# INFLUENCES OF LARUS GULLS AND NOCTURNAL ENVIRONMENTAL CONDITION OF LEACH'S STORM-PETREL ACTIVITY PATTERNS AT THE BREEDING COLONY



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# Influences of *Larus* Gulls and Nocturnal Environmental Condition on Leach's Storm-Petrel Activity Patterns at the Breeding Colony

By

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## Abstract

The risk of predation is perhaps the most serious pressure an animal must contend with during its lifetime. Predation risk has played a strong selective force in many aspects of life history, including the activity patterns of prey species. Leach's Storm-Petrels *(Oceanodroma leucorhoa)* arrive and depart from breeding colonies only at night. Anecdotal reports suggest that storm-petrels return to the colony later on bright nights than on overcast or foggy ones, and that fewer birds are seen at the colony on bright nights. These are considered predator avoidance behaviours as diurnal gulls prey on storm-petrels, especially on bright moonlit nights.

This study examined the effects of the presence of predators on the activity and parental care patterns at two Leach's Storm-Petrel colonies - one with gulls (Gull Island) and one without (Green Island). Data were collected on storm-petrel flight and vocalization activity, reproductive chronology, chick interfeed interval, and gull activity and predation on Leach's Storm-Petrels. A model gull experiment was conducted on Green Island to determine storm-petrel responsiveness to gulls at this colony. In addition, fledging mass and winglength measurements were collected from five colonies; four in Newfoundland and one in Maine.

Differences were found in storm-petrel responses to nocturnal environmental condition both between the colonies and between the reproductive phases of incubation and chick rearing. At both colonies, and over the entire reproductive season, storm-petrels arrived and began to vocalize later on bright evenings than on intermediate or dark ones, and under clear versus cloudy or foggy skies. Leach's Storm-Petrels on Gull Island were also quiet on arrival for a longer period than those on Green Island. Once at the colony, the behaviour of the storm-petrels was similar under a variety of nocturnal environmental conditions at Gull and Green Islands, although the storm-petrels at Green Island were apparently less affected by nocturnal environmental condition. Storm-petrels tended to be most affected by nocturnal environmental condition during incubation on Gull Island and during chick rearing on Green Island. The activity of Leach's Storm-Petrels at both colonies was affected by the presence of gulls (model gulls on Green Island). Gulls had a higher level of activity under those conditions that were more conducive to nocturnal hunting (i.e. brighter nights), and more storm-petrel remains were found after bright or moonlit nights. The reproductive season was somewhat attenuated at Gull Island compared to Green Island, and fledging mass and winglength tended to be lower at colonies with gulls, and at larger colonies compared to smaller ones. The results of this study indicate that many factors contribute

to the ultimate decision an individual storm-petrel makes to return to and land at the colony: a number of these factors are outlined in a model of *offshore*, *colony*, and *underlying influences*.

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# Chapter 1

# Introduction

## 1.1. Predatory and Environmental Constraints on Activity Patterns

Many physiological and behavioural processes follow regular, rhythmic patterns of occurrence (Enright, 1970). These biological rhythms result from interactions between the endogenous rhythm of the animal, and exogenous influences on that inherent rhythm. Activity patterns in particular reflect the benefits and costs associated with performing certain behaviours at particular times; Aschoff (1960) argued for the adaptive value of 'doing the right thing at the right time'. External constraints imposed by major environmental cycles or physical events (e.g. lunar, solar, tidal, seasonal), either permit or demand that certain activities be performed during particular environmental phases (e.g. the light/dark cycle of the solar day), and portions of the overall activity pattern can be accentuated or suppressed by environmental condition (Aschoff, 1960).

Activity patterns exhibited during the reproductive season may differ markedly from those at other times of the year (Enright, 1970; Harrington & Mech, 1982). Reproductive events have evolved to ensure that young are born or hatched at a time that maximizes their chances for survival (i.e., advantages afforded by food availability, seasonal changes in weather, etc.; Lack, 1968). Owing to temporal variation in foraging opportunities and predation risk to the individual, however, successful reproduction also depends on the individual's awareness of, and synchronization to the external world, and thus activities such as feeding and parental care tend to occur at specific times of the day (Silver & Norgren, 1987).

Predation has played a strong selective force on life history traits, habitat use, foraging behaviour, and the population and community structures of prey species (Martin, 1987; Sih, 1987). The risk of predation can also have an important influence on the activity patterns of prey. Decisions about when to perform certain behaviours will be influenced by the perceived risk of predation and these decisions change over an animal's lifetime (Lima & Dill, 1990). A variety of prey species have been known to completely reverse their activity patterns when they are under heavy predation pressure, most often by shifting from a diurnal to a nocturnal activity pattern, although the opposite has been reported occasionally (Curio, 1976). Less dramatic alterations in an animal's activity while under predation risk are more commonly reported, however (e.g., Owings & Lockard, 1971).

Almost all seabird species breed colonially (Furness & Monaghan, 1987). While affording many benefits to the individual (e.g., information transfer, reproductive synchrony, predator swamping), coloniality also provides a super-abundant resource to predators. Seabirds have evolved a diversity of anti-predator strategies however, including mobbing (Kruuk, 1964), habitat choice (Buckley & Buckley, 1980), camouflage (Cullen, 1960; Montevecchi, 1976), and the desynchronization of the daily activity pattern with those of their predators (Curio, 1976). The most conspicuous examples of this desynchronization of activity pattern in seabirds are seen in the nocturnal colony activity of storm-petrels, shearwaters and small alcids (e.g., Harris, 1965a; Corkhill, 1973; Manuwal, 1974; Warham *et al.*, 1977; Furness & Baillie, 1981; Simons, 1981; Jones *et al.*, 1990). Petrels are often referred to as 'nocturnal seabirds'; and of the 90-95 known species of petrels, only 7 are diurnal at the breeding colony (Bretagnolle, 1990). For convenience these birds will be referred to as nocturnal here, recognizing that this is not entirely accurate: while they are nocturnally active at the colony, very little is known about their activity patterns at sea, although some species are known to feed during the day as well as at night (e.g., Obst, 1985; Watanuki, 1985; Pitman & Ballance, 1989).

While restricting colony activity to the night may reduce predation risk, especially for small species, nocturnal predation nevertheless does occur. Peregrine Falcons (*Falco peregrinus*), Bald Eagles (*Haliaeetus leucocephalus*), Herring (*Larus argentatus*), Great Black-backed (*L. marinus*), and Lesser Black-backed Gulls (*L. fuscus*), and corvids (*Corvus spp.*) have all been known to prey on nocturnal seabirds at night, even though they themselves are typically considered to be diurnally active (see Table 1-1). These predator species tend to be generalists in their choice of prey and are able to alter their activity patterns so that they may take advantage of prey not normally available during daylight hours (Curio, 1976). Generalist predators tend to be less temporally specialized in their daily activity patterns; specialists tend to show activity rhythms closely correlated with those of the prey (Cloudsley-Thompson, 1960). The ability of a predator to modify its hunting behaviour is also limited by its sensory capabilities (Barry & Francq, 1982). The 'diurnal' predators noted above, when hunting at night, are likely constrained by their limited nocturnal perceptual capabilities, especially vision. Given these constraints, predation on nocturnal seabirds by 'diurnal' predators tends to be limited to a few specialists in a population (Harris, 1965a; Corkhill, 1973; Pierotti & Annett, 1991), although they nevertheless can exact a serious toll on their prey (e.g., Parslow, 1965; Watanuki, 1986; Paine *et al.*, 1990).

The risk of predation to the nocturnal seabird varies with nightly environmental condition. Conditions that are conducive to 'diurnal' predators hunting at night tend to be those that provide higher levels of nocturnal illumination. Many reports have indicated that predation on nocturnal seabirds is higher in bright moonlit conditions (Gross, 1935; Watanuki, 1986; Nelson, 1989). It is generally thought that in order to reduce the risk of predation, nocturnal seabirds visit the colony in large numbers during foggy, or overcast nights, and return later (or avoid the colony altogether) on bright moonlit nights. The tendency to avoid the colony on bright, moonlight nights is exhibited most strongly by non-breeders. Of those studies that have differentiated between breeders and non-breeders, breeders were found to either have no response to moonlight (Storey & Grimmer, 1986; Bretagnolle, 1990), or to have reduced activity in moonlight, however only during incubation (Scott, 1970; Watanuki, 1986; MacKinnon, 1988; Table 1-2). Non-breeders of 12 seabird species (10 Procellariidae, two Alcidae), were all found to have decreased flyover activity at the colony during bright nocturnal conditions, and nine of these had reduced vocalization activity (Scott, 1970; Manuwal, 1974; Imber, 1975; Watanuki, 1986; Storey & Grimmer, 1986; MacKinnon, 1988; Bretagnolle, 1990; Jones *et al.*, 1990; Table 1-2).

Furness and Baillie (1981) were unable to detect a correlation between activity and moonphase in British Storm-Petrels (*Hydrobates pelagicus*) on Hirta, St. Kilda. Predation pressure on these populations was only mild or nonexistant however, further supporting the hypothesis that predation pressure plays a significant role in the nocturnal colonial activity patterns of seabirds.

Weather variables, in particular those that affect light intensity (such as cloud or fog), have also been found to affect nocturnal seabird activity. Warham *et al.* (1977) and Storey and Grimmer (1986) found that birds arrive later on clear nights, and Scott (1970), Bretagnolle (1990) and Jones *et al.* (1990) report an immediate increase in activity when the moon becomes obscured by cloud or fog. Severe weather (high winds, heavy rains) has also been associated with fewer birds returning to the colony (MacKinnon, 1988; Jones *et al.*, 1990), and a decrease in non-breeder activity in particular has been associated with high winds (Scott, 1970; Furness & Baillie, 1981).

## 1.2. Leach's Storm-Petrels, *Oceanodroma leucorhoa*

This study examines the influences of *Larus* gulls and nocturnal environmental condition on the colony activity and parental care patterns of Leach's Storm-Petrels, *Oceanodroma leucorhoa*. The storm-petrels are the most abundant breeding seabird species in the North-west Atlantic (Cairns *et al.*, 1989), which has had large increases of *Larus* gull populations during the present century and in recent decades (Montevecchi & Tuck, 1987).

Leach's Storm-Petrels are small, long-lived pelagic seabirds that winter at sea and return to coastal islands to breed. Maturation is delayed with onset of breeding at four to five years (Wilbur, 1969; Morse & Buchheister, 1977). Breeding chronology in Leach's Storm-Petrel is highly variable and asynchronous (see Wilbur, 1969; Simons, 1981; Ricklefs *et al.*, 1985). In Newfoundland, arrival at the breeding colony begins in April when burrows and nest chambers are excavated, occupied, and courtship is initiated. Egg laying (1 egg/clutch) begins in mid-May and generally extends through late June, although R. Butler (unpubl. data) has found birds in North-west Atlantic colonies laying in late July. Incubation ranges 37 - 52 days (Butler, unpubl. data), averaging approximately 40 - 42 days. Both adults incubate, and shift changes occur every 2 - 4 days (Wilbur, 1969). After hatching, the chick is brooded for 1 - 5 days (Ricklefs *et al.*, 1980b), after which time the chick is left unattended with each adult returning to feed it approximately once every 2 days (Ricklefs *et al.*, 1985), although interfeed intervals are highly variable. Some of this variation may be accounted for by weather and other environmental conditions, both at sea and at the colony. Chicks fledge from mid-September to late October, at approximately 60 - 70 days post-hatch (Ricklefs *et al.*, 1980a). It is thought that Leach's Storm-Petrels feed from a few km to 150 km or more offshore (Linton, 1978; Steele & Montevecchi, 1993), although owing to their small size it has not yet been possible to track individual Leach's Storm-Petrels at sea.

As with other nocturnal seabirds that are under the risk of predation at the colony, anecdotal reports have indicated that Leach's Storm-Petrels return to the colony later, and/or in fewer numbers on bright nights (e.g., Gross, 1935; Waters, 1965). Recent studies (Watanuki, 1986; MacKinnon, 1988) have quantified Leach's Storm-Petrel colony activity and have substantiated the anecdotal reports.

The relative importance of individual environmental variables (lunar phase, moonlight, cloud, fog, wind) to nocturnal activity of Leach's Storm-Petrels has not yet been fully determined, although Watanuki (1986) and MacKinnon (1988) argue that lunar phase is the single most significant factor. Watanuki (1986) further suggests that Leach's Storm-Petrels in part anticipate the lunar cycle and synchronize their activity to hours of darkness during clear, half moon nights. It is most likely that an interaction exists between both moonlight and weather conditions, as various combinations act to increase or decrease predation risk to the birds, thereby affecting activity.

The late or diminished arrival of Leach's Storm-Petrels to the colony on bright moonlit nights and the increased activity on foggy/overcast nights has been interpreted by some (Grubb, 1974; Imber, 1975) as being related more closely to feeding opportunities than to predator avoidance. Imber (1975) reported that bioluminescent and vertically migrating species comprise a large part of petrel diets (80-100%) off the New Zealand coast. At Newfoundland colonies, approximately 80% of the Leach's Storm-Petrel diet consists of vertically migrating species, and about 50% are bioluminescent (Linton, 1978; Montevecchi *et al.*, 1992). During periods of high nocturnal illumination, these species would be less available to the storm-petrels: vertically migrating species would remain farther below the surface, and bioluminescent prey would be more difficult to detect (Imber, 1975). The birds would thus take a longer time (or not succeed at all) in obtaining enough food to warrant a return to the colony on bright nights, thereby arriving late, or not at all.

Regardless of the mechanism that brings an individual to the vicinity of the colony, once there, the decision to land may be influenced by environmental conditions and the correspondant level of predation pressure at the colony. The behaviour at the colony may therefore be limited by both foraging constraints and predation risk, each of which may be affected by environmental condition (Jones *et al.*, 1990). Individual variation in activity at the colony should thus reflect a balance between avoiding predation and satisfying reproductive requirements and nutritional needs of the chicks.

While it has been quite well documented that Leach's Storm-Petrels avoid, or have reduced colony activity in conditions of high nocturnal illumination, very little research has been conducted on the inter-relationship between environmental influences and the nocturnal activity of both predators and prey at a seabird colony. In addition, the extent and nature of the effects of particular environmental variables are still a matter of discussion. This study therefore sought to further elucidate the relationship between Leach's Storm-Petrel colony activity pattern, environmental condition and predation at the breeding colony. This was achieved by examining the Leach's Storm-Petrel nocturnal activity at Gull Island, a colony with a large population of breeding of Herring and Great Black-backed Gulls, to nocturnal activity at Green Island, a colony with no breeding gulls. Further examination of the effect of the presence of gulls on Leach's Storm-Petrel activity was obtained throught the experimental introduction of model gulls at Green Island. The study was designed to specifically test the following hypotheses:

1) Predation by gulls on Leach's Storm-Petrels is a) higher at Gull Island and, b) owing to the diurnal nature of these gulls, is highest under conditions of high nocturnal illumination.

2) The flyover and vocalization activity of Leach's Storm-Petrels differs in the presence of gulls at the breeding colony. As a consequence of predatory pressures imposed by gulls, Leach's Storm-Petrels are responsive to environmental conditions that affect their detectability (i.e., nocturnal ambient light level, cloud, fog, moonlight). It was expected that increased risk of predation (i.e., moonlit nights, nights with little or no cloud or fog) would result in later arrivals and lower Leach's Storm-Petrel activity at Gull Island. How differences in environmental condition would affect Leach's Storm-Petrel activity at Green Island were not anticipated *a priori*, but if responses to these conditions were strictly a proximate anti-predator strategy, then they should not influence individuals on Green Island, except perhaps during the introduction of model gulls.

3) Leach's Storm-Petrels were not expected to organize colony activity around the lunar phase, regardless of gull presence at the colony. Owing to frequent occurrences of fog and cloud along the Newfoundland coast, lunar phase is not a reliable predictor of moonlight illumination.

4a) Chick interfeed intervals will be longer during periods of high nocturnal illumination in the presence of hunting gulls (Gull Island). If parental feeding strategies are also anti-predator strategies for Leach's Storm-Petrels, then intervals between parental food deliveries should be greater at the colony where gulls are present; perhaps with larger, more concentrated, or higher quality feeds being provided less frequently. Alternatively, if parental feeding strategies are dependent on pelagic foraging constraints only, then assuming similar oceanographic conditions around them, intervals between parental food deliveries to young should be similar among both colonies, regardless of the presence of gulls.

4b) If interfeed interval is longer at the colony with gulls, these greater intervals between feeds may affect chick growth, and hence chicks reared at Gull Island may be expected to fledge at a lighter weight or later than those at Green Island. Leach's Storm-Petrel fledging weights at Gull and Green Islands were also compared with those at three other colonies. Except for Green Island, all colonies had breeding gulls.

*Post-hoc* analyses on the effects of colony size on fledgling weights and reproductive chronology were done in light of evidence suggesting that colony size and fledgling weights are inversely related (Gaston *et al.*, 1983; Birkhead & Nettleship, 1981; Hunt *et al.*, 1986). This study provided an opportunity to indirectly explore this possibility with Leach's Storm-Petrels. Data are reported from colonies ranging over three orders of magnitude in size (4,200 - 530,000 pairs: R. Butler, pers. comm; Cairns *et al.*, 1989).

**Table 1-1:** Examples of 'diurnal' predators and the nocturnal seabirds they have been known to prey on. Sources are listed in chronological order.

| Diurnal Predator | Nocturnal Seabird | Sources |
|---|---|---|
| **GULLS** | | |
| **Herring Gull** | **Leach's Storm-Petrel** | Harris, 1965a,b |
| (*Larus argentatus*) | (*Oceanodroma leucorhoa*) | Long, 1965 |
| **Great Black-backed Gull** | **British Storm-Petrel** | Parslow, 1965 |
| (*L. marinus*) | (*Hydrobates pelagicus*) | Scott, 1970 |
| **Lesser Black-backed Gull** | **Manx Shearwater** | Corkhill, 1973 |
| (*L. fuscus*) | (*Puffinus puffinus*) | Oades, 1974 |
| **Slaty-backed Gull** | **Cassin's Auklet** | Manuwal, 1974 |
| (*L. schistisagus*) | (*Ptychoramphus aleuticus*) | Watanuki, 1986 |
| **Western Gull** | **Xantus' Murrelet** | MacKinnon, 1988 |
| (*L. occidentalis*) | (*Synthliboramphus hypoleucus*) | Nelson, 1989 |
| | | Bretagnolle, 1990 |
| **BIRDS OF PREY** | | |
| **Bald Eagle** | **Leach's Storm-Petrel** | Harris, 1965b |
| (*Haliaeetus leucocephalus*) | | Scott, 1970 |
| **Peregrin Falcon** | **Fork-tailed Storm-Petrel** | Sealy, 1976 |
| (*Falco peregrinus*) | (*O. furcata*) | French, 1979 |
| **Long-eared Owl** | **British Storm-Petrel** | DeGange & Nelson, 1982 |
| (*Asio otus*) | | Quinlan, 1983 |
| **Short-eared Owl** | **Ancient Murrelet** | Vermeer *et al.*, 1984 |
| (*Asio flammus*) | (*S. antiquus*) | Jones *et al.*, 1987 |
| **Great Horned Owl** | **Cassin's Auklet** | Gaston, 1990 |
| (*Bubo virginianus*) | | Jones *et al.*, 1990 |
| **Little Owl** | | Paine *et al.*, 1990 |
| (*Athene noctua*) | | |
| **Western Screech Owl** | | |
| (*Otus kennicottii*) | | |
| **Northern Saw-Whet Owl** | | |
| (*Aegolius acadicus*) | | |
| **CORVIDS** | | |
| **Northern Raven** | **Leach's Storm-Petrel** | Quinlan, 1973 |
| (*Corvus corone*) | **Ancient Murrelet** | MacKinnon, 1988 |
| **North American Crow** | | Vermeer *et al.*, 1984 |
| (*C. brachyrhynchos*) | | Gaston, 1990 |
| | | W.A. Montevecchi, unpubl. data |

Table 1-2: Some nocturnal seabird species and the effects of bright nocturnal conditions on colony activity (flyovers, vocalizations, or both). Sources indicated by superscripts.

| Species | Activity in bright nocturnal conditions | |
|---|---|---|
| | **Breeders** | **Nonbreeders** |
| **British Storm-Petrel** *Hydrobates pelagicus* | *decreased* [1] | *decreased* [1] |
| **Leach's Storm-Petrel** *Oceanodroma leucorhoa* | *decreased* [4,5] | *decreased* [4,5] |
| **Madeiran Storm-Petrel** *Oceanodroma castro* | *no change* [6] | *decreased* [6] |
| **White-faced Storm-Petrel** *Pelagodroma marina* | *no change* [6] | *decreased* [6] |
| **Bulwer's Petrel** *Bulweria bulwerii* | *no change* [6] | *decreased* [6] |
| **Cory's Shearwater** *Calonectris diomedea* | *no change* [6] | *decreased* [6] |
| **Little Shearwater** *Puffinus assimilis* | *no change* [6] | *decreased* [6] |
| **Manx Shearwater** *Puffinus puffinus* | *no change* [3] | *decreased* [3] |
| **Cassin's Auklet** *Ptychoramphus aleuticus* | ------ | *decreased* [2] |
| **Ancient Murrelet** *Synthiboramphus antiquus* | ------ | *decreased* [7] |

**Sources:**
1 - Scott, 1970
2 - Manuwal, 1974
3 - Storey & Grimmer, 1986
4 - Watanuki, 1986
5 - MacKinnon, 1988
6 - Bretagnolle, 1990
7 - Jones *et al.*, 1990

# Chapter 2

# Methods

## 2.1. General Methods

### 2.1.1. Study Sites

Behavioural and fledging data were collected at two Leach's Storm-Petrel colonies off the Newfoundland coast (Fig 2-1). Green Island (46°53'N, 56°05'W), Fortune Bay is a small (0.8 x 0.4 km), gently sloping island that is predominately vegetated by ferns and grasses. The Leach's Storm-Petrel population is estimated to be 72,000 pairs (Cairns *et al.*, 1989), with the greatest density occurring along the slopes at the northwestern portion of the island. Gulls do not normally nest on Green Island, likely a result of a resident dog, belonging to the lightkeepers. In 1987, no gulls bred on the island, and in 1988, one pair of Herring Gulls hatched two chicks at Southwest Point. Both Herring and Great Black-backed Gulls breed on nearby islands and rest on Green Island during the day, however gulls were only very rarely seen or heard on the island at night. Gull Island (47°16'N, 52°46'W), Witless Bay, measures 1.6 x 0.8 km and has an estimated storm-petrel population of 530,000 pairs (Cairns *et al.*, 1989). The majority of storm-petrels nest in burrows in the fir and spruce forest which covers much of the island. Approximately 3,850 pairs of Herring Gulls (Cairns *et al.*, 1989) and 113 pairs of Great Black-backed Gulls (Roy, 1986) nest on Gull Island. As the larid populations have been increasing since 1951 (Montevecchi & Tuck, 1987), these populations may be higher now.

Additional fledging data were collected on Middle Lawn Island, (46°52'N, 55°37'W), Placentia Bay, and contributed by R. Butler for Great Island (47°11'N, 52°49'W), Witless Bay, and Little Duck Island (44°10'N, 65°15'W), Maine (Fig 2-1). Middle Lawn is a small (370 x 290 m) grass and fern covered island, with a Leach's Storm-Petrel population of about 26,313 pairs (Cairns *et al.*, 1989). Approximately 20 pairs of Herring Gulls and 6 pairs of Great Black-backed Gulls breed on the island (Cairns *et al.*, 1989). Great Island has a Leach's Storm-Petrel population of approximately 250,000 pairs, and approximately 2,770 pairs of Herring Gulls and 80 pairs of Great Black-backed Gulls (Cairns *et al.*, 1989), although as with Gull Island, these numbers may now be higher. Little Duck Island is a small (35 ha) spruce-fir forest and Rubus-grass meadow covered island with a Leach's Storm-Petrel population of 4,200 pairs, and approximately 600 pairs of Herring Gulls and 520 pairs of Great Black-backed Gulls (R. Butler, pers. comm.).

### 2.1.2. Observation Schedule

Eight visits were made to Gull and Green Islands in 1988; these were scheduled so that observations could be conducted in all lunar phases and during both incubation and chick rearing periods (Table 2-1). Comparative measurements between the colonies were made by two field teams during simultaneous trips (9 - 22 July, 29 July - 7 August). In order to obtain a more extensive coverage of the breeding season, additional trips were made to Green Island during 12 - 20 June and 21 - 29 August. Fifty-seven days were spent at the colonies in 1988, totalling 129 hr of observation on Gull Island, and 172 hr on Green. Fledging data were collected during brief visits to Green Island (17 - 18 September), Middle Lawn Island (18 - 19 September) and Gull Island (25 - 26 September). Simultaneous trips were made in the hopes that inter-colony comparisons would be possible by reducing variance in storm-petrel behaviour caused by variation in reproductive chronology. Reproductive chronology between Gull and Green Islands was found to differ nonetheless however, reducing the utility of analyzing the data on the basis of date. Data were instead analyzed and compared in terms of reproductive stage (i.e., incubation, chick rearing). A colony was considered to be incubating or chick rearing when $\geq$ 75% of the study burrows (see below) were in one or the other phase.

### 2.1.3. Observation Procedures

Methods were refined in 1987 during one trip to Great Island and three trips to Green Island. Observers were trained and interobserver reliabilities were established either in 1987, or early in the 1988 season. All auditory measurements of activity were recorded on tape and counted later by the author (see 2.3.2), however visual measurements of activity were done on site. Four observers in total recorded behaviour (observer 1 - 4). During bright and intermediate nocturnal conditions interobserver reliabilities were very good ($\bar{x}$=85%, range=75-96%, n=11 comparisons). During dark nights however differences between observers were quite apparent, with the exception of observers 1 and 2, who had 85% agreement on average (range=71-90%, n=16 comparisons). During dark nights observer 3 consistantly counted approximately 25% more Leach's Storm-Petrels in flight than either observer 1 or 2 (n=22 comparisons). A correction factor was therefore applied to observer 3's counts made during dark nights: they were reduced by 25% to be approximately equivalent to observer 1 and 2. Conversely, observer 4 was consistantly lower than either observer 1 or 2 by approximately 33% (n=25 comparisons); thus the correction factor of a 33% increase was applied to this observer's counts. The occasions when observer counts needed to be corrected for were actually quite few in number: this was only necessary when either observers 1 or 2 were not present. Overall, only 1/10 dark nights had observations that were corrected for on Gull Island. On Green Island, 3/12 dark nights had observations that were corrected for.

#### 2.1.3.1. Colony Activity

Observations of environmental condition, Leach's Storm-Petrel and gull activity (see below) were made from the same location each evening. On Green Island, birds were observed from a point near the apex at the NW end of the island. Observations on Gull Island were made from a point ~15 m north of the research cabin on the western edge of the island. The cabin provided a visual barrier between the observer and the gulls, thereby reducing the chance of an artificial elevation in gull activity. The observer sat near the edge of the forest, overlooking a clearing to Witless Bay. At both colonies, the observers sat within 0.5 m of active storm-petrel burrows, though this did not appear to have any effect on those individuals, as they would often land nearby and enter their burrows. Observations began at dusk, and continued throughout the night until first light, except on a few occasions during very stormy weather when observations were terminated early.

#### 2.1.3.2. Environmental Conditions

The following environmental information was recorded hourly throughout the nightly observations: a) *Cloud cover* was estimated as the percentage of the sky covered in cloud, and later classified as light (5% - 25%), intermediate (30% - 70%) or heavy (75% - 100%). Type of cloud present (cirrus, stratus, cumulus) was also considered in this classification; b) *Fog* was classified as light, intermediate, or thick; c) *Wind* was estimated in km/hr, and later checked for accuracy against data from weather stations at Torbay (25 km north of Gull Island) and St. Pierre

(12 km south of Green Island); d) *Visibility* was measured in m by mounting an 18 x 13 cm card, divided into four black and white rectangles at eye level and walking away from it until the white portion of the card could just be detected; e) *Moonlight* was recorded as present or absent i.e., whether the moon had risen, or was obscured by cloud or fog; f) *Nocturnal illumination* was noted and classified as bright, intermediate, or dark; following Storey and Grimmer (1986). (The classification of this variable was somewhat subjective and included several meteorological/environmental variables - cloud, fog, moonlight and lunar phase. For example, a bright classification was typically characterised by a full or partial moon, and little or no cloud or fog. A night classified as dark typically had no moon, and/or was heavily overcast or foggy. Intermediate nights were more varied, but generally occurred when the moon was partially to fully illuminated, and cloud cover or fog level blocked much of the lunar illumination. The classification of nocturnal illumination often changed from one level to another throughout a night, as meteorological/environmental variables changed, e.g., the moon rising or setting, cloud cover forming, or a fog bank rolling in). g) At the nightly onset of Leach's Storm-Petrel activity, *evening illumination* was also classified as bright, intermediate, or dark; and *sky condition* was classified as either clear, cloudy or foggy.

## 2.2. Predation by Gulls on Leach's Storm-Petrels

Predation by gulls was estimated by the daily searching of a 458 x 1 m pathway on Gull Island for storm-petrel remains. All remains were collected and counted: full carcasses, gull regurgitation pellets packed with feathers, and pairs of wings were counted as single kills, individual wings were counted as 0.5 kills. The approximate positioning of the remains were noted, although not in detail; e.g., in the immediate vicinity of a known gull nest (< .5 m) or not. Very little predation of storm-petrels occurred on Green Island, nevertheless a 500 x 1 - 1.5 m pathway was searched for storm-petrel remains approximately once every 3 days, and a separate 450 x 1 m path was searched daily.

## 2.3. Nocturnal Activity of Leach's Storm-Petrels and Gulls

### 2.3.1. First Flyovers (FFO) and First Air Calls (FAC)

The time of the tenth storm-petrel seen in flight over the colony was used to indicate the nightly commencement of flyover activity (FFO). These times were later converted to a value in min after sunset. Sunrise and sunset times were obtained from Environment Canada Atmospheric Weather Service for St. John's (25 km north of Gull Island) and adjusted for Green Island. Accordingly, the tenth aerial vocalization heard was used to indicate the commencement of vocalization activity (FAC). Air calls were discerned from burrow calls based on the loudness and clarity of the call, and the height at which the call was emitted. On-site observations indicated that vegetative cover (clearing vs forest) and proximity of gulls affected time of storm-petrel FAC. To quantify this, additional FAC data were obtained on 6 nights (Aug 1 - 6) on Gull Island from a clearing near nesting gulls, approximately 55 m south of the observation point.

### 2.3.2. Flyover and Aerial Vocalization Activity

One min counts of storm-petrel flyover and vocalization activity were conducted every 15 min throughout the night. Flyover counts consisted of the number of storm-petrels flying within 4 m (Gull Island), or 6 m (Green Island) of the observer. These distances were determined to be the distance at which the storm-petrels could be reliably counted, even on very dark or foggy nights; Green Island had a larger detection distance due the lighthouse beam periodically sweeping the area. Natural vegetation or wooden stakes indicated the detection distance for the observer. Because meterological information was collected only every hour, hourly averages of storm-petrel flyovers were analysed.

Radio Shack CTR-55 cassette recorders with microphones mounted on 2 m poles were used to record air calls. Recordings were made along with flyover counts, usually during the same 1 min period, but occasionally in the min following the flyover count. Cassette tapes were later played back and air calls counted by the author, reducing the likelihood of observer errors in the discrimination of the calls. Checks throughout the season of recorded counts against counts made in the field indicated that the counts from cassette recordings differed only slightly from direct counts. Again, hourly averages were analysed.

On-site observations indicated that vegetative cover tended to affect storm-petrel vocalization rate. To quantify this, additional data were collected from July 30 - Aug 6 on Gull Island on the ratio of air calls emitted from the wooded area behind and beside the observer to calls from the clearing in front of the observer.

### 2.3.3. Activity at the Burrow

The activity of breeding birds was assessed by latticing with vegetation the entrances of a number of active burrows each evening. When an adult bird passed through the lattice to relieve its mate or feed its chick, the lattice would be disturbed. The status of each lattice was checked every hr throughout the night. Uncertain breakages (likely due to an adult only partially entering or exiting) were not included in the analysis; broken lattices were reset immediately.

Because other birds may break the lattice, or an incubating bird may exit and then re-enter the burrow, the accuracy of this technique was established during the first trip to Green Island during incubation, and again at both Gull and Green Islands during chick rearing. If a lattice was found broken, the burrow was investigated to determine if a bird had left or returned, or a mate change had occurred. Individual birds were identified by numbered U.S. Fish and Wildlife Service metal leg bands. In an attempt to minimize disturbance and reduce desertions, each burrow was investigated for only three nights. During incubation at Green Island 53 broken lattices were sampled from 18 burrows, and indicated that 79% (42/53) of the broken lattices were due to an actual mate change, or a bird returning to or leaving the burrow. During chick rearing (eight nights of observation), a broken lattice indicated that a parent had returned to feed its chick (determined by weighing of chicks the following day, see 2.6 for methods) on 89% (72/81) and 85% (160/189) of the occasions, at Gull and Green Islands respectively.

The number of burrows monitored varied throughout the season from 20 - 30 for each study site due to desertions and egg or chick mortality. Deserted burrows were replaced with others within 1 - 3 days. Desertion rate was high, with nine of 37 (24%) burrows deserted over the season on Gull Island, and 14 of 49 (29%) on Green Island. Most desertions were of eggs (67% on Gull Island, 64% on Green Island), and occurred following disturbance early in the nesting period; a time when Leach's Storm-Petrels were particularly sensitive to interference.

### 2.3.4. Gull Activity

Gull activity was measured simultaneously with storm-petrel activity. Gulls flying by during the storm-petrel activity counts were recorded. Gull vocalizations were counted from the same 1 min cassette recordings used to measure storm-petrel aerial vocalizations.

## 2.4. Model Gull Experiment

This project was carried out on Green Island in August, 1988 to determine what effect the presence of model gulls and gull vocalizations have on storm-petrel activity at this colony. Seven Herring Gull models were carved out of styrofoam and marked with wings, bills, and eyes. Five were carved in a sitting position with folded wings, and two had outstretched wings. Models were mounted on wooden stakes and positioned in a 100 $m^2$ area around the observer, approximately 30 min before the anticipated time of storm-petrel arrival. In addition, a Uher model 4400 reel to reel, and a Radio Shack CTR-55 cassette recorder played a 60 min series of single and group Herring Gull calls. The calls were played at a volume similar to that heard on Gull Island at dusk, as judged by two observers. FFO and FAC data were collected as described above. The models were left in position and the tapes were played for either 1 or 2 hr after storm-petrel arrival. The models were then covered in dark plastic and the recorders turned off for 1 hr. Activity data were collected during both 'gull' and 'no gull' conditions. Periods of 'gull/no gull' conditions were alternated throughout the remainder of the night. This procedure was used on four nights from 25 - 28 Aug, totalling 21 hr of observation. To test the effectiveness of the visual models plus auditory cues versus the auditory cues from the gull vocalizations alone, an additional 5 hr of observations were made using only the taped vocalizations in the 'gull' condition. Two bright nights, and one intermediate and dark night occurred during the sampling period.

Data collected on FFO and FAC times and during the first 60-90 minutes of storm-petrel activity were compared with data obtained from the previous four evenings of observation, before the experiment began. These data were analysed in this fashion because storm-petrels are generally fewer and quieter in the early evening, and the 'gull' condition was always present during the first hour of storm-petrel arrival. It was thought that the data obtained during this 'gull' condition might therefore be artificially lowered, and thus the first 60 - 90 min of measurements were excluded from these analyses to remove the possibility of this bias. For FFO, FAC and activity during the first 60-90 minutes of activity then, a total of eight nights of observations were obtained (four before and four during the experiment). A total of three bright, three intermediate and two dark evenings illuminations occurred.

## 2.5. Interfeed Interval

Chicks from the 20 - 30 study burrows were weighed daily between 1200 and 1500 h (Gull Island, 30 July - 07 Aug; Green Island, 21 - 29 Aug) using a 50 or 100 g Pesola spring scale measurable to 0.5 or 0.1 g units. In order to reduce chick mortality, chicks were not weighed until they reached ~ 20 g at about 10 d posthatch (Ricklefs *et al.*, 1985). The difference in mass from day to day was determined and used to indicate whether a chick had been fed on the previous night. Following Ricklefs *et al.* (1985), a 24 hr mass change of -1.5 to +5.5 g was taken to indicate that the chick had been fed once the previous night, and increments of $\geq$ 6.0 g indicated a double feed. A loss in mass of $\geq$ 2.0 g indicated that the chick had not been fed the previous night.

## 2.6. Fledging Measurements

Mass and wing length (wrist to tip of longest primary) measurements of fledging or near to fledging storm-petrel chicks were collected on Green, Gull and Middle Lawn Islands. Chicks found during the night in vegetation and along pathways were measured, as well as chicks found in burrows during the day. Mature chicks were distinguished from adults by meeting one or several of these criteria: peeping; not quite fully feathered; a mass $\geq$ 55 g; an inability to fly when gently tossed into the air. Data from Gull and Green Islands were compared with data supplied by R. Butler for Great Island and Little Duck Island.

## 2.7. Statistical Treatment of Data

Early examination of the data revealed that they were not normally distributed and colonies were not homogeneous in their variances. Data were therefore analysed separately for each colony, and nonparametric analysis were used. The environmental and gull effects on Leach's Storm-Petrel activity were determined using Kruskal-Wallis one way ANOVA. All statistics were performed using the Statistical Analysis System (SAS), version 6.06.

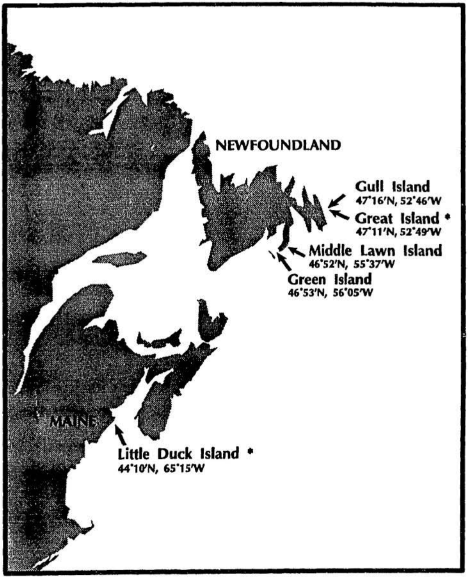



Figure 2-1: Location of study colonies. Asterisks (*) indicate colonies for which data were contributed by R. Butler.

**Table 2-1:** Observation schedule (date and lunar phase) of study sites visited in 1988.

| Colony | Date | Lunar phase |
|---|---|---|
| Gull Island | July 9 - 21 | Last - First Quarter |
| | July 29 - August 7 | Full - Last Quarter |
| | September 25 - 26 | Last Quarter |
| Green Island | June 12 - 20 | New - First Quarter |
| | July 13 - 22 | New - First Quarter |
| | July 30 - August 7 | Full - Last Quarter |
| | August 21 - 29 | First Quarter - Full |
| | September 17 - 18 | Full |
| Middle Lawn Island | September 18 - 19 | Full |

# Chapter 3

# Results

## 3.1. Nocturnal Activity of Gulls and Predation on Leach's Storm-Petrels (Gull Island)

In general, nocturnal activity of gulls was highest in conditions conducive to visually oriented hunting. Significantly more gulls were seen flying and heard calling when nocturnal illumination and visibility were greatest, and in moonlight (Tables 3-1 - 3-3). Gull activity level was also significantly higher (Chi-square, $\chi^2$=8.7, df=1, p=.003) in the period around the full moon ($\bar{x}$ flyovers=0.7/min, sd=0.7; $\bar{x}$ vocalizations=1.9/min, sd=0.7), than around the new moon ($\bar{x}$ flyovers=0.5/min, sd=0.8; $\bar{x}$ vocalizations=1.6/min, sd=0.7).

On Gull Island, most predation on storm-petrels occurred under bright, moonlit skies. Significantly more storm-petrel remains were found after bright or intermediately lit nights, as compared to dark nights (Kruskal-Wallis one way ANOVA, $H$=6.1, df=2, p=.048). Predation rate was positively correlated with both nocturnal illumination level (Spearman $r_s$=.61, p=.009) and number of hours of moonlight (Spearman $r_s$=.59, p=.01). More remains were collected after nights with moonlight ($\chi^2$=5.3, p=.02, Fig 3-1), and on bright nights compared to intermediate and dark ($H$=6.08, df=2, p=.05, Fig 3-2). Numbers of remains found in the period during the full moon were only slightly higher overall than during the new moon however (full moon $\bar{x}$=4.4 sd=2.3; new moon $\bar{x}$=3.8, sd=2.8). The majority of storm-petrel remains were consistently found at only a few sites, normally very near particular gull nests. This suggests that nocturnal predation is not widespread among the gull population, but rather was limited to a small number of 'specialists' that were successful nocturnal hunters.

Predation on storm-petrels on Green Island was infrequent. While a few storm-petrel remains were found on Green Island over the season, none were found on the path that was searched for storm-petrel remains. All storm-petrel remains were discovered after a 1 - 2 week observer absence from the colony, and hence the cause of predation could not be ascertained. Gulls were very rarely seen or heard at the colony at night however, and it is felt that they were not likely to visit the colony from their nearby nesting sites to hunt storm-petrels.

Table 3-1: Effects of nocturnal illumination level on gull activity level (Gull Island) over the reproductive season:
$H$ = Kruskal-Wallis one way ANOVA; * = $p < .05$; ** = $p < .01$.

| | Nocturnal illumination level (n = # of hrs) | | | |
|---|---|---|---|---|
| Gull activity /min | Bright (n=21) | Intermediate (n=36) | Dark (n=70) | $H$ value |
| Flyovers | | | | |
| $\overline{x}$ (sd) | 1.9 (1.8) | 2.0 (3.8) | 0.6 (2.1) | 29.8 ** |
| Vocalizations | | | | |
| $\overline{x}$ (sd) | 13.8 (6.2) | 11.6 (9.4) | 6.0 (6.0) | 18.2 ** |

**Table 3-2:** Effects of visibility level on gull activity level (Gull Island) over the reproductive season:
$H$ = Kruskal-Wallis one way ANOVA; * = $p < .05$; ** = $p < .01$.

| | Visibility level (n = # of hrs) | | | |
|---|---|---|---|---|
| **Gull activity /min** | High 11m+ (n=23) | Intermediate 6 - 10m (n=27) | Low 0 - 5m (n=81) | $H$ value |
| Flyovers | | | | |
| $\bar{x}$ (sd) | 2.4 (1.9) | 1.4 (1.9) | 0.7 (3.1) | 39.6 ** |
| Vocalizations | | | | |
| $\bar{x}$ (sd) | 14.9 (5.7) | 12.5 (9.9) | 5.7 (5.8) | 35.2 ** |

**Table 3-3:** Effects of moonlight on gull activity level (Gull Island) over the reproductive season:
$H$ = Kruskal-Wallis one way ANOVA; * = $p < .05$; ** = $p < .01$.

| | Moonlight periods (n = # of hrs) | | |
|---|---|---|---|
| **Gull activity /min** | Moonlit (n=26) | Moonless (n=102) | $H$ value |
| Flyovers | | | |
| $\bar{x}$ (sd) | 1.6 (1.7) | 1.1 (2.9) | 22.6 * |
| Vocalizations | | | |
| $\bar{x}$ (sd) | 12.8 (5.9) | 7.9 (7.9) | 6.2 ** |

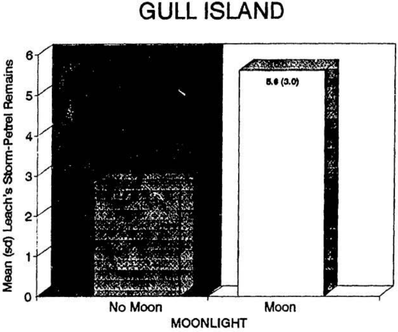



**Figure 3-1: Relationship between presence and absence of moonlight and the number of storm-petrel remains collected the following day (Gull Island).**

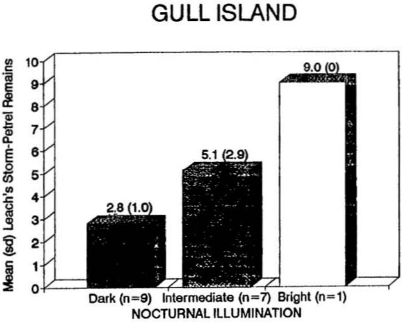



**Figure 3-2: Relationship between level of nocturnal illumination and number of storm-petrel remains collected the following day (Gull Island).**

## 3.2. Environmental Effects on Leach's Storm-Petrel Activity

### 3.2.1. First Flyovers (FFO) and First Air Calls (FAC)

At both colonies over the entire reproductive season, storm-petrels arrived and began to vocalize later on bright evenings than on intermediate or dark ones, and under clear versus cloudy or foggy skies (Tables 3-5, 3-6). In general however, time of first flyover (FFO) and first air call (FAC) on Green Island varied more with evening condition than on Gull Island. Table 3-4 is a summary of the associations between environmental condition and FFO and FAC. Evening illumination level and sky condition affected FFO and FAC times at both colonies, although effects on FFO were not statistically significant for Gull Island over the entire reproductive season.

Storm-petrel FFO time was not significantly different between the 2 colonies (Gull Island n=21, FFO=73.1 $\pm$ 11.6 min post sunset; Green Island n=28, FFO=71.9 $\pm$ 14.1 min post sunset) (Fig 3-3). FAC at both colonies varied significantly with evening illumination level ($p<.02$). In addition, FAC times were consistently later on Gull Island, regardless of evening illumination level (Table 3-7). As a result, the interval between time of FFO and FAC was significantly greater on Gull than on Green Island ($H$=12.4, df=1, $p$=.0004). This indicates that while the birds at both colonies arrived at approximately the same time, the storm-petrels on Gull Island were quieter for a longer period after arrival than those on Green Island. Data collected at the clearing on Gull Island (see FAC methods) indicated that average FAC time at the clearing was a further 10.8 (n=6 nights, sd=4.5) min later than FAC at the edge of the wood, a doubling of the length of time the storm-petrels were quiet on arrival. This indicates that under topographical conditions similar to those on Green Island (clear areas, without immediate opportunity for cover), the storm-petrels on Gull Island differed even more from those on Green Island.

**Table 3-4:** Summary of effects of evening environmental condition on time of Leach's Storm-Petrel first flyover (FFO) and first air call (FAC), over the entire reproductive season and during the separate periods of incubation and chick rearing. Double asterisks indicate significance $\leq .05$ (Kruskal-Wallis one way ANOVA).

| | Gull Island | | Green Island | |
|---|---|---|---|---|
| | Evening illumination | Sky condition | Evening illumination | Sky condition |
| **FFO** | | | | |
| Entire season | -- | -- | ** | -- |
| Incubation | -- | -- | -- | ** |
| Chick rearing | -- | ** | ** | -- |
| **FAC** | | | | |
| Entire season | ** | ** | ** | -- |
| Incubation | -- | -- | ** | -- |
| Chick rearing | -- | -- | ** | -- |

**Table 3-5:** Effects of evening nocturnal illumination level on Leach's Storm-Petrel FFO and FAC times over the reproductive season: *H* = Kruskal-Wallis one way ANOVA; * = $p < .05$; ** = $p < .01$.

| | Nocturnal illumination level (n = # of evenings) | | | |
|---|---|---|---|---|
| | **Gull Island** | | | |
| | Bright (n=2) | Intermediate (n=9) | Dark (n=10) | *H* value |
| min after sunset | | | | |
| FFO | | | | |
| $\bar{x}$ (sd) | 87 (24) | 72 (10.1) | 68.7 (8.3) | 1.6 |
| FAC | | | | |
| $\bar{x}$ (sd) | 102 (24) | 87.7 (13.3) | 77.3 (6.8) | 7.9 ** |
| | **Green Island** | | | |
| | (n=10) | (n=6) | (n=12) | |
| FFO | | | | |
| $\bar{x}$ (sd) | 84.1 (9) | 75.0 (4.4) | 63.1 (5.6) | 21.0 ** |
| FAC | | | | |
| $\bar{x}$ (sd) | 93.1 (10.7) | 78.3 (5.9) | 67.3 (6.8) | 20.8 ** |

**Table 3-6:** Effects of sky condition on Leach's Storm-Petrel FFO and FAC times over the reproductive season: *H* = Kruskal-Wallis one way ANOVA; * = p < .05; ** = p < .01.

| | Sky condition (n = # of evenings) | | |
|---|---|---|---|
| | **Gull Island** | | |
| | Clear (n=12) | Overcast/Foggy (n=9) | *H* value |
| **min after sunset** | | | |
| FFO | | | |
| $\bar{x}$ (sd) | 73.7 (13.2) | 69.4 (8.4) | 0.1 |
| FAC | | | |
| $\bar{x}$ (sd) | 88.8 (15.5) | 77.9 (7.0) | 4.9 ** |
| | **Green Island** | | |
| | (n=14) | (n=14) | |
| **min after sunset** | | | |
| FFO | | | |
| $\bar{x}$ (sd) | 83.9 (19.4) | 64.5 (10.4) | 15.8 ** |
| FAC | | | |
| $\bar{x}$ (sd) | 89.1 (11.4) | 68.6 (7.6) | 17.5 ** |

**Table 3-7:** Leach's Storm-Petrel FAC times (min after sunset) on Gull and Green Islands in different nocturnal illumination levels over the reproductive season: $\chi^2$ = chi-square test; * = $p < .05$; ** = $p < .01$.

| Nocturnal Illumination | Gull Island (n=21 nights) | Green Island (n=28 nights) | $\chi^2$ value |
|---|---|---|---|
| Bright (sd) (n=12) | 102.0(24.0) | 93.1(10.7) | .1 |
| Intermediate (sd) (n=15) | 87.7(13.3) | 78.3(5.9) | 3.8 * |
| Dark (sd) (n=22) | 77.3(6.8) | 67.3(6.8) | 9.9 ** |

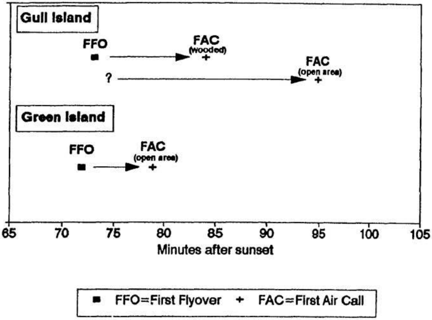



Figure 3-3: Observed nightly sequence of events during Leach's Storm-Petrel arrival to Gull and Green Islands. Data are averaged over the entire reproductive season.

### 3.2.2. Flyover Activity

Analysis of the number of storm-petrels present at the colonies indicated that the birds on Gull and Green Islands responded similarly to different environmental conditions. Significantly fewer storm-petrels were present at Gull Island over the entire reproductive season (n=139 hr) when nocturnal illumination and visibility were highest. On Green Island, flyover rate was higher in low visibility (Tables 3-8, 3-9). Greater numbers of storm-petrels on Green Island were also associated with thick fog (Table 3-10). Fewer storm-petrels were present in moonlight both colonies, although this was not statistically significant (Table 3-11). An almost immediate decrease or increase in flyover activity occurred at both colonies with the appearance or disappearance of the moon.

On Gull Island, the peak of flyover activity was 2.5 hr later under bright nocturnal illumination, as compared to both intermediate and dark nights ($H$=5.9, df=2, p=.05). Flyover peak was also later on Green Island during bright nights, although not significantly so.

During incubation on Gull Island (n=65 hr), significantly fewer storm-petrels were counted when nocturnal illumination ($H$=10.6, df=2, p=.005) and visibility ($H$=12.4, df=2, p=.002) were highest, and in moonlight ($H$=3.8, df=1, p=.05). The same pattern, although statistically nonsignificant, was seen on Green Island during incubation for nocturnal illumination, visibility and moonlight.

During chick rearing on Gull Island (n=64 hr), a significantly lower storm-petrel flyover rate was associated with higher visibility levels ($H$=15.4, df=2, p=.0005). During chick rearing on Green Island (n=97 hr) significantly fewer storm-petrels were counted in moonlight ($H$=3.9, df=1, p=.05) and when visibility ($H$=8.3, df=1, p=.004) was highest.

### 3.2.3. Aerial Vocalizations

Leach's Storm-Petrel aerial vocalization rates varied similarly with environmental condition at both colonies over the entire reproductive season. Significantly fewer storm-petrels were heard at the Gull Island colony (n= 129 hr) when nocturnal illumination and visibility were highest, cloud cover was not heavy, and in moonlight (Tables 3-8, 3-9, 3-12, 3-11, respectively). On Green Island (n=172 hr), significantly more aerial vocalizations were heard when nocturnal illumination and visibility were low, fog was thick, and in moonless conditions (Tables 3-8 - 3-11).

During incubation on Gull Island (n=65 hr), significantly fewer aerial vocalizations were associated with higher nocturnal illumination ($H$=10.3, df=2, p=.006) and visibility ($H$=26.0, df=2, p<.0001) levels.

During chick rearing on Gull Island (n=64 hr), storm-petrels called significantly less when visibility was highest ($H$=14.4, df=2, p=.0008). Results obtained at Green Island during chick rearing (n=101 hr) indicated that significantly fewer vocalizations were heard in moonlight ($H$=14.9, df=1, p<.0001) and when nocturnal illumination ($H$=18.4, df=2, p<.0001) and visibility ($H$=16.1, df=1, p<.0001) were highest.

Data collected at Gull Island on the ratio of calls emitted from the wooded area to calls emitted from the clearing (n=69) indicated that when nocturnal illumination was high, significantly more calls were emitted from the woods ($H$=10.2, df=2, p=.006). An average of 80% (sd=14.9) of the calls were heard from the wooded area during bright periods; while only 64% (sd=12.7) of the calls were emitted from the woods in intermediate periods and 66% (sd=19.8) during dark periods.

As with flyover activity, an almost immediate decrease or increase in vocalization activity was noted at both colonies with the appearance or disappearance of the moon.

### 3.2.4. Call:Flyover Ratio

As reported above, storm-petrels emit fewer aerial vocalizations under certain environmental conditions (e.g., bright nights, moonlight). While this may be a function of fewer storm-petrels present at the colony under these conditions, it may also be due to an actual reduction in aerial vocalization rate by birds that are present. In order to elucidate this, the ratio of calls to flyovers under different environmental conditions was examined. Call:flyover ratio was determined by dividing the number of flyovers by the number of calls, for each one minute sampling period.

Over the entire reproductive season, calls:flyovers on both Gull and Green Island were significantly lower when nocturnal illumination and visibility levels were high (Tables 3-8, 3-9). On Green Island (n=172 hr), call:flyover ratio was also lower under moonlit conditions (Table 3-11).

During incubation on Gull Island (n=65 hr), a significantly lower call:flyover ratio was was associated with high nocturnal illumination ($H$=6.5, df=2, p=.04) and high visibility ($H$=10, df=2, p=.007). Call:flyover ratio on Green Island during incubation (n=75 hr) was not significantly affected by any of the environmental variables measured.

During chick rearing on Gull Island (n=64 hr) the call:flyover ratio was not significantly affected by any of the environmental variables measured. On Green Island however (n=97 hr), higher nocturnal illumination ($H$=15.9, df=2, p=.0004) and visibility ($H$=13.3, df=1, p=.0003) levels, and moonlight ($H$=19.7, df=1, p<.0001) were associated with a significantly lower call:flyover ratio during chick rearing.

**Table 3-8:** Effects of nocturnal illumination level on Leach's Storm-Petrel flyover and aerial vocalization rates, and call:flyover ratio over the reproductive season:
$H$ = Kruskal-Wallis one way ANOVA; * = $p < .05$; ** = $p < .01$.

| Storm-petrel activity/min | Nocturnal illumination level (n = # of hrs) | | | |
|---|---|---|---|---|
| | **Gull Island** | | | |
| | Bright (n=21) | Intermediate (n=36) | Dark (n=72) | $H$ value |
| Flyovers | | | | |
| $\bar{x}$ (sd) | 18.7 (11.1) | 17.2 (14.4) | 23.8 (12.0) | 6.2 * |
| Vocalizations | | | | |
| $\bar{x}$ (sd) | 7.6 (4.5) | 6.9 (6.1) | 16.6 (9.3) | 33.9 ** |
| Calls:Flyovers | | | | |
| $\bar{x}$ (sd) | 0.5 (0.2) | 0.4 (0.4) | 0.8 (0.6) | 22.1 ** |
| | **Green Island** | | | |
| | (n=42) | (n=20) | (n=110) | |
| Flyovers | | | | |
| $\bar{x}$ (sd) | 22.8 (13.8) | 24.5 (15.4) | 29.6 (16.4) | 5.2 |
| Vocalizations | | | | |
| $\bar{x}$ (sd) | 7.5 (4.8) | 9.5 (6.3) | 13.0 (6.5) | 22.0 ** |
| Calls:Flyovers | | | | |
| $\bar{x}$ (sd) | 0.3 (.2) | 0.4 (.2) | 0.5 (.2) | 19.8 ** |

**Table 3-9:** Effects of visibility level on Leach's Storm-Petrel flyover and aerial vocalization rates, and call:flyover ratio over the reproductive season: $H$ = Kruskal-Wallis one way ANOVA; * = p < .05; ** = p < .01.

| | Visibility level (n = # of hrs) | | | |
|---|---|---|---|---|
| | **Gull Island** | | | |
| | 0-5 m (n=32) | 5-10 m (n=27) | 10-15 m (n=21) | $H$ value |
| **Storm-petrel activity/min** | | | | |
| Flyovers | | | | |
| $\overline{x}$ (sd) | 25.1 (10.6) | 16.2 (14.4) | 12.7 (11.8) | 23.4 ** |
| Vocalizations | | | | |
| $\overline{x}$ (sd) | 16.9 (8.6) | 6.9 (6.1) | 5.3 (4.9 | 44.8 ** |
| Calls:Flyovers | | | | |
| $\overline{x}$ (sd) | 0.8 (0.6) | 0.5 (0.6) | 0.4 (0.3) | 14.9 ** |
| | **Green Island** | | | |
| | (n=147) | (n=15) | | |
| Flyovers | | | | |
| $\overline{x}$ (sd) | 29.3 (15.9) | 16.5 (7.4) | | 10.6 ** |
| Vocalizations | | | | |
| $\overline{x}$ (sd) | 12.0 (6.3) | 5.5 (5.1) | | 14.0 ** |
| Calls:Flyovers | | | | |
| $\overline{x}$ (sd) | 0.4 (.2) | 0.3 (.2) | | 3.9 * |

**Table 3-10:** Effects of fog on Leach's Storm-Petrel flyover and aerial vocalization rate over the reproductive season (Green Island): $H$ = Kruskal-Wallis one way ANOVA; * = p < .05; ** = p < .01.

| | Fog Condition (n = # of hrs) | | | | |
|---|---|---|---|---|---|
| | none (n=68) | light (n=24) | intermediate (n=21) | thick (n=59) | $H$ value |
| **Storm-petrel activity/min** | | | | | |
| Flyovers | | | | | |
| $\bar{x}$ (sd) | 22.1(13.3) | 28.5(14.2) | 27.7(17.9) | 32.8(17.0) | 14.0 ** |
| Vocalizations | | | | | |
| $\bar{x}$ (sd) | 8.6(5.6) | 11.3(5.4) | 12.2(7.3) | 13.9(6.8) | 19.5 ** |

**Table 3-11:** Effects of moonlight on Leach's Storm-Petrel flyover rate and aerial vocalizations and call:flyover ratio over the reproductive season: $H$ = Kruskal-Wallis one way ANOVA; * = p < .05; ** = p < .01.

| | Moonlight periods (n = # of hrs) | | |
|---|---|---|---|
| | **Gull Island** | | |
| **Storm-petrel activity/min** | Moonlit (n=26) | Moonless (n=103) | $H$ value |
| Flyovers | | | |
| $\bar{x}$ (sd) | 17.4 (10.5) | 22.0 (13.3) | 2.9 |
| Vocalizations | | | |
| $\bar{x}$ (sd) | 8.0 (4.4) | 13.6 (9.7) | 7.5 ** |
| Calls:Flyovers | | | |
| $\bar{x}$ (sd) | 0.5 (.4) | 0.7 (.6) | 0.7 |
| | **Green Island** | | |
| | (n=45) | (n=125) | |
| Flyovers | | | |
| $\bar{x}$ (sd) | 23.2 (13.5) | 28.9 (16.6) | 3.5 |
| Vocalizations | | | |
| $\bar{x}$ (sd) | 7.4 (4.8) | 12.6 (6.6) | 20.6 ** |
| Calls:Flyovers | | | |
| $\bar{x}$ (sd) | 0.3 (.2) | 0.5 (.2) | 26.3 ** |

**Table 3-12:** Effects of cloud cover on Leach's Storm-Petrel aerial vocalization rate over the reproductive season (Gull Island): $H$ = Kruskal-Wallis one way ANOVA; * = $p < .05$; ** = $p < .01$.

| | Cloud cover (n = # of hrs) | | | | |
|---|---|---|---|---|---|
| | none (n=22) | light (n=27) | intermediate (n=12) | heavy (n=74) | $H$ value |
| **Storm-petrel activity/min** | | | | | |
| Flyovers | | | | | |
| $\bar{x}$ (sd) | 19.8(12.6) | 21.2(12.1) | 18.3(15.1) | 21.7(12.7) | 1.2 |
| Vocalizations | | | | | |
| $\bar{x}$ (sd) | 8.9(7.1) | 9.7(7.1) | 7.4(6.7) | 15.8(9.8) | 18.0 ** |

### 3.2.5. Activity at the Burrow

Activity at burrows with breeding Leach's Storm-Petrels on Gull Island varied considerably more with environmental condition than those on Green Island. On Gull Island over the reproductive season (n=108 hr), significantly fewer burrow lattices were broken when nocturnal illumination levels were high (Table 3-13). Fewer lattices were broken in moonlit periods, and although this was not statistically significant ($H$=3.3, df=1, p=.07).

During chick rearing on Gull Island (n=84 hr), significantly less activity at the burrow occurred during moonlit periods ($H$=6.5, df=1, p=.01). Fewer lattices were broken during periods of high nocturnal illumination, although this was nonsignificant. Activity at the burrow on Green Island during chick rearing was not significantly affected by any of the environmental variables measured.

**Table 3-13:** Effects of nocturnal illumination level on Leach's Storm-Petrel burrow activity (/hr) over the reproductive season (Gull Island): $H$ = Kruskal-Wallis one way ANOVA; * = $p < .05$; ** = $p < .01$.

| | Nocturnal illumination (n = # of hrs) | | | |
|---|---|---|---|---|
| | bright (n=20) | intermediate (n=26) | dark (n=62) | $H$ value |
| **% lattices broken** | | | | |
| $\bar{x}$ (sd) | 11.2(5.1) | 19.4(12.8) | 14.5(9.3) | 6.7 * |

## 3.3. Effects of Gulls on Leach's Storm-Petrel Activity

### 3.3.1. Flyover and Aerial Vocalization Activity

The presence of gulls exerted a strong influence on the colony activity of Leach's Storm-Petrels. Storm-petrel activity was significantly lower during periods of higher gull activity, and gull activity level was often a strong predictor of both storm-petrel flyover and aerial vocalization rate. Storm-petrel activity was consistently negatively correlated with nocturnal gull activity (Table 3-14).

On Gull Island, storm-petrel activity varied significantly with gull activity level over the reproductive season ($n=129$ hr), with fewer storm-petrel flyovers, vocalizations, and a lower call:flyover ratio when gull activity levels were high (Table 3-15).

Effects of gulls on Leach's Storm-Petrel activity levels at Green Island were documented on the few occasions that gulls were heard calling nearby, and throughout the model gull experiment. The few occasions that gulls were heard calling on Green Island ($n=16$) were significantly associated with lower Leach's Storm-Petrel flyover and vocalization rates over the entire season (Table 3-16), as well as during incubation (flyovers: $n=9$, $H=15.5$, $df=1$, $p<.0001$; vocalizations: $n=9$, $H=11.5$, $df=1$, $p=.0007$). During chick rearing, storm-petrels in flight called less when gulls were heard calling nearby, although this association was not statistically significant ($p=.06$).

**Table 3-14:** Spearman correlations between Leach's Storm-Petrel and gull nocturnal activity.

| | Storm-petrel activity (n = # of hrs) | |
|---|---|---|
| | **Gull Island** | |
| | Flyovers (n=135) | Vocalizations (n=135) |
| **Gull activity** | | |
| Flyovers (n=133) | -.57 (p<.0001) | -.65 (p<.0001) |
| Vocalizations (n=134) | -.47 (p<.0001) | -.63 (p<.0001) |
| | **Green Island** | |
| | (n=172) | (n=168) |
| Flyovers (n=165) | -.13 (p=.0973) | -.13 (p=.1059) |
| Vocalizations (n=164) | -.26 (p=.0008) | -.28 (p=.0004) |

Table 3-15: Effects of gull activity level on Leach's Storm-Petrel activity level over the reproductive season (Gull Island):
$H$ = Kruskal-Wallis one way ANOVA; * = $p < .05$; ** = $p < .01$.

| | Gull vocalization level (calls/min) | | | | |
|---|---|---|---|---|---|
| Storm-petrel activity/min | 0 (n=1) | 1-10 (n=98) | 11-20 (n=25) | > 21 (n=10) | $H$ value |
| Flyovers | | | | | |
| $\bar{x}$ (sd) | 35.8(0) | 24.9(10.7) | 10.0(10.4) | 8.5(13.3) | 38.4 ** |
| Vocalizations | | | | | |
| $\bar{x}$ (sd) | 33.0(0) | 15.5(8.2) | 4.7(5.6) | 1.8(3) | 9.5 ** |
| Calls:Flyovers | | | | | |
| $\bar{x}$ (sd) | 0.9(0) | 0.8(0.5) | 0.5(0.5) | 0.5(0.7) | 16.8 ** |

| | Gull flyover level (flyovers/min) | | | |
|---|---|---|---|---|
| Storm-petrel activity/min | 0 (n=70) | 1-10 (n=61) | 11-20 (n=2) | $H$ value |
| Flyovers | | | | |
| $\bar{x}$ (sd) | 26.6(9.9) | 15.2(12.8) | 0.9(1.3) | 29.9 ** |
| Vocalizations | | | | |
| $\bar{x}$ (sd) | 18.0(7.7) | 6.8(6.9) | 0.3(0.4) | 55.4 ** |
| Calls:Flyovers | | | | |
| $\bar{x}$ (sd) | 0.8(0.6) | 0.5(0.3) | 0.2(0.3) | 23.5 ** |

**Table 3-16:** Effects of gull vocalization level on Leach's Storm-Petrel activity level over the reproductive season (Green Island): $H$ = Kruskal-Wallis one way ANOVA; * = p < .05; ** = p < .01.

| | Gull vocalization level (calls/min) | | |
|---|---|---|---|
| | 0 (n=148) | 1-10 (n=16) | $H$ value |
| **Storm-petrel activity/min** | | | |
| Flyovers | | | |
| $\bar{x}$ (sd) | 29.6 (15.4) | 16.0 (13) | 13.1 ** |
| Calls | | | |
| $\bar{x}$ (sd) | 12.2 (6.3) | 6.3 (4.9) | 12.9 ** |

### 3.3.2. Activity at the Burrow

At Gull Island burrow activity was significantly reduced over the season when gull flyover activity was high (Table 3-17). During incubation, gull flyover activity was the only variable that affected activity at the burrow ($H$=6.2, df=2, p=.05). During chick rearing, burrow activity was lower when gull activity was high (gull flyovers: $H$=10.4, df=2, p=.02; gull vocalizations: $H$=6.5, df=3, p=.04).

At Green Island over the reproductive season and during incubation, activity at the burrow was significantly lower only on the few occasions that gulls were heard calling nearby (Table 3-18).

**Table 3-17:** Effects of gull flyover activity level on Leach's Storm-Petrel activity at the burrow (/hr) over the reproductive season (Gull Island): *H* = Kruskal-Wallis one way ANOVA; * = p < .05; ** = p < .01.

| | Gull flyover level (flyovers/min) | | | |
|---|---|---|---|---|
| | 0 (n=68) | 1-10 (n=42) | 11-20 (n=1) | *H* value |
| **% lattices broken/hr** | | | | |
| $\bar{x}$ (sd) | 17.0(10.7) | 12.2(7.4) | 0(-) | 8.8 ** |

**Table 3-18:** Effects of gull vocalization activity on Leach's Storm-Petrel activity at the burrow (/hr) (Green Island) over the entire reproductive season and during incubation only:
$H$ = Kruskal-Wallis one way ANOVA; * = p < .05; ** = p < .01.

| | Gull vocalization level (calls/min) | | |
|---|---|---|---|
| | **Reproductive Season** | | |
| | 0 (n=125) | 1-10 (n=11) | $H$ value |
| % lattices broken/hr | | | |
| $\bar{x}$ (sd) | 16.5(11.0) | 11.6(12.8) | 5.9 ** |
| | **Incubation** | | |
| | (n=50) | (n=6) | |
| $\bar{x}$ (sd) | 18.9(14.4) | 9.5(8.4) | 3.8 * |

### 3.3.3. Model Gull Experiment

Results of the model gull experiment on Green Island indicated that the presence of model gulls and vocalizations did not significantly affect FFO or FAC times. However, Leach's Storm-Petrel flyover rates during the first 60 - 90 min of activity were significantly lower when exposed to model gulls and gull vocalizations (Table 3-19). Not only were fewer storm-petrels seen at the colony in the 'gull' condition, but the ratio of calls:flyovers was significantly lower, indicating that those that were present were less vocal. Storm-petrel aerial vocalizations and call:flyover ratio were significantly lower in the 'gull' condition during the remainder of the night (Table 3-20).

Leach's Storm-Petrels were found to respond equally to the gull models plus taped vocalizations as to taped vocalizations only. Neither flyover rate, aerial vocalization rate, nor call:flyover ratio differed significantly between the two conditions.

Table 3-19: Model gull effects on Leach's Storm-Petrel flyover and vocalization levels, and call:flyover ratio during the first 60-90 min of storm-petrel activity (Green Island):
$H$ = Kruskal-Wallis one way ANOVA; * = p < .05; ** = p < .01.

| | Experimental condition (n = # of hrs) | | |
|---|---|---|---|
| Storm-petrel activity/min | Gull (n=20) | No gull (n=20) | $H$ value |
| Flyovers | | | |
| $\bar{x}$ (sd) | 9.7 (6.4) | 14.8 (5.7) | 7.29 ** |
| Vocalizations | | | |
| $\bar{x}$ (sd) | 2.2 (1.8) | 2.0 (1.7) | 0.11 |
| Calls:Flyovers | | | |
| $\bar{x}$ (sd) | 0.1 (0.1) | 0.3 (0.2) | 5.15 * |

**Table 3-20:** Model gull effects on Leach's Storm-Petrel flyover and vocalization levels and call:flyover ratio excluding first 60-90 min of activity (Green Island): $H$ = Kruskal-Wallis one way ANOVA; * = $p < .05$; ** = $p < .01$.

| | Experimental condition (n = # of hrs) | | |
|---|---|---|---|
| Storm-petrel activity/min | Gull (n=31) | No gull (n=47) | $H$ value |
| **Flyovers** | | | |
| $\bar{x}$ (sd) | 16.8 (7.7) | 17.4 (13.8) | 0.4 |
| **Vocalizations** | | | |
| $\bar{x}$ (sd) | 4.1 (2.4) | 6.5 (5.1) | 4.3 * |
| **Calls:Flyovers** | | | |
| $\bar{x}$ (sd) | 0.3 (0.2) | 0.4 (0.2) | 12.5 ** |

## 3.4. Summary of Environmental and Gull Activity Effects on Leach's Storm-Petrel Activity

Tables 3-21 and 3-22 provide a summary of the effects of environmental variables and gulls on Leach's Storm-Petrel activity at the colony. Possible environmental determinants of storm-petrel activity level measured were nocturnal illumination level, visibility level, moonlight, cloud, fog, wind speed, and gull activity level. Wind speed did not predict storm-petrel activity level except in a few instances in very high winds; storm-petrel activity was lower during these occasions. The presence of cloud or fog alone rarely had a significant influence on storm-petrel behaviour. Moonlight occasionally resulted in reduced storm-petrel activity. Not surprisingly, the most significant environmental effects on storm-petrel activity level were seen in those variables that are a composite of two or more environmental variables; such as nocturnal illumination and visibility levels. At Gull Island, gull activity had the most consistent effect on Leach's Storm-Petrel activity. Fig 3-4 shows the relationship between Leach's Storm-Petrels, gulls and nocturnal environmental condition at Gull Island. Gulls also had a strong effect on the activity of storm-petrels on Green Island, where gulls do not breed, but occasionally fly or call nearby. The results of the model gull experiment at this colony further illustrate the effects of gulls on the activity of Leach's Storm-Petrels. Fig 3-5 is an example of the relative importance of the environmental determinants of Leach's Storm-Petrel activity at each colony.

**Table 3-21:** Summary of effects of environmental variables on Leach's Storm-Petrel activity on Gull Island over the entire reproductive season, and during the separate periods of incubation and chick rearing. Double asterisks indicate significance $\leq .05$ (Kruskal-Wallis one way ANOVA).

| | GULL ISLAND | | | | | | |
|---|---|---|---|---|---|---|---|
| | NOCT ILLUM | VIS | MOON | FOG | CLOUD | GULL FLYS | GULL CALLS |
| **Flyovers** | | | | | | | |
| Entire season | ** | ** | -- | -- | -- | ** | ** |
| Incubation | ** | ** | | | | ** | ** |
| Chick rearing | -- | ** | -- | -- | -- | ** | ** |
| **Vocalizations** | | | | | | | |
| Entire season | ** | ** | ** | -- | ** | ** | ** |
| Incubation | ** | ** | -- | -- | -- | ** | ** |
| Chick rearing | -- | ** | -- | -- | -- | ** | ** |
| **Calls:Flyovers** | | | | | | | |
| Entire season | ** | ** | -- | -- | -- | ** | ** |
| Incubation | ** | ** | -- | -- | -- | ** | ** |
| Chick rearing | -- | -- | -- | -- | -- | -- | -- |
| **Burrow activity** | | | | | | | |
| Entire season | ** | -- | -- | -- | -- | ** | -- |
| Incubation | -- | -- | -- | -- | -- | ** | -- |
| Chick rearing | -- | -- | ** | -- | -- | ** | ** |

**Table 3-22:** Summary of effects of environmental variables on Leach's Storm-Petrel activity on Green Island over the entire reproductive season, and during the separate periods of incubation and chick rearing. Double asterisks indicate significance $\leq .05$ (Kruskal-Wallis one way ANOVA).

| | GREEN ISLAND | | | | | | |
|---|---|---|---|---|---|---|---|
| | NOCT ILLUM | VIS | MOON | FOG | CLOUD | GULL FLYS | GULL CALLS |
| **Flyovers** | | | | | | | |
| Entire season | -- | ** | -- | ** | -- | -- | ** |
| Incubation | -- | -- | -- | -- | -- | -- | ** |
| Chick rearing | ** | ** | ** | -- | -- | -- | -- |
| **Vocalizations** | | | | | | | |
| Entire season | ** | ** | ** | -- | -- | ** | ** |
| Incubation | ** | -- | -- | -- | -- | -- | ** |
| Chick rearing | ** | ** | ** | -- | -- | -- | -- |
| **Calls:Flyovers** | | | | | | | |
| Entire season | ** | ** | ** | -- | -- | -- | -- |
| Incubation | -- | -- | -- | -- | -- | -- | -- |
| Chick rearing | ** | ** | ** | -- | -- | -- | -- |
| **Burrow activity** | | | | | | | |
| Entire season | -- | -- | -- | -- | -- | -- | ** |
| Incubation | -- | -- | -- | -- | -- | -- | ** |
| Chick rearing | -- | -- | -- | -- | -- | -- | -- |

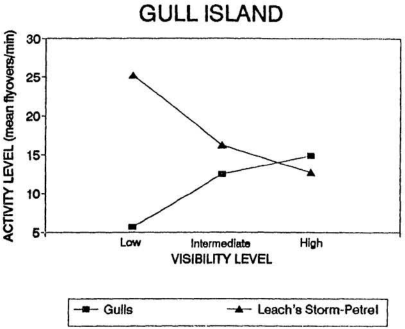
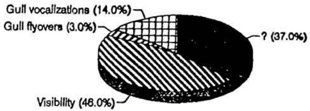



Figure 3-4: Gull and storm-petrel activity levels under various nocturnal visibility levels (Gull Island).

# Gull Island




# Green Island

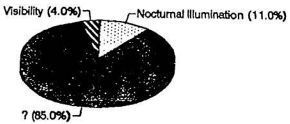



**Figure 3-5: Relative importance of effect of environmental variables on Leach's Storm-Petrel vocalization activity at Gull and Green Islands. Percentages indicate amount of variance in Leach's Storm-Petrel behaviour accounted for by the variable.**

### 3.5. Interfeed Interval

There was no overall difference between Gull and Green Islands in percentage of chicks fed either one or two times per night. On Gull Island, an average of 59% of the study chicks were fed at least once per night, and 27% were fed twice. Sample size at this colony ranged from 8-20 chicks over the study period. On Green Island, 58% were fed at least once, and 23% were fed twice per night; sample size here ranged from 21-30 chicks over the study period.

On a night by night basis, and when categorized by nocturnal illumination level, it was found that more chicks were fed both once and twice per night on Gull Island during dark nights compared to intermediate or bright nights (Fig 3-6). On Green Island, numbers of chicks fed either once or twice per night was not affected by nocturnal illumination level (Fig 3-6). Over the entire season, dark nights occurred only once every two days on average. Therefore, the interval between double feeds was, on average, longer on Gull than Green Island.

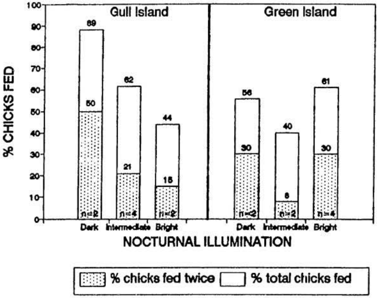



Figure 3-6: Nocturnal illumination level and percent of chicks fed at Gull and Green Islands. Hatched bars indicate double feeds.

### 3.6. Reproductive Chronology and Fledging Size

General data collection on reproductive parameters over the season indicated that the reproductive season on Gull Island was later than on Green Island. Three reproductive parameters support this suggestion:

a) Hatching date - On 16 July 1988, 60% of the study chicks (12/20) had hatched on Green Island, and by 21 July, 75% had hatched (15/20). On Gull Island however, only 63% had hatched by 01 Aug (19/30), and 77% by 6 Aug (23/30). Hatch rates were similar at the colonies, with an average of 3% of the monitored chicks hatching/day on both Green and Gull Islands. Using this hatch rate, dates can be established where the islands would be roughly equal in the percentage of chicks hatched. On 16 July (Green Island) and on 31 July (Gull Island), the colonies should have been equal had ~ 60% of the chicks hatched. The difference in days between these two estimates indicates that Gull Island was about 15 days later than Green Island.

b) Chick mass - Chicks averaged 31 g on 21 July (n=6) at Green Island and on 30 July (n=9) at Gull Island. This may indicate that chick growth was later on Gull Island, although sample sizes are very small. It does not appear however that chick growth rate is slower on Gull Island, as average mass increase/chick/day during this time was equal between the 2 colonies (Gull Island, 2.3 g $chick^{-1}$ $day^{-1}$; Green Island, 2.2 g $chick^{-1}$ $day^{-1}$.

c) Fledging date - On 17 Sept 24% of the chicks from the monitored burrows on Green Island had fledged, and by 26 Sept, 25% had fledged on Gull Island, indicating a span of approximately nine days between the two colonies at early fledging. In addition, while no very young chicks were found on Green Island, five chicks from the study burrows on Gull Island had only recently hatched. Peak fledging might be expected to be considerably later on Gull Island, and the fledging period would continue well into October at this colony.

In addition to the extended reproductive season, chicks on Gull Island were lighter and had shorter wing lengths at fledging than chicks from both Green Island (mass $H$=23.4, p<.0001; wing $H$=6.4, p=.01) and Middle Lawn Island (mass $H$=9.6, p=.002; wing $H$=5.5, p=.02) (Table 3-23). Green and Middle Lawn Island chicks did not differ in size. Although unable to test for statistical significance, fledging size at Great Island was smaller than at Gull Island, and Little Duck Island was intermediate between the Newfoundland colonies.

Table 3-23: Fledging mass and winglength of chicks from four Newfoundland colonies and one Maine colony. Asterisks indicate colonies for which data were contributed by R. Butler.

| Colony | Sample year(s) | n | Mass g(sd) | Winglength mm(sd) |
|---|---|---|---|---|
| Gull Island | 1988 | 43 | 63.0 (6.2) | 154.8 (5.2) |
| Green Island | 1988 | 38 | 67.9 (9.8) | 159.3 (6.1) |
| Middle Lawn Island | 1988 | 6 | 73.3 (3.1) | 160.3 (5.1) |
| Great Island * | 1982-84 | 494 | 58.7 (n/a) | 156.8 (n/a) |
| Little Duck Island * | 1988-89 | 73 | 65.4 (n/a) | 156.5 (n/a) |

# Chapter 4

# Discussion

The risk of predation is perhaps the most serious pressure an animal must contend with during its lifetime. If an animal has difficulty finding food or a mate, it will simply go hungry for the day, or fail to reproduce that season (Lima & Dill, 1990). If, however, the animal fails to detect a predator, or respond properly to it, the consequence may be death. Predation risk is often higher during the breeding season than at other times of the year because reproductive activities can put adults at additional risk, and predators are also feeding their young, as well as themselves. The colonial nature of seabirds puts them at further predation risk during the breeding season. A variety of species are often found at a colony, and both inter-specific (Buckley & Buckley, 1980) and intra-specific (Parsons, 1971) predation is common. Leach's Storm-Petrels, like other seabird species, frequently breed in mixed-species communities, and returning to the colony to breed places these birds in close proximity to predators at the colony. Most predators of these seabirds are diurnal, and the Leach's Storm-Petrel has adapted to this pressure by restricting its colony visitation to the night. Leach's Storm-Petrels are dark gray-brown in colour, which helps to camouflage them at the colony at night. On bright, moonlit nights however, their movement at the colony renders them quite conspicuous. As a consequence of this, individual storm-petrels have further adjusted their nocturnal behaviour at the colony to avoid predation.

Evidence of Leach's Storm-Petrel behaviour at the colony has indicated that colony visitation is later and is reduced in conditions of high nocturnal illumination (Watanuki, 1986; MacKinnon, 1988); The most apparent explanation for this is that gull predation risk is higher under these conditions. Higher nocturnal illumination levels would intuitively seem to be more conducive to diurnal gulls hunting Leach's Storm-Petrels, however this supposition has only been supported by anecdotal reports (Gross, 1935; MacKinnon, 1988). Also, whether the increase in predation is attributed to more gulls being active under these conditions, or whether those that are active are simply more successful, had not yet been addressed before this study. Watanuki (1986) quantified gull activity under different nocturnal illumination conditions but did not report whether predation level varied accordingly.

## 4.1. Nocturnal Activity of Gulls, Gull Predation, and Leach's Storm-Petrel Activity

The results of this study indicate that at a colony with breeding gulls and Leach's Storm-Petrels (Gull Island) gull activity is indeed higher under brighter nocturnal environmental conditions, and that predation on Leach's Storm-Petrels is also higher under these conditions. Increases in gull predation under bright nocturnal conditions were likely attributed to a combination of more gulls being active in bright conditions, as well as the individuals that are active having a greater hunting success. Much of the predation on Gull Island could be attributed to individual gulls specializing on Leach's Storm-Petrels. This was evidenced by increases in number of remains found around particular nests after a bright or moonlit night. Specialization among individuals of a population has been reported for fishes, amphibians, birds and mammals, and these differences may reflect corresponding individual variation in the perceptual abilities, search and capture techniques, foraging site, and feeding rhythm (Curio, 1976). Individuals in a population of gulls likely also vary in these qualities, enabling some individuals to specialize on the nocturnal seabirds. A number of gull species have been known to specialize on Leach's Storm-Petrels (e.g., Harris, 1965a; Parsons, 1971; Corkhill, 1973; Watanuki, 1986; Pierotti & Annett, 1991). While these specialists typically comprise only a small proportion of the total predator population, and are often specialists in the short-term because of a change in food abundance or type (Curio, 1976), they nevertheless pose a very real threat to individual Leach's Storm-Petrels and to their populations (Montevecchi & Tuck, 1987).

Moonlight appears to play an especially important role in the nocturnal hunting success of gulls. Significantly more Leach's Storm-Petrel remains were found following nights of moonlight than nights with no moonlight. Further, the number of hours of moonlight in a particular night was positively associated with number of storm-petrel remains found. More predation on Leach's Storm-Petrels occurred around the full moon phase compared to the period around the new moon, as Nelson (1988) found with the predation of Cassin's Auklets. Corkhill (1973) found that gull predation on Manx Shearwaters was higher during periods of moonlight, as well as during extremely dark nights.

Gulls appear to locate Leach's Storm-Petrels by audition (pers. obs.; Watanuki, 1989), waiting and listening in vegetation for a bird to land nearby, or emerge from a burrow. Nevertheless, a sufficient level of illumination would likely be necessary for the final moment of location and capture of the storm-petrel. Moonlight, along with providing a greater level of illumination overall, facilitates the location of prey because of the quality of light it provides. Moonlight is a direct source of light which can create shadows, and prey should be more easily detected when they cast shadows. A higher level of illumination alone would not provide this additional contrast cue for the predator. For a diurnal species, hunting at night poses the problem of avoiding collision with objects in its environment (vegetation, etc.). Higher levels of illumination, and direct moonlight in particular, better enable gulls to avoid these collisions. Presumably gulls are less active in levels of low nocturnal illumination to avoid collision, and also perhaps because hunting success is too low to be energetically profitable, due to increased capture time required in low light levels.

### 4.1.1. Leach's Storm-Petrel Behaviour on Arrival to the Colony (FFO, FAC)

The results of this study indicated that nocturnal predation pressure plays an important role in the Leach's Storm-Petrel behaviour on arrival at the colony. The absence of gull predation at Green Island provides an opportunity for comparison of behaviour of Leach's Storm-Petrels on arrival to the colony. Behaviour in the early evening indicated that, in general, while the birds arrived at the colonies at essentially the same time (FFO), the storm-petrels at Gull Island were quiet on arrival (FAC) for a longer period of time than those at Green Island. It is likely that light levels must go below a certain threshold before the storm-petrel will vocalize, presumably because predation risk is somewhat reduced as light levels decrease. On Gull Island, light levels may need to be lower than on Green Island, and hence the storm-petrels wait until additional time has elapsed after sunset. The difference between colonies is further apparent when activity is measured in similar habitats. Green Island is treeless, and hence measurements were taken in an open habitat. Gull Island has both wooded and open areas. Most data were collected at the edge of a wooded area, however a small number of first air call (FAC) measurements were made in a nearby open area. In this open area, time of FAC was later than at the edge of the wood on the same evenings. This suggests that cover afforded by vegetation affects the storm-petrel's decision to begin to vocalize at the colony. Had the two observation sites been more equivalent (both open or wooded), first flyover (FFO) at Gull Island would have likely also been later at this colony than at Green Island. Preliminary data collected at Great Island in 1987 (an island with gulls) in open habitat indicated that FFO was indeed significantly later than on Green Island in the same year.

Leach's Storm-Petrel FFO and FAC times varied with evening environmental condition at both colonies over the reproductive season. FFO and FAC were later on clear, bright evenings at both colonies, although the birds at Green Island appeared to be more strongly affected than at Gull Island. This difference between the colonies is contrary to what was initially expected; if any difference was detected, it was expected that Leach's Storm-Petrels on Gull Island would be more sensitive to environmental condition in the early evening, because of the risk of predation at that time.

The difference may instead be explained by the actual presence and activity levels of the gulls on Gull Island in the early evening. Evening environmental condition may factor into the storm-petrel's decision to come to the vicinity of the colony, but once there, the bird likely makes the decision to land and vocalize at the colony based on the perceived risk of predation (influenced by the activity level of the gulls), thereby masking the effects of environmental condition. Gull activity is of obvious greater importance in predation risk assessment than overall evening illumination level. The behaviour of the storm-petrels on Green Island may therefore be most influenced by general environmental conditions, while those birds on Gull Island are instead influenced firstly by gull presence, and then by general environmental conditions. Presumably, gull activity must be below a certain threshold before storm-petrels will land at the colony. Unfortunately, gull activity level was not measured in this study until Leach's Storm-Petrel activity had begun each evening, so this threshold was not quantified. As a subjective indication however, part of the observer's decision to begin the nightly observation session was based on the general activity of the gulls declining, i.e., when gull vocalizations began to decrease, the observers readied themselves to begin the session in anticipation of Leach's Storm-Petrel activity commencing.

The presence of model gulls and gull vocalizations on Green Island did not affect FFO or FAC times, although the number of evenings of observation in each condition are small, and only two or three of each of bright, intermediate, and dark nights occurred.

### 4.1.2. Leach's Storm-Petrel Activity Once at the Colony

#### 4.1.2.1. Nocturnal Environmental Condition

Once at the colony, Leach's Storm-Petrels behaved quite similarly under a variety of nocturnal environmental conditions at Gull and Green Islands, although the storm-petrels at Green Island were apparantly less affected by nocturnal environmental condition. In general, Leach's Storm-Petrel activity at both colonies tended to be lowest during those nocturnal environmental conditions under which gulls were most likely to be active and hence most conducive to gulls hunting.

Other research has indicated that individual environmental variables (cloud, fog, moonlight, wind) can affect nocturnal activity at the colony (Furness & Baillie, 1981; Watanuki, 1986; MacKinnon, 1988; Bretagnolle, 1990; Jones *et al.*, 1990). In this study, individual variables in themselves very rarely influenced storm-petrel activity, at either colony. Cloud was more common than fog at Gull Island, however it only affected storm-petrel vocalizations, and only when data collected during incubation and chick rearing were combined. On the other hand, fog was more common at Green Island, however it only affected flyovers, and, like Gull Island, only when data collected during incubation and chick rearing were combined. Wind did not affect Leach's Storm-Petrel activity in any predictable fashion at either colony, except during stormy conditions with high winds. These conditions were associated with low activity. Although activity immediately decreased or increased with the appearance or disappearance of the moon at both colonies, effects of moonlight on storm-petrel activity were more frequently seen at Green Island than at Gull Island. This may be attributed to the fact that a large number of bright, moonlit nights occurred at Green Island during the chick rearing sampling period, while only a few of these nights occurred at Gull Island throughout the entire sampling period. Even though moonlight was relatively infrequent at Gull Island, when it was present, storm-petrel activity was reduced. This is likely because of the greatly increased risk of predation during moonlit periods, as discussed above.

Overall nocturnal illumination and visibility levels often affected storm-petrel activity, and especially vocalization activity at Gull Island. Storm-petrel activity was lower under higher visibility levels. Peak of flyover activity was 2.5 hr later on Gull Island under conditions of bright nocturnal illumination, compared to intermediate or dark nights. Because visibility is a composite of a number of variables that affect illumination, overall visibility level likely represents a more reliable indication of environmental condition with regard to predation risk. Hence it is not surprising that this composite variable played a larger role than individual environmental variables alone. Composite variables (such as nocturnal illumination and visibility level) may therefore be a better type of variable (in terms of significance to the animal) to choose in future studies of nocturnal seabirds. Storey and Grimmer (1986) used a similar composite variable with Manx Shearwaters. Leach's Storm-Petrel activity at Green Island was also more affected by the composite variables (nocturnal illumination, visibility) than the individual variables, although to a lesser degree than at Gull Island. Fewer storm-petrel behaviours were affected by these composite variables overall at Green Island. Peak of flyover activity at this colony was also later under bright nocturnal conditions, although not significantly so.

#### 4.1.2.2. Gull Activity

Bright conditions and gull activity are clearly associated and will likely be assessed in conjunction with one another by the storm-petrel when making decisions about activity once at the colony (i.e., after the decision to land has been made). The results of this study indicated that nocturnal predation pressure plays an important role in the shaping of Leach's Storm-Petrel's activity patterns at the colony. Gull activity level had the most consistant influence on storm-petrel activity at Gull Island. Significant associations of lower storm-petrel behaviour with higher gull activity levels were common across behaviours, and reproductive phases. These results are consistant with what Watanuki (1986) found with Leach's Storm-Petrels in Japan.

The later peak in flyover activity in bright nocturnal conditions at Gull Island suggests that the storm-petrels at this colony may wait offshore for a window of opportunity until it is safer to return to the colony. The immediate and rapid increase in storm-petrel activity when the moon was obscured by cloud or fog further supports this notion. Gull nocturnal activity patterns tend to be bimodal (Galusha & Amlander, 1978), so gulls may be less active on average in the middle portion of the night, regardless of nocturnal illumination levels. Therefore, Leach's Storm-Petrels may remain just slightly offshore, assessing the level of gull activity (using visual and auditory cues), and coming to the colony when relative safety has been established.

The reduction of flyover and vocalization activity in higher nocturnal illumination, visibility and gull activity levels at Gull Island may be explained by fewer birds actually coming to the colony in brighter nocturnal conditions when gulls are active. The reduction in call:flyover ratio in these conditions on Gull Island indicates however that the birds that did return to the colony were quieter in brighter nocturnal conditions when gulls were active. This suggests that estimates of the numbers of birds present at the colony (flyovers, vocalizations) under various nocturnal conditions reflect gross behaviour of the birds, and that a finer measure of risk assessment by Leach's Storm-Petrels is call:flyover ratio. Because gulls often hunt by audition, refraining from vocalizing represents a sort of auditory camouflage, and indicates that Leach's Storm-Petrels assessed their predation risk, and adjusted their behaviour accordingly. This is further supported by the result that storm-petrels vocalized significantly less during bright periods in the open area compared to the wooded area on Gull Island. Again, it appears that the storm-petrels are assessing the risk of predation at this colony and adjusting their behaviour to account for the risk. Storey and Grimmer (1986) also found that Manx Shearwaters reduced their conspicuousness by reducing vocalizations on bright nights at a colony with gulls.

There is likely some trade-off for remaining offshore for longer periods of time, or for being quiet at the colony to avoid predation. Because of the risk imposed by predation and short nightime hours, especially early in the season, the window of opportunity for colony activity is a narrow one. Vocalizations may play an important role early in the reproductive season in courtship and mate selection, and during incubation (through communication with the mate) in finding the burrow. Vocalizations are of great importance to Leach's Storm-Petrels (Taoka et al., 1989) and Manx Shearwaters (Brooke, 1978; Storey, 1984) in mate attraction and recognition. By not vocalizing, the individual may take longer to secure a mate, or in finding that mate to switch incubation duties. Although not yet known, chicks may peep in response to their parent's vocalizations. This peeping may also help guide the parent to the burrow, and, if so, would also be hindered by the parent remaining quiet. These trade-offs however are quite small when compared to the increased risk of predation by being vocal.

The results from Green Island indicate that Leach's Storm-Petrel activity was quite strongly affected by gull activity, even though gulls do not breed at the colony. Gulls only flew by or called infrequently, however storm-petrel flyover and vocalization activity was reduced during these occasions; especially when gulls vocalized. Call:flyover ratios were not reduced on the few occasions when gulls were present. This result was surprising given the overall response of flyovers and vocalizations alone to gull presence, and the response of call:flyover ratio to other environmental conditions. Call:flyover ratios were however reduced during exposure to the model gulls and vocalizations. The presence of the model gulls and vocalizations may have been perceived as a real threat by the storm-petrels, and they responded by being less vocal. Flyovers were not reduced in the 'gull' condition, except during the first 60 - 90 min of the night. During these higher light levels, the model gulls would be more easily seen and the storm-petrels may have avoided the area with the model gulls, or not come to the colony at all. Once light levels decreased however, the storm-petrels may have come to the colony, but reduced their vocalizations, creating the auditory camouflage discussed above. Gull vocalizations alone were sufficient to elicit a response in the storm-petrels: when the tapes were played, but the model gulls covered, storm-petrel activity was still reduced. These results suggest that Leach's Storm-Petrels are responsive to auditory cues at the colony, perhaps because auditory cues are more reliable (i.e., can still be detected) in fog or darkness. This is supported by Taoka *et al.*, (1989), who suggested that vocalizations are so important to Leach's Storm-Petrels in mate attraction and recognition, because visual stimuli are not available to these birds at the colony at night.

The overall differences in activity between the colonies under different nocturnal conditions may exist because of an increased sensitivity to nocturnal environmental condition at Gull Island, perhaps because of the heightened awareness created by the presence of gulls and the associated risk of predation at this colony. Differences in Leach's Storm-Petrel population sizes at the colonies may also play a role. Gull Island has a much larger storm-petrel population than Green Island (530,000 and 72,000 pairs, respectively). Social stimulation and information transfer may therfore be greater and/or more efficient at Gull Island. During increased nocturnal illumination, storm-petrels are less active. At Gull Island, many more individuals are present, and the reduction in activity, especially vocal activity, may be more apparent to individual Leach's Storm-Petrels than at Green Island. In addition, there are more individuals at Gull Island to transfer information about the perceived risk of predation to other individuals, and this may contribute to accentuating the overall response seen at the colony.

Similarities between the colonies, on the other hand, are likely due to the importance of the risk of predation to an individual. Predation is an 'all or nothing' type of pressure. If an animal fails to avoid predation, all chances for future feeding or reproductive success die with it. As a result, predation has had important influences on most, if not all, aspects of animal behaviour (Lima & Dill, 1991). In addition, Leach's Storm-Petrels may show a tendency toward a low degree of natal philopatry (Huntington, 1963; Podolsky & Kress, 1989). It is assumed that those individuals that possess adaptations to deal with predators at the colony would be most likely to reproduce.

Thus, a low level of natal philopatry could lead to similar anti-predator behaviour patterns among colonies, regardless of gull presence. Even if philopatry were high in Leach's Storm-Petrels, gulls may have nested at Green Island in the past (before lighthouse keepers and their dogs were present), and adaptations needed to avoid nocturnal predation by gulls would not likely be selected out of the population, even after long periods of gull absence. Regardless of gull presence directly at the colony, the storm-petrels in this study at Green Island would likely have had some experience with gulls, as gulls nest nearby and were very occasionally present at the colony at night.

## 4.2. Leach's Storm-Petrel Activity Around the Lunar Phase

Lunar phase did not predict Leach's Storm-Petrel activity at either colony. Unlike what Watanuki (1986) and MacKinnon (1988) found, there was no suggestion of a synchronization of activity around any lunar phase. Instead, the storm-petrels appeared to be responsive to the proximate environmental situation with which they were faced. This would seemingly be a better strategy for the bird to use, especially off the coast of Newfoundland where fog and cloud frequently obscure the moon. To organize colony activity around lunar phase, and avoid the colony, on the basis that nocturnal illumination may be high at the colony under the partial or full moon, would greatly reduce the available time for the bird to fulfill reproductive duties. A large portion of Leach's Storm-Petrel diet are bioluminescent and vertically migrating species (Linton, 1978; Montevecchi *et al.*, 1992). In moonlit conditions, these species may not come as close to the surface of the water, and feeding may be more difficult (Imber, 1975). Moonlight offshore may therefore ultimately influence the decision to return to the colony. The finding that peak of flyover activity was later in bright nights may relate to the increased length of time required for the storm-petrel to procure food. It is possible then that colony return may show some correlation with lunar phase, perhaps with predictable lags between lunar phase and colony return. Although an interesting question, this was not addressed in the present study and remains a point for future research to consider.

## 4.3. Behaviour of Breeding Leach's Storm-Petrels

### 4.3.1. Activity at the Burrow

A decision not to return to the colony clearly works as an anti-predator strategy, although it is not without implications to the individual bird, especially if it is breeding. By not returning to the colony, the mate may be required to remain in the burrow for a longer period of time, or the chick may go without food. Individual Leach's Storm-Petrels have been known to incubate for up to five days (Gross, 1935), and (Ricklefs *et al.*, 1985) reported that chicks unfed for up to seven days apparently suffer no ill effect. The age or fat reserves of these chicks was not indicated however, and it is possible that a young chick might not have the fat reserves to sustain itself for that period of time. At some point the breeding adult may have to take additional risks if its chick is to survive.

In this study, activity at the burrow was used to measure breeding bird activity; all other measurements include both breeding and nonbreeding birds. At Gull Island, burrow activity was apparently less affected by nocturnal environmental condition than were the other activitieies monitored. Nocturnal illumination level, moonlight and nocturnal gull activity level resulted in a lower burrow activity, although not to the extent that the other behaviours were affected. These results are consistent with suggestions made from other research on nocturnal seabirds (Scott, 1970; Watanuki, 1986; MacKinnon, 1988), and indicate that breeding birds may indeed take additional risk because of reproductive responsibilities, or that breeders have more experience than nonbreeders, and have better learned how to avoid predators. While breeders may not have avoided the colony altogether, they may have indeed been more careful, perhaps by remaining offshore until relatively safe to land. If this were the case, it may account for the 2.5 hr delay in activity peak in bright conditions at Gull Island. Breeding Leach's Storm-Petrels at Green Island were less influenced by environmental condition at the colony. Burrow activity over the season was only reduced during the occasions when gulls were heard calling nearby, but never in any other environmental condition. This indicates that breeding storm-petrel behaviour on Green Island was relatively robust to nocturnal environmental condition, but that special attention was paid to gulls, an indication that the breeders were quite directly assessing risk of predation.

### 4.3.2. Behavioural Differences During Incubation and Chick Rearing

Studies have indicated that breeding storm-petrels are most sensitive to nocturnal environmental condition during incubation. Breeding British (Scott, 1970) and Leach's (Watanuki, 1986; MacKinnon, 1988) Storm-Petrels have been found to have activity correlated with lunar phase during incubation. The explanation most frequently provided for this is that reproductive responsibilities during chick rearing are greater than during incubation (because chicks require more attention than eggs, and incubating adults can go without food for longer periods than can chicks), and that the level of parental investment increases as the season progresses (e.g., Carlisle, 1982). It has been suggested that both of these factors act to put additional pressure on the parent, and their likelihood of risk taking behaviour increases accordingly. Another explanation may come from the actual risk of predation associated with each of the reproductive phases. Watanuki (1986) found that predation was higher during the early part of the season, and Pierotti and Annett (1991) found that gulls that specialized on Leach's Storm-Petrels reduced their predation on the storm-petrels by switching to capelin, once gull chicks had hatched. These pieces of information suggest that the risk of predation by gulls to Leach's Storm-Petrels becomes smaller over the reproductive season, and that breeding birds, by being sensitive to environmental condition early in the season, are responding to the actual risk.

Because Pierotti and Annett (1991) obtained their data from Great Island, only a short distance from Gull Island, predation risk over the season was expected to vary similarly at Gull Island. The results obtained in this study were contrary to this expectation, however: gulls had a greater level of activity during chick rearing, although predation was equivalent during incubation and chick rearing. Burrow activity was less affected by environmental condition during incubation than during chick rearing. These results are possibly due to the full moon and chick rearing sampling periods coinciding. Gull activity and gull predation are both higher under conditions of bright nocturnal illumination and the full moon clearly contributes to nocturnal illumination, increasing the likelihood of predation. Entering and exiting the burrow is especially risky for the storm-petrel, given that gulls often wait just outside the burrow entrance for Leach's Storm-Petrels. If Leach's Storm-Petrels are responding to the actual level of predation risk, then breeders would respond to this increased risk by reducing activity, no matter where in the breeding season this risk occurred. It is also possible that the individuals that specialized on Leach's Storm-Petrels on Gull Island continued to do so into and beyond their own chick rearing period. Specialization may also be influenced by prey availability (Pierotti & Annett, 1991). The Leach's Storm-Petrel population on Gull Island is estimated to be more than double that of Great Island, but the gull population is only approximately 25% greater, hence storm-petrels may also be more available to individual gulls at Gull Island than at Great Island.

Leach's Storm-Petrel flyovers and vocalizations at Gull Island were significantly affected by nocturnal environmental condition and gull activity during both incubation and chick rearing, but call:flyover ratio was affected only during incubation. While the reasons for this are not entirely clear, it is known that nonbreeding storm-petrels are often most numerous at the colony during the early part of the season (Furness & Baillie, 1981; Simons, 1981), and it has been suggested that nonbreeding birds are in general more sensitive to nocturnal environmental condition (Scott, 1970; Manuwal, 1974; Imber, 1975; Watanuki, 1986; Storey & Grimmer, 1986; MacKinnon, 1988; Bretagnolle, 1990; Jones *et al.*, 1990).

Because nonbreeders do not have the pressures associated with nest duties, the threat of predation may act to shape their activity patterns to a larger degree than for breeders. Nonbreeders may also lack the experience necessary to fully assess predation risk, and some research has indicated that nonbreeders and young birds are likely killed more often than breeding birds (see Corkill, 1973; Lima & Dill, 1990). In addition, nonbreeders may not have burrows in which to escape if the nocturnal illumination level suddenly increases or if dawn approaches. As a result of these considerations, nonbreeders may be more cautious in their nocturnal activity. In this study, measurements of general Leach's Storm-Petrel activity were made of both breeding and nonbreeding birds, and the results may mainly be a reflection of the activities of the nonbreeders.

Another explanation for why call:flyover ratio was lower only during incubation at Gull Island may come from differences in the actual level of predation risk during the two reproductive periods. Unfortunately, the sampling periods for incubation and chick rearing are not directly comparable. As noted above, the incubation sampling period fell during a new moon (i.e., the dark phase), and the chick rearing sampling period occurred during a full moon. In this study, predation was found to be higher in moonlit conditions. Predation was similar during incubation and chick rearing periods, but because predation is higher in moonlight, had sampling during incubation been done during a full moon, predation would likely have been even greater than during chick rearing.

At Green Island, Leach's Storm-Petrel activity was rarely influenced by environmental condition during incubation. When it was, it was typically only during those occasions when gulls were present. Activity was instead influenced by nocturnal environmental condition at this colony during chick rearing. Most of the bright, moonlit nights at this colony occured during the chick rearing period, and this may account for the influences on behaviour.

### 4.3.3. Interfeed Interval, Reproductive Chronology, and Fledging Size

Nocturnal illumination levels clearly affected the percentage of chicks fed in total and twice per night on Gull Island. Significantly more chicks were fed during dark nights, fewer in intermediate conditions, and fewest in bright conditions. Nocturnal illumination did not influence chick feeds on Green Island. This difference between the colonies is likely the result of increased predation pressure during bright nights on Gull Island. Breeding Leach's Storm-Petrels on Gull Island appeared to attempt to make up for the lost feeding time during bright and intermediate nights by greatly increasing feeding rate during dark nights. Percentage of chicks fed in total on dark nights was twice that on bright nights, and double feeds were three times more frequent during dark compared to bright nights. This strategy appeared to be somewhat successful, as feeding rate when averaged overall was similar between Gull and Green Islands and chicks gained an equal amount of mass per day at the two colonies, at least early in the season (although sample sizes were small). The overall percentages of chicks fed per night found in this study were similar to what Ricklefs *et al.* (1985) found at Kent Island, New Brunswick, although they found that nocturnal environmental condition affected the probability of a chick being fed in only one of two study years.

At fledging, chick mass was significantly smaller at Gull Island than at Green Island. This suggests that the strategy of increasing feeding rate during dark nights was not sufficient to counter the effects that the gulls had on storm-petrel parental behaviour at Gull Island. This may be explained by the result that chicks from the study burrows on Gull Island hatched and fledged later than those on Green Island; reproductive chronology at Gull Island appeared to be behind Green Island by about two weeks. Fledging at a lighter mass may represent a balance between optimal fledging mass and date: it may be more beneficial for the chick to fledge smaller than to fledge too late in the season. Perrins (1970) and Watanuki (1982), among others, found that survival of late chicks was less than for earlier ones.

Reproductive chronology at Gull Island may have lagged behind Green Island because of interference in pair synchrony caused by gulls. Interference in pair synchrony may have resulted in poorly organized activity between the parents, and the egg may have been left unattended more frequently, causing chilling and delayed development. In some species pair synchrony affects breeding success (Simons, 1981; Koenig, 1982; Pietz, 1986). Egg neglect in procellariiforms is well documented and has been found to delay embryo development (Wilbur, 1969; Boersma & Wheelwright, 1979, and references therein). Hence, laying dates for each colony may have actually been the same, but because of gull interference, incubation may have been extended. It is also possible that egg laying was actually later at Gull Island, and the later reproductive chronology may have begun from the season's onset. Gull Island is further north, and due to ice on the water, ambient air and water temperatures remain cool later into the season. Burrows on Gull Island may have remained snowed over or frozen (compounded by the fact that most burrows are in the forest, and sunshine would not reach them as readily), and hence not become accessible to the storm-petrels until later, resulting in delayed egg laying. A third possibility for delayed fledging at Gull Island has been suggested by Ainley *et al.*(1975): that the birds delay nesting (and hence delay the entire reproductive season) to reduce the likelihood of predation on newly fledged chicks. At colonies with gulls, the number of gulls reduces as the season progresses. As long as there is not too great a cost to delaying fledging, avoiding gull predation by fledging later would greatly enhance the reproductive success of an individual.

Evidence has suggested that in some seabird species colony size and fledging weight are inversely related (Gaston *et al.*, 1983; Birkhead & Nettleship, 1981; Hunt *et al.*, 1986). The explanation provided for this is that competition or interference at the feeding grounds results in less food being available to each individual (Furness & Birkhead, 1984). In addition, egg neglect may increase due to a need to increase foraging time or distance. This study provided an opportunity to indirectly explore the colony size/fledging weight hypothesis with Leach's Storm-Petrels. The storm-petrel population at Gull Island is estimated to be 530,000 pairs while the Green Island population is only about 72,000 pairs (Cairns *et al.*, 1989). Additional data (see Methods) were collected at Middle Lawn Island, Newfoundland (26,313 pairs), and contributed by R. Butler for Great Island, Newfoundland (250,000 pairs) and Little Duck Island, Maine (4,200 pairs). All colonies but Green Island had populations of breeding gulls.

Of the four Newfoundland colonies, fledging mass was significantly larger at the two smallest colonies. Gull population size at these colonies confounds interpretation of these results, however. The smallest Newfoundland colonies also have the smallest numbers of breeding gulls (Green Island - 0; Middle Lawn Island Island - 26 pairs). Additional problems exist because the sample size at Middle Lawn was very small, and the data from Great Island and Little Duck Island were collected by another researcher, thus the potential exists for different measurement techniques. The Maine colony, while being the smallest, nevertheless had a mean fledging mass and winglength that was intermediate between the large and small Newfoundland colonies. This may be because Maine is at the lower edge of the Leach's Storm-Petrel breeding range, and breeding habitat (i.e., food) might be expected to be of a lower quality. It is also noteworthy that this colony proportionally had the largest population of gulls, yet it still had a larger fledging mass than either of the large Newfoundland colonies. These data are suggestive of the importance of colony size to Leach's Storm-Petrel fledging size, and provide an initial point for research on this question in this species.

## 4.4. Summary: Factors Contributing to Leach's Storm-Petrel Colony Visitation

The results of this study indicate that many factors contribute to the ultimate decision that an individual Leach's Storm-Petrel makes to return to and land at the colony. Fig 4-1 is a schematic representation of some of these effects and the points at which they may influence this decision. These influences pertain to both breeding and nonbreeding Leach's Storm-Petrels, except where obviously related only to breeding birds. A number of these influences have been addressed in some detail in this study, others are only touched on and are interesting questions for future research.

*Offshore influences* are those that affect food availability and the energy expended to obtain that food. Weather conditions, moonlight and tides influence food availability by affecting sea surface state, upwelling and the probability that food will be near to the surface. Foraging interference or competition (perhaps influenced by colony size) may also affect foraging success. If the individual does not succeed in obtaining enough food to sustain itself (and its chick) that individual will likely decide to remain offshore until it does so. If, however, the individual does obtain enough food, it may decide to return to the vicinity of the colony. *Underlying influences* such as reproductive phase (and associated parental committment), state of the chick, and the predator swamping benefits associated with the underlying 2 - 4 day cycle may contribute to this decision. The decision to actually land at the colony may then be affected by proximate *colony influences* such as the presence and activity of gulls and whether they are likely to be hunting Leach's Storm-Petrels (seasonal specialization), and overall visibility or nocturnal illumination level. Gulls appear to have the strongest influence on this decision to land, overall visibility or nocturnal illumination level are secondary. Vegetative cover also appears to play a role in Leach's Storm-Petrel vocalization activity. Individual environmental variables such as lunar phase, moonlight, cloud or fog alone have the least influence. The decision to land at the colony may ultimately have implications for reproduction insofar as reproductive chronology and chick mass at fledging may be influenced by predation risk by gulls and the size of Leach's Storm-Petrel colonies.

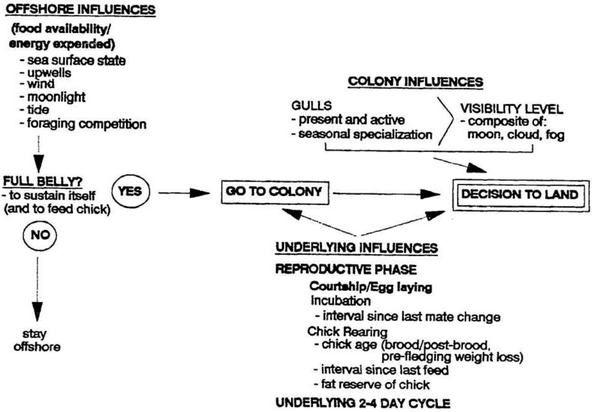



Figure 4-1: Influences on colony visitation by Leach's Storm-Petrels

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