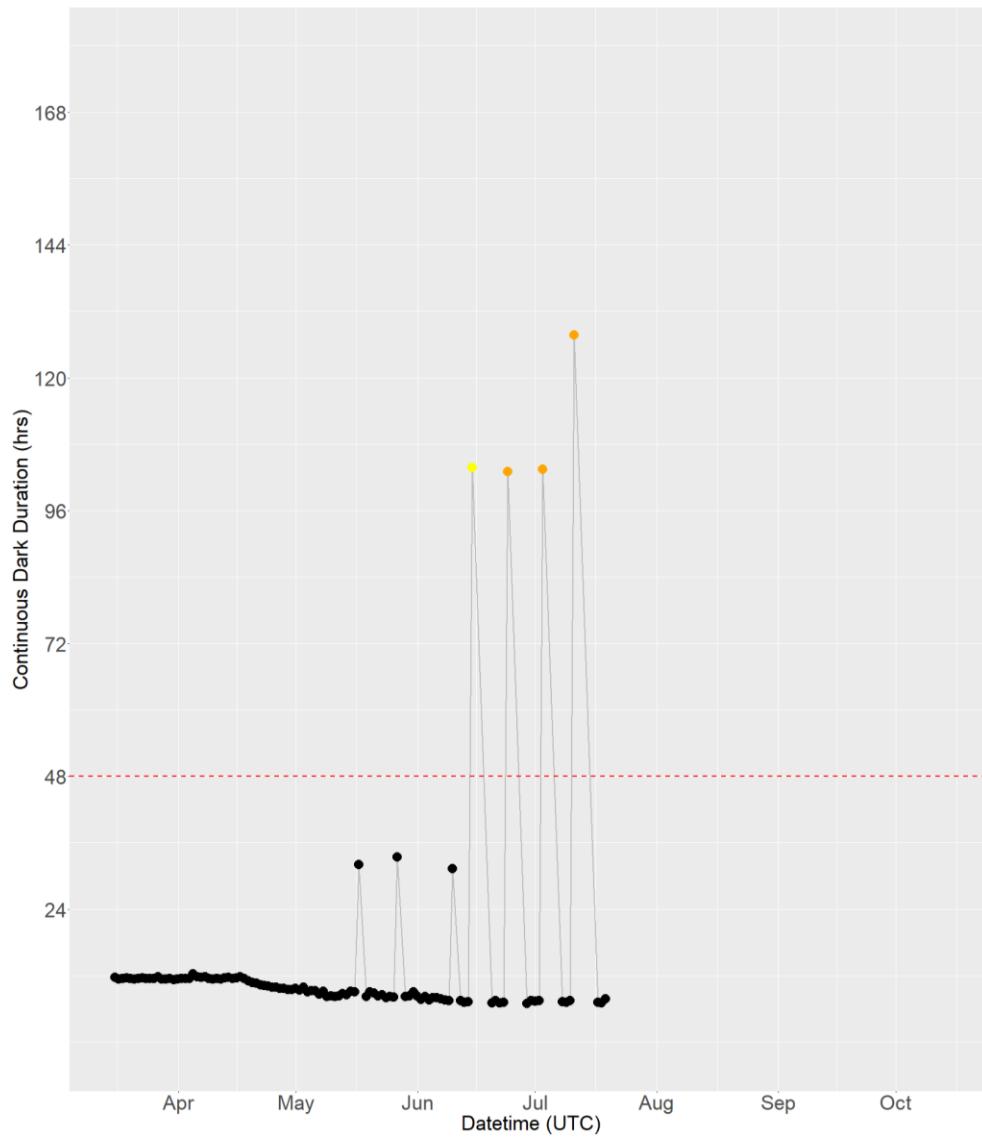
## **APPENDIX**



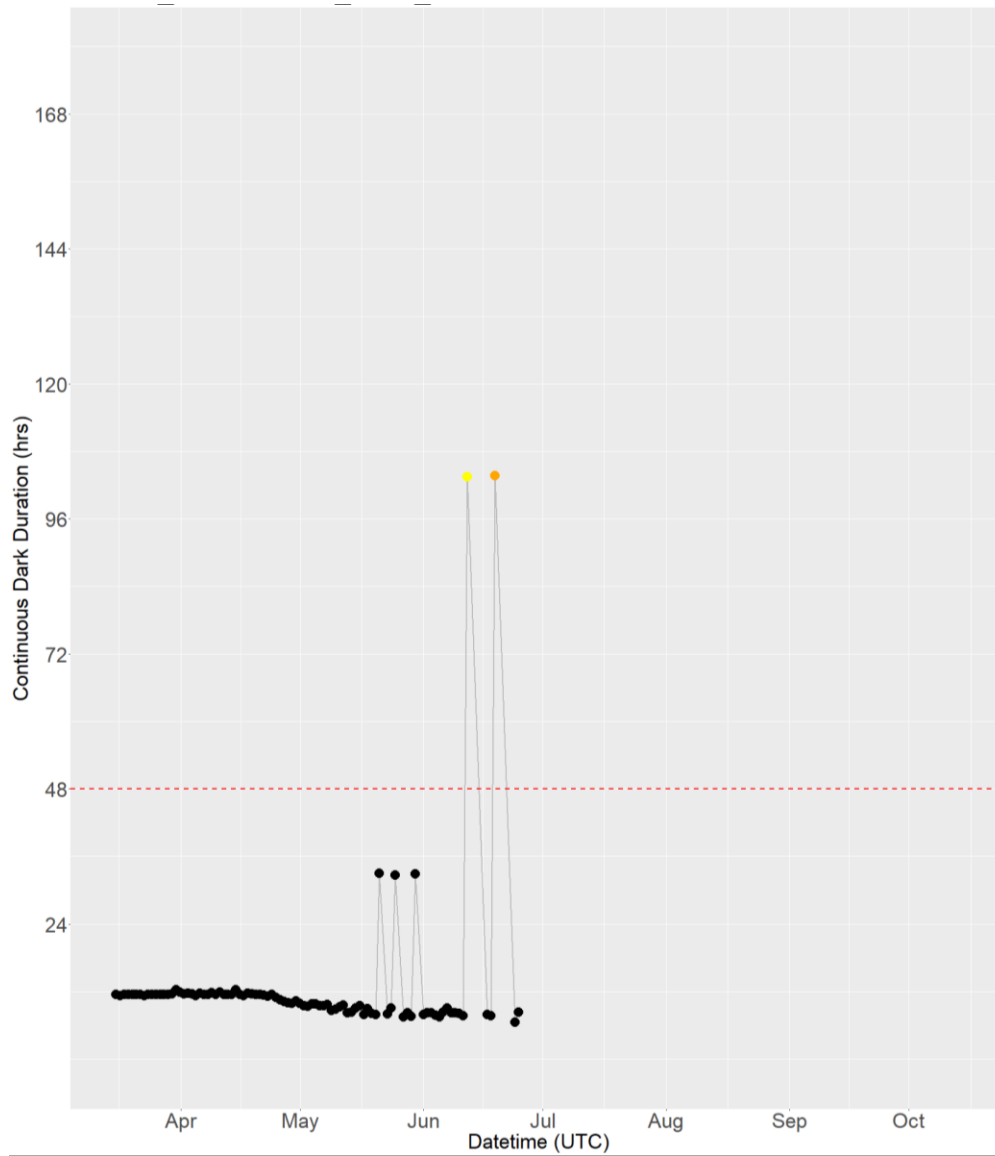
Appendix A.1: Example of charted burrow usage for a failed male breeder with no clear patterns in burrow usage. Dashed red line indicating 48 hours of dark period. Black markers indicate potential pre-laying activity, yellow potential start of incubation, and orange potential incubation stints.



Appendix A.2: Example of charted burrow usage for a failed male breeder with few patterns in burrow usage. Dashed red line indicating 48 hours of dark period. Black markers indicate potential pre-laying activity.



Appendix A.3: Example of charted burrow usage for a successful male breeder with three pre-lay visits and four incubation visits. Dashed red line indicating 48 hours of dark period. Black markers indicate potential pre-laying activity, yellow potential start of incubation, and orange potential incubation stints. Note large gap between last two pre-lay visits that was assumed to be potential pre-lay exodus.



Appendix A.4: Example of charted burrow usage for a successful unknown sex breeder with three pre-lay visits and two incubation visits. Dashed red line indicating 48 hours of dark period. Black markers indicate potential pre-laying activity, yellow potential start of incubation, and orange potential incubation stints. Note large gap between last pre-lay visit and start of incubation that was assumed to be potential pre-lay exodus.