HABITAT UTILIZATION AND BREEDING SUCCESS OF LEACH'S STORM-PETREL, Oceanodroma leucorhoa

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HABITAT UTILIZATION AND BREEDING SUCCESS OF LEACH'S STORM-PETREL, *Oceanodroma leucorhoa*.

by

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ABSTRACT

It is generally assumed that individual organisms behave optimally. In terms of habitat utilization, the optimal habitat for any species is that which provides the optimum conditions for survival and reproduction.

This study compared how Leach's Storm-Petrels, *Oceanodroma leucorhoa*, utilized forest and open habitat on Great Island, Newfoundland. Specifically, nesting habitats were compared in terms of slope, aspect, and peat compaction. The adaptive significance of habitat utilization was assessed through comparisons of burrow density, the proportions of active and occupied burrows, hatching success, chick growth, breeding success and predation risk.

Forest and open habitats differed; open habitat had steeper slope and more compact soil than forest, which had deeper peat. Burrow density and activity were greater in forest than open habitat, indicating that Leach's Storm-Petrels actively selected forest over open habitat. Clearly, based on area, forest habitat supported a greater number of breeding pairs. Moreover, birds nesting in forest exhibited greater hatching and breeding success than birds nesting in open habitat, thus storm-petrels nesting in forest were disproportionately more productive than storm-petrels nesting in open habitat.

Avian predation of Leach's Storm-Petrels did not differ between forest and open habitats, but varied seasonally in both. Predation was much reduced in both habitats following the inshore movement of spawning Capelin, *Mallotus villosis*.

The terrestrial flora of the habitats utilized by Leach's Storm-Petrels change over time, being influenced by other seabirds (e.g. gulls and puffins on Great Island). Forest habitat is estimated to have decreased by 17 % on Great Island over the past 25 years. Open habitat has been expanding, which will negatively affect the overall productivity of the Leach's Storm-Petrel colony. Generalizations to other Leach's Storm-Petrel colonies in the northwest Atlantic are also made.

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Chapter 1

INTRODUCTION

1.1. Habitat utilization

Habitat utilization is a universal activity in animals. Most of the advances in habitat utilization theory have been derived from studies of avian biology, from Darwin (1872) to the present (Block & Brennan 1993). Habitat utilization could be defined simply as the use of one habitat over another or others. However, the word 'habitat' in itself is somewhat ambiguous, and requires clear definition. The term habitat is used here to describe a combination of physical and biotic characteristics which constitute the environment in which an individual lives. In this context then, climate, topography, substrate, food resources, nesting sites, and social interactions are all considered important elements of habitat (see Cody 1985).

Lack (1944, 1949) provided one of the earliest and most clearly worded views on habitat utilization. He concluded that the choice of habitat is adaptive and "released" by specific characters of the habitat. Lack (1937) also considered that "psychological factors" played an important role in habitat utilization.

Habitat utilization is influenced by ultimate and proximate factors (Hildén 1965). Ultimate factors are environmental components deemed essential in survival and reproductive success, while proximate factors are environmental stimuli that influence settling behaviour (Orians 1971). Ultimate factors include the availability of, or proximity to, food, shelter from predators and adverse conditions, requirements imposed by structural and functional characteristics of the species. Proximate factors are more difficult to determine, but are likely to include features of landscape, aspect, terrain, vegetation structure, presence of suitable nest sites, and the presence or absence of conspecifics and other species. Proximate factors will be highly influenced by an animal's sensory capacity to perceive its environment (Montevecchi 1998). What may appear to the human observer to be a homogeneous environment may be perceived by another organism as a complex mosaic with distinct boundaries (Klopfer & Hailman 1965). This may be due entirely to the scale of environmental features considered (Orians & Wittenberger 1991). Investigation of macro-habitat features may easily overlook utilization based on features at the micro-habitat level, and vice versa.

The majority of the individuals in a species are expected to utilize habitat which provides the optimum conditions for survival and reproduction (Buckley & Buckley 1980). Ultimately, the utilization of a particular habitat by an individual will be the outcome of a fine balance between the costs and benefits of utilizing that habitat.

1.2. Nest-site utilization

1.2.1. Social interactions

Sociality is widespread among birds and has been considered to regulate the habitat utilization of most species (Hildén 1965). Social stimulation may contribute to the onset/development of breeding condition as well as the timing and success of breeding. The social attractiveness of the sight and sound of conspecifics has long been recognized as an important factor in nest-site utilization and breeding synchrony in colonial nesters (Darling 1938). Synchronized production of young may enhance breeding success by reducing the period over which vulnerable adults or chicks are available to predators (Darling 1938). Social attraction is also considered an important mechanism in the recruitment of young birds to colonies (Gochfeld 1980).

However, colonial nesting and variation in habitat quality will lead to intra-specific competition for access to the best habitat (Partridge 1978). The intensity of intra-specific competition will be driven by the scarcity of critical resources. Experienced birds often gain access to the best habitat, while inexperienced birds are forced to utilize sub-optimal habitat (Hildén 1965). Intra-specific competition may then broaden the range of habitats utilized by a species, or increase the proportion of non-breeders in the population.

In seabirds, there appears to be little in the way of inter-specific interactions. This is due to the development of a clear breeding habitat partitioning (Nelson 1980), which may reflect historical competition between seabird species. However, inter-specific competition for nest-sites may occur between similarly-sized burrow/crevice-nesting seabird species.

Breeding close to neighbours may also be disadvantageous through an increase in the extent of physical interference and disturbance between conspecifics. In some species, particularly the gulls (*Laridae*), increasing density may increase the likelihood of misdirected parental care or infanticide due to territorial disputes or cannibalism (Hunt & Hunt 1976).

1.2.2. Predation

Colonial nesting provides greater predator defence through increased vigilance, as well as predator mobbing and swamping opportunities (Kruuk 1964, Lack 1968, Wittenberger & Hunt 1985). Large colonies have been shown to suffer lower rates of predation than smaller colonies, and it has been proposed that the proportion of eggs and chicks lost to predators may be reduced in large colonies through synchronized breeding (Darling 1938, Patterson 1965).

Some burrowing species attend the colony only under cover of darkness to further reduce the risk from avian predators. In seabirds, nocturnality is generally interpreted as avoidance of diurnal predators and kleptoparasites (McNeil *et al.* 1993).

The main avian predators, the gulls, may be active at night, particularly on moonlit nights (Gross 1935). Species which are vulnerable to predation, such as shearwaters and storm-petrels, are less active at colonies on clear moonlit nights than dark foggy nights (Storey & Grimmer 1986, Watanuki 1986, Bryant 1993).

Seabird colonies are generally highly conspicuous concentrations which may attract predators, including humans. Colony peripheries tend to suffer higher predation rates than central areas, and small colonies suffer higher predation than large ones (Kruuk 1964; cf. Montevecchi 1977). The potential safety provided by a colonial situation may depend on a critical density.

1.3. Breeding success

1.3.1. Population density

It is generally expected that the majority of individuals in a species will utilize the habitat which provides the optimal conditions for survival and reproduction (Buckley & Buckley 1980). Thus, in a species with a low population density, it is expected that only the optimal habitats will be exploited. However, where population density is high, it is expected that less suitable habitats will be utilized in rank order (Hildén 1965, Rodway 1994). This process depends on the existence of a specific population density threshold (Fretwell 1972). That is, a specific density beyond which foraging or breeding success in optimal habitat is affected, by a variety of factors, to the extent that it is rivalled by the success in sub-optimal habitats. Such a threshold will be determined by the territorial and colonial tendencies of a given species.

Distribution models are designed to predict the spatial and temporal distributions of individuals, based on the assumption that individuals will attempt to maximize fitness (Fretwell & Lucas 1970, Rosenzweig 1981, Holt 1987, Morris 1991. Rodway 1994). Models typically assume that population density will correlate with resource abundance and high densities will occur in preferred habitats (Rosenzweig 1991). Ideal-free and ideal-despotic models (Fretwell & Lucas 1970) assume that habitat quality declines with increasing density, due to factors such as increased predator activity and competition. In an ideal-free distribution, individuals can move freely among habitats and should distribute themselves such that individual fitness is similar across habitats. However, it is expected that individual fitness will be dissimilar across habitats where established individuals are despotic i.e. can prevent others from accessing preferred habitat.

Many studies have shown a positive correlation between density and breeding success, although this is often associated with the risk of predation (Nettleship 1972, Harris 1980, Hatchwell 1991). However, Van Horne (1983) concluded that high density alone does not infer habitat quality and provided a few examples of situations where the density-habitat relationship has been "decoupled". Van Horne also pointed out that great care must be taken in the development of wildlife management plans, which are often based on inferred habitat quality, since many other factors may influence population density e.g. habitat loss or fragmentation. In species such as gulls, with a high degree of intra-specific predation and cannibalism, individuals may exhibit greater reproductive success at low densities (Pierotti 1982). In species such as storm-petrels, which utilize burrows or crevices, density may be limited by substrate (Harris 1974).

1.3.2. Age and experience

Foraging ability improves with age in many species, and undoubtedly affects breeding success (Gauthreaux 1988). In some species, however, experienced breeders have greater breeding success than inexperienced breeders, despite their age (e.g. Thick-billed Murres, *Uria lomvia* ; A. Gaston pers. comm.), suggesting that age alone is not the only, or indeed major, influence. This difference in breeding success is likely the result of substantial advantages gained from access to higher quality habitat, such as a central location in colonial situations. The earlier arrival of experienced breeders clearly facilitates a greater choice of available breeding sites (Coulson & White 1960). It is also recognized that practice in breeding, greater knowledge of a particular breeding site, precise location of the nest, increased synchrony or coordination with partner, and an experienced partner are all likely to contribute to breeding success (Warham 1990, De Forest & Gaston 1996). Experienced breeders are more likely to mate first, as well as to mate with birds of equal breeding experience, foraging abilities, and social standing. However, it is difficult to separate the effects of age and experience on habitat utilization and breeding success from that of increased breeding effort due to a decrease in life expectancy (Pugesek 1981).

Most seabird species are long-lived and defer breeding for several years, during which they spend much time prospecting possible breeding locations and establishing pair bonds (Lack 1968, Warham 1990). Prospecting by young birds of many species tends to take place late in the season (Boulinier *et al.* 1996), when the greatest potential exists to use the success of breeding birds as an indicator of nest-site quality and a cue for habitat utilization.

1.4. Leach's Storm-Petrels

Leach's Storm-Petrel is the most widely distributed procellariiform in the Northern Hemisphere, breeding on small islands across the northern Atlantic and Pacific Oceans. Recent estimates suggest a world population of more than 8 million breeding pairs (Huntington *et al.* 1996) plus an inestimable number of non-breeders, mostly immature birds, which remain at sea most of the year.

Leach's Storm-Petrels reach reproductive maturity in their fourth or fifth year, and are thought to form a life-long monogamous pair bond, probably based on strong nest-site fidelity (Cramp & Simmons 1977). They are colonial breeders, and nest in burrows or crevices, where both adults share incubation of their single egg in average shifts of 2.7 days (Wilbur 1969). Four or five days after hatching the chick is left alone and each adult returns on average every 2-3 days to feed the chick (Huntington *et al.* 1996). Although it has been suggested that the frequency of feeding visits slowly decreases until the chick is abandoned a few days prior to fledging (Ricklefs *et al.* 1980), it has been shown that chicks may be fed until the night before fledging, and adults may continue to visit the burrow after the chick has fledged (Huntington *et al.* 1996). Chicks fledge at approximately 60-70 days after hatching, at which point the chick is fully independent (Gross 1935, Ricklefs *et al.* 1980). Outside this long breeding season, Leach's Storm-Petrels are migratory and disperse widely across the Atlantic and Pacific Oceans, wintering south to the equator particularly in regions of tropical oceanic convergences (Cramp & Simmons 1977).

Leach's Storm-Petrel is the smallest and most abundant seabird to breed in the Northwest Atlantic (Montevecchi *et al.* 1992). Their breeding range is centred on the eastern and southern coasts of Newfoundland, where over half of the world's breeding population is found, as well as the largest breeding concentrations in the world (Sklepkovych & Montevecchi 1989). Despite these vast numbers, Leach's Storm-Petrels are rarely observed. Being small and dark, and remaining low over the water, they are inconspicuous at sea, and activity at colony islands is strictly nocturnal.

Leach's Storm-Petrels are pelagic planktivores, that feed on zooplankton and nekton at the sea surface in areas of deep water (Cramp & Simmons 1977). They forage by picking up individual organisms while flying or hovering low over the surface of the water, and occasionally patter over the surface with their feet or sit on the surface while foraging (Warham 1990). Zooplankton provides a lipid-rich food source which storm-petrels concentrate into a stomach oil stored in the proventriculus, or foregut (Place *et al.* 1989). The dense aqueous phase is eliminated, and oils and suspended solids retained (Duke *et al.* 1989), which may be easily transported over long distances and provides a high energy meal for the chick (Ricklefs *et al.* 1980). Breeding Leach's Storm-Petrels may forage more than 200 km from colonies (Steele & Montevecchi 1994).

1.5. The current study of habitat utilization by Leach's Storm-Petrels

This study compares micro-habitat features and breeding success in forest and open meadows to determine optimal breeding habitat of Leach's Storm-Petrels, at the centre of the species breeding range in the North Atlantic. Another focal objective is to investigate trade-offs between predation risk and nesting patterns.

Leach's Storm-Petrels nest in a variety of habitats on marine islands, and in Atlantic colonies these range from densely-canopied coniferous forest to open meadow (Gross 1935, Sklepkovych 1986, Huntington *et al.* 1996). To date, however, no study has compared Leach's Storm-Petrel utilization of, and breeding success in, forest and open habitats.

Within forest and open habitats, nest-site selection of Leach's Storm-Petrels may be determined by micro-habitat features. Characteristics of soil (Harris 1974, Grimmer 1980, Watanuki 1985), slope (MacKinnon 1988, Sklepkovych & Montevecchi 1989, Huntington *et al.* 1996) and vegetation (Harris 1974, Grimmer 1980, MacKinnon 1988, Vermeer *et al.* 1988, Sklepkovych & Montevecchi 1989) have all been suggested as important factors in breeding success. This study compares key micro-habitat features in forest and open habitats.

Predation risk is also an important aspect of habitat suitability (Lima & Dill 1990). This may be particularly critical for Leach's Storm-Petrels which, due to their small size and lack of direct defences, are heavily preyed upon by larger birds at breeding colonies. In fact the species' major life-history traits (i.e. coloniality, nocturnality, burrow-nesting, pelagic-feeding, and overall dark colour) have been largely shaped by predator avoidance. Gulls are the main predators at most colonies (Huntington *et al.* 1996), where Leach's Storm-Petrel activity is reduced on bright moonlit nights due to their greater visual detectability (Watanuki 1986, Bryant 1993). Therefore, this study also focuses on predation risk in forest and open habitats.

The current study addresses the following specific predictions:

1) Micro-habitat features are compared between forest and open habitat and:
    a) due to a greater build up of humus, peat is expected to be deeper in forest than open habitat.
    b) due to exposure and shallower peat, soil is expected to be more compact in open than forest habitat.
    c) average slope and aspect are not expected to differ between forest and open habitats.

2) Leach's Storm-Petrels are expected to burrow more densely in areas of deep peat, low soil compaction and steep slopes. Therefore, burrow density is expected to be greater in forest than open habitat.

3) Owing to the proximity of predatory gulls, breeding success is expected to be compromised to a greater extent in open than forest habitat.

Chapter 2

METHODS

2.1. Study site

Great Island (47°11' N, 52°49' W) in the Witless Bay Ecological Reserve lies approximately 2.4 km off the eastern shore of the Avalon Peninsula on the southeast coast of Newfoundland (Fig. 1). The island is approximately 1200 m long (N-S) and ranges between 150 to 700 m wide (E-W). The island consists of a precipitous rocky shoreline, topped by steep grassy slopes, levelling out to gently sloping grass-*Rubus* meadows and a central area of dense conifers, predominantly dwarfed Balsam Fir, *Abies balsamea*, and Black Spruce, *Picea mariana*. However, the forested area is thought to have contracted over the past 20-30 years, while the perimeter grass and meadow habitats have expanded (Rodway 1994). Nine seabird species breed on the island, including an estimated 340,000 pairs of Leach's Storm-Petrels; 123,000 pairs of Atlantic Puffins, *Fratercula arctica*; 2,770 pairs of Herring Gulls, *Larus argentatus*; and 80 pairs of Great Black-backed Gulls, *Larus marinus* (Cairns *et al.* 1989, Rodway *et al.* 1996).

2.2. Sampling methods

This study was conducted from 17 May to 14 September 1996 and from 16 May to 26 August 1997. Two habitat types, were identified and characterized -

Forest = an area of grass, shrub or fern vegetation and/or bare peat under a dense canopy of coniferous forest

Open = an area of grass and shrub vegetation open to the sky and sea.

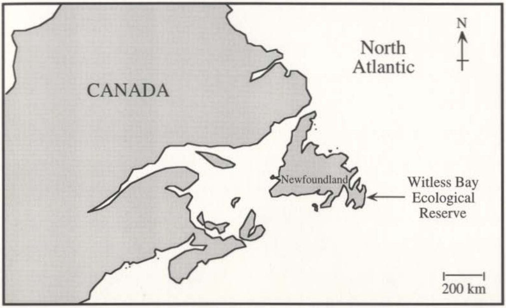

Figure 1: Location of the Witless Bay Ecological Reserve, Newfoundland, Canada, in the northwest Atlantic.

In 1996, burrow density and breeding success were recorded in two 10 x 10 m study plots, chosen in areas of similar slope and aspect, in each of the habitat types. Throughout this season, burrows in open habitat were explored first, followed by burrows in forest. In 1997, a random sampling method was used, with samples being stratified by habitat. An existing transect grid, running E-W at 100 m intervals (Rodway *et al.* 1996), was used to establish random points (Fig. 2), although transects 9 and 10 were excluded from the study to avoid excessive disturbance to areas of cliff-nesting seabirds. A transect number (1-8) and direction of travel (E or W) was randomly generated. Then, two coordinates, at 10 m intervals, were randomly generated; the first represented the distance along the transect in the selected E or W direction; the second represented the distance directly south of the transect (up to 90 m). Each random point was marked with a stake, and a provided the SE corner for a 2 x 2 m plot. Random points which did not fall in forest or open habitat were omitted; the process was repeated until 50 random plots were established in each habitat. Burrow density, breeding success, and habitat variables were recorded in each plot in forest and open habitats. In 1997, all burrow interventions and habitat variables were recorded in an equal number of forest and open plots on each day, thus exploring each habitat over the same time period and under the same environmental conditions. To lessen disturbance, burrow intervention was minimized throughout this study, with four visits to each burrow in 1996 and three in 1997. Nest chambers which could not be reached, due to the shape of the burrow and/or the presence of rocks or roots, were considered inaccessible and were not disturbed i.e. unreachable burrows were not accessed by digging hatches.

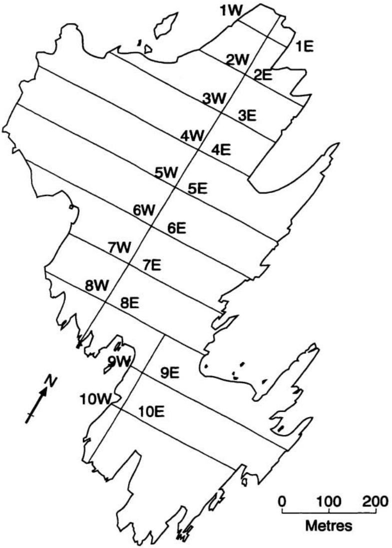

Figure 2: Layout of permanently marked transect grid on Great Island, Newfoundland (from Rodway *et al.* 1996).

2.2.1. Micro-habitat features

In 1997, aspect, slope, peat depth and soil compaction were measured for each plot. Aspect, the direction of greatest slope, was measured to the nearest degree, at the central point of each plot, using a Silva sighting compass. Slope, peat depth and soil compaction were measured at five points within each plot, at the central point and half way between the central point and each corner of the plot. Slope was measured to the nearest degree using an MJP Mini-Gradometer (Michael Jay), which measured the angle of the surface over a 20 cm span. Soil compaction was measured using a Lang Penetrometer (Blue Generation, James D. Lang, Alabama), which was used to record the peat resistance to penetration i.e. dense peat has a high resistance and thus a high compaction score. Peat depth was measured to the nearest 5 cm using an iron rod approximately 1 cm in diameter and marked at 10 cm intervals.

2.2.2. Reproductive parameters

2.2.2.1. Density

In 1996, burrows were counted in each plot in open habitat, between 17 and 18 May, and in forest habitat, between 25 and 26 May, and in four random 10 x 10 m plots in each habitat type, between 16 and 18 August. In 1997, burrows were counted in each plot in both habitat types, between 25 and 31 May.

2.2.2.2. Activity

The activity at each burrow was assessed by placing a lattice of grasses from the surrounding area over the entrance, which was later examined for evidence of disturbance. In 1996, all burrow lattices were examined each day, over a period of 6 nights, from 25 May to 1 June. In 1997, all burrow lattices were examined once, 7 nights after latticing, between 25 May and 7 June.

2.2.2.3. Occupancy

A burrow was considered to be occupied when two adults were found during the day on at least one occasion, a single adult was found during the day on more than one occasion, or an egg was laid. Throughout the study, the proportion of occupied burrows was considered to be the number of burrows in which birds attempted to breed divided by the total number of burrows in each plot.

2.2.2.4. Egg characteristics

In 1996, egg length, breadth and mass were recorded in each plot, between 22 June and 1 July, between 0800 and 1300 h in dry conditions. Maximum egg length and breadth were measured with calipers to the nearest 0.1 mm, and eggs were weighed with a 50 g Pesola scale to the nearest 0.5 g. Egg shape index was calculated using the formula $ESi = B \times 100/L$ (Coulson 1963), where B = breadth and L = length, and egg volume was calculated using the formula $V = 0.51 \times L \times B^2$ (Preston 1974, Hoyt 1979). These measurements were not taken in 1997, resulting in an overall less invasive study design.

2.2.2.5. Hatching success

The presence of adults and/or eggs (i.e. reproductive attempts) were established by exploration of each burrow between 22 June and 1 July 1996, and between 28 June and 8 July 1997. Hatching success was the number of eggs hatched divided by the number of eggs laid in each plot.

2.2.2.6. Chick morphometrics

As an index of growth, chicks were weighed with a 100 g Pesola scale to the nearest 0.5 g and the right wing chord of each chick was measured with a wing rule to the nearest 1 mm. In 1996, chicks in open plots were weighed and measured once between 27 and 28 August, and in forested plots between 31 August and 1 September, and re-weighed between 12 and 13 September. In 1997, chicks in both habitats were weighed and measured once between 18 and 23 August.

2.2.2.7. Breeding success

In this study, breeding success was defined as the number of chicks surviving at the last burrow exploration divided by the number of eggs laid in each plot. Breeding success was determined between 12 and 14 September 1996, and between 18 and 23 August 1997, at which time surviving chicks were assumed to fledge.

2.2.3. Predation Risk

2.2.3.1. Gull nests

In 1997, the distance from the central point of each plot to the nearest gull nest was measured along the ground to the nearest 0.1 m using a 60 m tape. The area around each plot was searched in a concentric circling pattern up to 25 m, all nests over 25 m from the plot, or where no nests were found, were recorded as >25 m.

2.2.3.2. Gull predation

Gull predation of Leach's Storm-Petrels was examined from June to September 1996, and from May to August 1997. A 435 m x 2 m transect, established in early June 1996, passed through each of the habitat types. Leach's Storm-Petrel "kills" (i.e. many loose feathers and evidence of a struggle on the ground) and pellets (i.e. a solid mass of oily feathers and/or bones regurgitated by gulls) were recorded along the transect weekly throughout the season. On each survey, all evidence of a kill or pellet was removed from the transect allowing new sites to be clearly identified.

2.2.4. Habitat changes

The area of each habitat type on Great Island was determined by placing a fine grid over habitat maps (Nettleship 1972, Rodway *et al.* 1996) and counting the number of grid squares in each habitat. The area of each habitat was calculated as a percentage of the total area of vegetation of the island.

2.3. Statistical Analyses

In 1996, the effects of habitat variables were explored using the G-test of Independence, employing the Williams' correction for a 2 x 2 table (Sokal & Rohlf 1995). In 1997, the effects of habitat variables were explored using the General Linear Model, and relationships between variables were examined using ANOVA, ANCOVA, Simple and Multiple Regression (Data Desk 5.0, Data Description Inc., Ithaca, NY, USA). Error distributions were examined for homogeneity, normality, and independence of residuals (Simpson & Schneider, submitted). Where error distributions were deemed unacceptable, sample size was low ($n < 30$), and p was close to α (0.05), the p-value was re-calculated ($n = 5000$) using a randomization test (Minitab 10.2, Minitab Inc., PA, USA).

Chapter 3

RESULTS

Analyses focus on comparisons of forest and open habitat and other finer-scale environmental variables (slope, aspect, soil) in terms of reproduction and predation.

3.1. Forest and Open habitats

Mean slope was significantly less steep in forest (12 ± 7°; range 2 - 32°) than in open habitat (16 ± 10°; range 2 - 36°; $F_{1,99} = 5.01$, $P = 0.03$; Table 1). Aspect did not differ between forest (157 ± 108°; range 0 - 332°) and open habitats (148 ± 88°; range 8 - 354°; $F_{1,99} = 0.21$, $P = 0.6$; Table 1). Soil was less compact in forest (1.65 ± 0.48; range 1 - 3) than in open habitat (2.52 ± 8.39; range 1 - 3; $F_{1,99} = 39.73$, $P = <0.001$), and peat was deeper in forest (38.2 ± 6.59 cm; range 25 - 51) than open habitat (29.46 ± 9.75 cm; range 17 - 66; $F_{1,99} = 27.56$, $P = <0.001$; Table 1). Peat depth and soil compaction were negatively related ($r^2 = 0.05$, $F_{1,98} = 4.61$, $P = 0.03$): with deeper peat showing lower soil compaction (Fig. 3). Peat depth was not included in further statistical analysis, because peat in both habitats, and across the island, was deep enough to support storm-petrel burrows. Soil compaction was much more variable, and therefore considered the more important determinant of habitat utilization.

In 1996, the mean number of inaccessible nest chambers was higher in forest (0.23 ± 0.021 burrows/m^2; range 0.28 - 0.33) than in open plots (0.04 ± 0.056 burrows/m^2; range 0 - 0.14; Table 2), and there was a significant difference in the proportion of inaccessible nest chambers in each habitat ($G_{adj} = 14.02$, $df = 1$, $P =$

Table 1: Summary of means (± SD) and significance of ANOVA results for comparison of micro-habitat variables in forest and open habitats on Great Island, Newfoundland, in 1997.

Variable	Units	Forest	Open	Significance[1]
Slope	degrees	12 ± 7	16 ± 10	*
Aspect	degrees	157 ± 108	148 ± 88	NS
Soil compaction	category	2.51 ± 0.83	1.65 ± 0.48	**
Peat depth	centimetres	38.2 ± 6.59	29.5 ± 9.75	**

[1] NS = not significant, * indicates $p < 0.05$, ** indicates $p < 0.01$

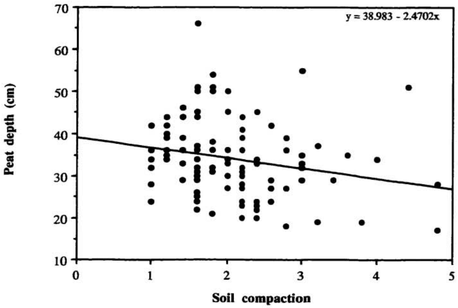

Figure 3: Relationship between peat depth (cm) and soil compaction across forest and open habitats on Great Island, Newfoundland, in 1997.

Table 2: Summary of means (± SD) and significance of ANOVA and G-test results for comparison of variables in forest and open habitats on Great Island, Newfoundland, in 1996.

Variable	Units	Forest	Open	Significance[1]
Density (ANOVA)	burrows/m^2	2.03 ± 0.74	0.95 ± 0.43	*
Activity	proportion of burrows	0.87 ± 0.09	0.76 ± 0.19	NS
Occupancy	proportion of burrows	0.76 ± 0.01	0.60 ± 0.22	*
Eggs	no. laid/occupied burrow	1.00 ± 0.00	0.98 ± 0.03	NS
Hatching success	no. hatched/egg laid	0.87 ± 0.02	0.78 ± 0.01	NS
Breeding success	no. chicks/egg laid	0.85 ± 0.04	0.74 ± 0.00	NS
Inaccessible nests	proportion of burrows	0.23 ± 0.02	0.04 ± 0.05	**

[1] NS = not significant, * indicates $p < 0.05$, ** indicates $p < 0.01$

Table 3: Summary of means (± SD) and significance of ANOVA results for comparisons of variables in forest and open habitats on Great Island, Newfoundland, in 1997.

Variable	Units	Forest	Open	Significance[1]
Density	burrows/m^2	2.21 ± 1.23	1.53 ± 1.13	**
Activity	proportion of burrows	0.95 ± 0.09	0.71 ± 0.31	**
Occupancy	proportion of burrows	0.70 ± 0.25	0.56 ± 0.24	**
Eggs	no. laid/occupied burrow	0.93 ± 0.17	0.98 ± 0.08	NS
Hatching success	no. hatched/egg laid	0.72 ± 0.31	0.52 ± 0.44	*
Breeding success	no. chicks/egg laid	0.71 ± 0.31	0.52 ± 0.44	*
Proximity of gull nest	category	4.68 ± 1.94	2.54 ± 1.28	**
Inaccessible nests	proportion of burrows	0.34 ± 0.21	0.26 ± 0.10	NS

[1] NS = not significant, * indicates $p < 0.05$, ** indicates $p < 0.01$

<0.001). In 1997, however, the proportion of inaccessible nest chambers (Table 3) was not significantly different in forest (0.34 ± 0.21; range 0.08 - 1.0) and open plots (0.26 ± 0.10; range 0.11 - 0.5; $F_{1,69} = 2.98$, $P = 0.09$). The following results, other than the consideration of overall burrow density and activity, refer to statistical analysis of accessible burrows only.

3.2. Reproduction in Forest and Open habitats

3.2.1. Density

In 1996, mean burrow density was over double in forested (2.03 ± 0.74 burrows/m^2; range 1.1 - 2.7) than in open habitat (0.95 ± 0.43 burrows/m^2; range 0.5 - 1.5; $F_{1,7} = 7.63$, $P = 0.03$; Fig. 4). Similarly, in 1997, mean burrow density was significantly higher in forests (2.21 ± 1.23 burrows/m^2; range 0.2 - 6.7) than in the open (1.53 ± 1.13 burrows/m^2; range 0 - 5; $F_{1,99} = 8.41$, $P= 0.004$; Fig. 4). The Linear Model showed significant effects of habitat ($F_{1,99} = 7.60$, $P = 0.007$) and slope ($F_{1,99} = 16.05$, $P = <0.001$) on burrow density (Table 4), with a higher burrow density in forest, and on steeper slopes in both habitats. Aspect and soil compaction showed no effect on burrow density, although soil compaction was close to α ($F_{17,99} = 1.71$, $P = 0.06$). Five to 10 % of variance in burrow density was explained by a positive relationship with slope ($r^2 = 0.11$, $F_{1,98} = 12.8$, $P = <0.001$) and a negative relationship with soil compaction ($r^2 = 0.05$, $F_{1,98} = 5.6$, $P = 0.02$).

3.2.2. Activity

In 1996, the number of active burrows per m^2 was higher in forest (0.77 ± 0.04; range 0.7 - 0.8) than in open habitat (0.40 ± 0.19; range 0.3 - 0.5). However, the proportion of active burrows did not differ between forest (0.87 ± 0.09; range 0.8 - 0.9) and open habitats (0.76 ± 0.19; range 0.6 - 0.9; Table 2; Fig. 5), although this

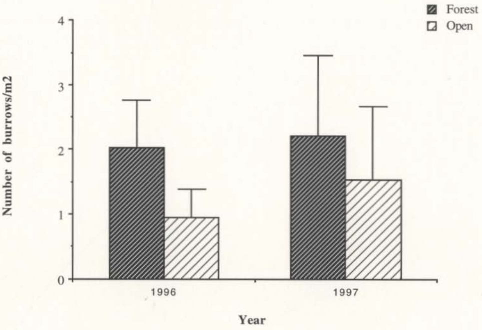

Figure 4: Mean burrow densities (+SD) for forest and open habitat on Great Island, Newfoundland, in 1996 and 1997.

Table 4: Summary of General Linear Model results for comparisons of variables on Great Island, Newfoundland, in 1997.

Model	Variables	df	F	P	Significance[1]
Density	Habitat	1	7.60	0.007	**
	Slope	1	16.05	<0.001	**
	Aspect	8	0.96	0.47	NS
	Soil compaction	17	1.71	0.06	NS
Activity	Habitat	1	5.50	<0.001	**
	Slope	1	0.09	0.7	NS
	Aspect	8	1.65	0.13	NS
	Soil compaction	17	0.09	0.77	NS
	Gull nest proximity	5	5.94	<0.001	**
Occupancy	Habitat	1	2.65	0.11	NS
	Slope	1	0.32	0.57	NS
	Aspect	8	1.39	0.22	NS
	Soil compaction	13	0.67	0.78	NS
	Gull nest proximity	5	0.75	0.58	NS
Breeding success	Habitat	1	1.72	0.20	NS
	Slope	1	0.08	0.78	NS
	Aspect	8	1.08	0.39	NS
	Soil compaction	13	1.06	0.41	NS
	Gull nest proximity	5	1.47	0.22	NS

[1] NS = not significant, * indicates $p < 0.05$, ** indicates $p < 0.01$

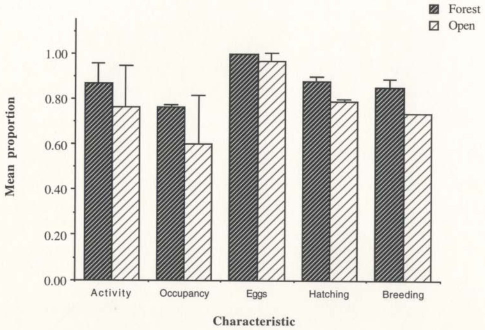

Figure 5: Mean proportions of accessible burrows (+SD) for Leach's Storm-Petrel breeding characteristics in forest and open habitat on Great Island, Newfoundland, in 1996.

Activity = no. of active burrows/total burrows, Occupancy = no. of occupied burrows/total burrows, Eggs = no. of eggs laid/occupied burrow, Hatching = hatching success (no. of chicks hatched/no. eggs laid), Breeding = breeding success (no. of surviving chicks/no. eggs laid).

was close to α (G_{adj} = 3.693, df = 1, P = 0.05). In 1997, the number of active burrows per m^2 was significantly higher in forest (2.1 ± 1.19; range 0.25 - 6.25) than open habitat (1.27 ± 1.03; range 0 - 4.5; $F_{1,99}$ = 13.7, P = <0.001). The proportion of active burrows was also significantly higher in forest (0.95 ± 0.09; range 0.5 - 1) than open habitat (0.71 ± 0.31; range 0 to 1; $F_{1,99}$ = 27.38, P = <0.001; Table 3; Fig. 6). The Linear Model showed significant effects of habitat ($F_{1,99}$ = 17.14, P = <0.001), soil compaction ($F_{17,99}$ = 5.49, P = <0.001), and proximity of gull nest ($F_{5,99}$ = 5.94, P = <0.001) on the proportion of active burrows in a plot (Table 4). Slope and aspect did not show significant effects on the proportion of active burrows. The proportion of active burrows was, however, positively related to burrow density (r^2 = 0.17, $F_{1,98}$ = 20.0, P = <0.001).

3.2.3. Occupancy

In 1996, the number of occupied burrows per m^2 was higher in forest (0.56 ± 0.007; range 0.56 - 0.57) than in open habitat (0.32 ± 0.18; range 0.2 - 0.4). The proportion of occupied burrows (Table 2, Fig. 5) was higher in forest (0.76 ± 0.01; range 0.7 - 0.8) than in open plots (0.60 ± 0.22; range 0.4 to 0.8), and there was a significant difference in proportion of occupied burrows in each habitat (G_{adj} = 4.40, df = 1, P = 0.4). In 1997, the number of occupied burrows per m^2 was significantly higher in forest (1.18 ± 0.84; range 0.25 - 4.7) than in open habitat (0.70 ± 0.58; range 0 - 2.7; $F_{1,97}$ = 10.7, P = 0.001). The proportion of occupied burrows was also significantly higher in forest (0.70 ± 0.25; range 0 - 1) than in open habitat (0.56 ± 0.24; range 0 - 1; $F_{1,92}$ = 6.82, P = 0.01; Table 3; Fig. 6). The Linear Model showed no significant effects of habitat, slope, aspect, soil compaction or proximity of gull nests on the proportion of occupied burrows (Table 4). There was no significant relationship between burrow density and occupancy. However, there was a significant

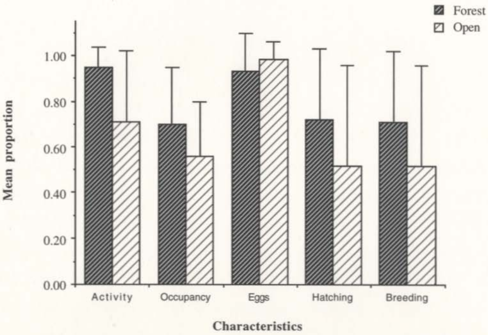

Figure 6: Mean proportions of accessible burrows (+SD) for Leach's Storm-Petrel breeding characteristics in forest and open habitat on Great Island, Newfoundland, in 1997.

Activity = no. of active burrows/total burrows, Occupancy = no. of occupied burrows/total burrows, Eggs = no. of eggs laid/occupied burrow, Hatching = no. of chicks hatched/no. eggs laid, Breeding = no. of surviving chicks/no. eggs laid.

positive relationship between activity and occupancy ($r^2 = 0.11$, $F_{1,91} = 11.4$, $P = 0.001$).

3.2.4. Number of eggs laid

In 1996, the number of eggs laid per m^2 was higher in forest (0.56 ± 0.007; range 0.56 - 0.57) than open habitats (0.31 ± 0.17; range 0.19 - 0.43). There was no significant difference in the number of eggs laid per occupied burrow in forest and open habitats; all occupied burrows in forest and 98 % of occupied burrows in the open contained an egg (Table 2, Fig. 5). In 1997, the number of eggs laid per m^2 was significantly higher in forest (1.08 ± 0.81; range 0 - 4.5) than open habitats (0.69 ± 0.56; range 0 - 2.5; $F_{1,98} = 8.08$, $P = 0.005$). The number of eggs laid per occupied burrow was also high in 1997 (Table 3, Fig.6), and, although slightly more variable, did not significantly differ between forest (0.93 ± 0.168) and open habitats (0.98 ± 0.081; $F_{1,79} = 2.927$, $P = 0.09$).

3.2.5. Egg characteristics

None of the Leach's Storm-Petrel egg characteristics measured in 1996, or subsequently calculated, differed between forest and open habitats on Great Island (Table 5).

3.2.6. Hatching success

In 1996, the number of eggs hatched per m^2 was higher in forest (0.49 ± 0.02; range 0.48 - 0.51) than open habitat (0.24 ± 0.13; range 0.15 - 0.34). The hatching success was also higher in forest (0.87 ± 0.02; range 0.86 - 0.89) than in open habitat (0.78 ± 0.01; range 0.77 - 0.79), although the difference in the proportion of burrows

Table 5: Leach's Storm-Petrel egg characteristics in forest and open habitats on Great Island, Newfoundland, in 1996, and ANOVA results for habitat comparisons.

Characteristic	Habitat	n	Mean	SD	Range	F	P
Length (mm)	Forest	93	33.08	0.98	30.05 - 35.10		
	Open	50	33.02	1.07	30.68 - 35.35	0.14	0.71
Breadth (mm)	Forest	93	23.79	0.60	22.20 - 25.25		
	Open	50	23.89	0.57	22.61 - 24.86	0.89	0.35
Mass (g)	Forest	93	9.84	0.73	8.00 - 12.00		
	Open	50	10.04	0.68	8.75 - 12.00	2.68	0.10
Volume (ml)	Forest	93	9.56	0.64	7.90 - 11.41		
	Open	50	9.61	0.56	8.56 - 10.95	0.25	0.62
Shape Index	Forest	93	71.95	2.22	66.44 - 78.51		
	Open	50	72.42	2.85	66.69 - 79.29	1.19	0.28

successfully hatching an egg in forest and open habitat was not significant (G_{adj} = 2.15, df = 1, P = 0.1; Table 2; Fig. 5). In 1997, the number of eggs hatched per m^2 was significantly higher in forest (0.96 ± 0.65; range 0 - 3.25) than open habitat (0.57 ± 0.54; range 0 - 2.5; $F_{1,90}$ = 9.37, P = 0.003). Hatching success (Table 3, Fig. 6) was also significantly higher in forest (0.72 ± 0.31; range 0 - 1) than open habitat (0.52 ± 0.44; range 0 - 1; $F_{1,64}$ = 4.26, P = 0.04). Across both habitats, there were significant positive relationships between hatching success and (1) burrow density (r^2 = 0.08, $F_{1,63}$ = 5.85, P = 0.02), (2) burrow activity (r^2 = 0.34, $F_{1,63}$ = 32.3, P = <0.001), (3) burrow occupancy (r^2 = 0.26, $F_{1,57}$ = 20.3, P = <0.001), and (4) proximity of gull nest (r^2 = 0.08, $F_{1,63}$ = 5.60, P = 0.02), and a significant negative relationship with (5) soil compaction (r^2 = 0.10, $F_{1,63}$ = 7.23, P = 0.009; Fig. 7). Multiple regression analysis, including all these factors (1-5), showed only a significant positive relationship between occupancy (R^2 = 0.39, $F_{7,32}$ = 2.93, P = 0.002) and hatching success across both habitats (Table 6).

3.2.7. Chick condition

In 1996, there was a positive linear relationship between chick mass and wing length in forest (r^2 = 0.57) and open (r^2 = 0.76) habitats ($F_{1,116}$ = 134.7, P = <0.001; Fig. 8). The relationships did not differ in magnitude ($F_{1,116}$ = 0.41, P = 0.5) or in slope ($F_{1,116}$ = 0.57, P = 0.4) for forest and open habitats. Similarly, in 1997, there was a positive linear relationship between chick mass and wing length in forest (r^2 = 0.66) and open (r^2 = 0.69) habitats ($F_{1,203}$ = 289.5, P = <0.001; Fig. 8), and again, the relationships did not differ in magnitude ($F_{1,203}$ = 0.28, P = 0.9) or in slope ($F_{1,203}$ = 0.004, P = 0.9) in forest and open habitats.

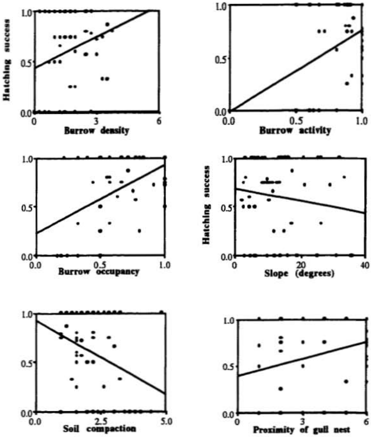

Figure 7: Relationships between Leach's Storm-Petrel hatching success and micro-habitat features on Great Island, Newfoundland, in 1997.

Table 6: Summary of Multiple Regression results for habitat variables against hatching success and breeding success on Great Island, Newfoundland, in 1997.

Variable	R^2	F	t	P	Significance[1]
Hatching success	0.39	2.93			
Habitat			-1.53	0.14	NS
Density			1.50	0.14	NS
Activity			0.58	0.57	NS
Occupancy			3.39	0.002	**
Slope			-0.55	0.59	NS
Soil compaction			0.69	0.50	NS
Gull nest proximity			0.19	0.85	NS
Breeding success	0.37	2.82			
Habitat			-1.52	0.14	NS
Density			1.50	0.14	NS
Activity			0.22	0.83	NS
Occupancy			3.57	0.001	**
Slope			-0.71	0.48	NS
Soil compaction			0.57	0.57	NS
Gull nest proximity			0.04	0.97	NS

[1] NS = not significant, * indicates $p < 0.05$, ** indicates $p < 0.01$

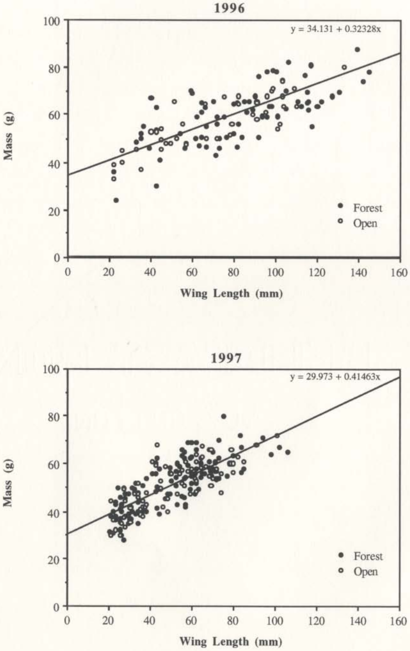

Figure 8: Relationship between chick mass (g) and wing length (mm) in forest and open habitat on Great Island, Newfoundland, in 1996 and 1997.

3.2.8. Breeding success

In 1996, more chicks survived per m^2 in forest (0.48 ± 0.03; range 0.46 - 0.50) than in open habitat (0.23 ± 0.13; range 0.14 - 0.32). Breeding success was higher in forest (0.85 ± 0.04; range 0.82 - 0.88) than in open habitats (0.74 ± 0.00; Table 2; Fig. 5), although the difference in the proportion of successful burrows in each habitat was not significant ($G_{adj} = 2.91$, df = 1, $P = 0.09$). In 1997, more chicks survived per m^2 in forest (0.74 ± 0.49; range 0 - 1.75) than in open habitat (0.38 ± 0.38; range 0 - 1.25; $F_{1,65} = 10.77$, $P = 0.002$). Breeding success was significantly higher in forest (0.71 ± 0.31; range 0 - 1) than in open habitats (0.52 ± 0.44; range 0 - 1; $F_{1,66} = 4.34$, $P = 0.04$; Table 3; Fig. 6). The Linear Model showed no significant effects of habitat, slope, aspect, soil compaction, or nearest gull nest on breeding success. Across both habitats, there were significant positive relationships between breeding success and (1) burrow density ($r^2 = 0.08$ $F_{1,65} = 5.40$, $P = 0.023$), (2) activity ($r^2 = 0.31$, $F_{1,65} = 29.9$, $P = <0.001$), (3) occupancy ($r^2 = 0.26$, $F_{1,59} = 20.5$, $P = <0.001$), (4) the proximity of gull nests ($r^2 = 0.07$, $F_{1,65} = 4.95$, $P = 0.03$), and a negative relationship with (5) soil compaction ($r^2 = 0.09$, $F_{1,65} = 7.08$, $P = 0.009$; Fig. 9). The relationship between breeding success and soil compaction was similar for forest and open habitats ($F_{1,66} = 0.76$, $P = 0.4$), and although overall soil compaction did not have a significant effect on breeding success ($F_{1,66} = 3.89$, $P = 0.05$) it was close to α in a low power test. Multiple regression analysis, including all these factors (1-5), showed only a significant positive relationship between occupancy ($R^2 = 0.37$, $F_{7,33} = 2.82$, $P = 0.001$) and breeding success across both habitats (Table 6).

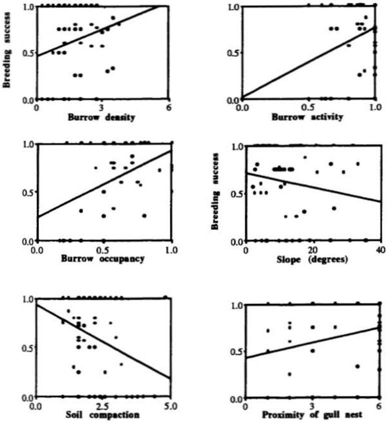

Figure 9: Relationships between Leach's Storm-Petrel breeding success and micro-habitat features on Great Island, Newfoundland, in 1997.

3.3. Predation risk in Forest and Open habitats

3.3.1. Gull nests

In 1996, the number of gull nests within 10 m of plot boundaries was lower in forest (2.0 ± 1.4; range 1 to 3) than open habitat (4.0 ± 1.4; range 3 to 5). In 1997, where gull nests were found within 25 m, mean distance to the nearest nest was not significantly different for forest (9.20 ± 6.06 m; range 2.1 - >25 m) and open plots (9.67 ± 5.57 m; range 0.9 - >25 m; $F_{1,65} = 0.088$, $P = 0.8$). However, gull nests were found within 25 m of 96 % of open plots, but only 36 % of forest plots. The proportion of plots with a gull nest within 25 m was significantly lower in forest than open habitat ($G_{adj} = 45.3$, df = 1, $P = <0.001$), and when categorized in blocks of 5 m to the nearest gull nest, the mean category distance was a significantly greater in forest (4.68 ± 1.94) than in open habitat (2.54 ± 1.28; $F_{1,99} = 42.3$, $P = < 0.001$).

3.3.2. Gull predation

In 1996, kills/occupied burrow was not significantly different in forest (0.007 ± 0.006; range 0 - 0.02) and open habitat (0.004 ± 0.003; range 0 to 0.01; $F_{1,21} = 1.449$, $P = 0.2$). In 1997, again kills/occupied burrow was not significantly different in forest (0.016 ± 0.012; range 0 - 0.03) and open habitat (0.014 ± 0.010; range 0 - 0.03; $F_{1,29} = 0.143$, $P = 0.7$). In both years, predation was high in May and June, lowest in July, and increased slightly again in August (Fig. 10). There was a significant difference between years ($F_{1,49} = 14.7$, $P = <0.001$), with a greater number of kills/occupied burrow in both habitats in 1997 than in 1996.

3.4. Habitat changes

Based on a 1969 habitat map (Nettleship 1972) for Great Island, coniferous forest covered 59 % of the total area of vegetation, while grass-*Rubus* meadow covered

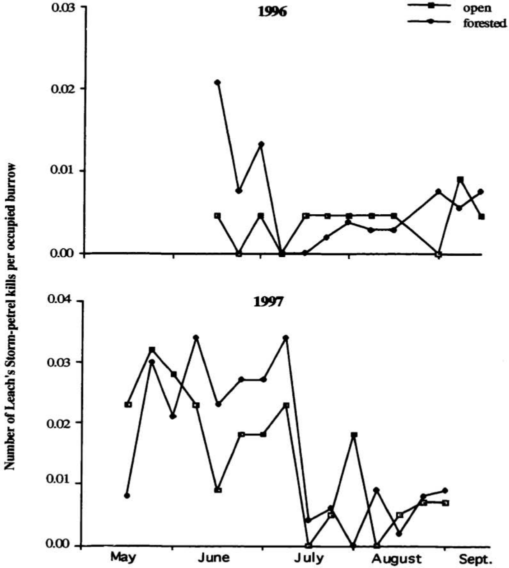

Figure 10: Number of Leach's Storm-petrels killed per occupied burrow in forest and open habitat on Great Island, Newfoundland, in 1996 and 1997.

14 % and grass-tussock slope covered 19 %. In comparison, a 1994 habitat map (Rodway *et al.* 1996) showed coniferous forest covering 42 % of the vegetated area, while grass-*Rubus* meadow covered 23 % and grass-tussock slope covered 33 % (Fig. 11). This suggests a decrease of 17 % in forest habitat, and an increase of 9 % in open habitat (grass-*Rubus*) over the 25 year period (Table 7).

Table 7: Percentage area of each habitat type on Great Island, Newfoundland, in 1969 (from Nettleship 1972) and 1994 (from Rodway *et al.* 1996) and the change in % area of each habitat over 25 years.

	Percentage area		
Habitat type	1969	1994	**Change**
Forest	59	42	**- 17**
Grass-*Rubus* (open)	14	23	**+ 9**
Grass tussock	19	33	**+ 14**
Exposed peat	7	2	**- 5**

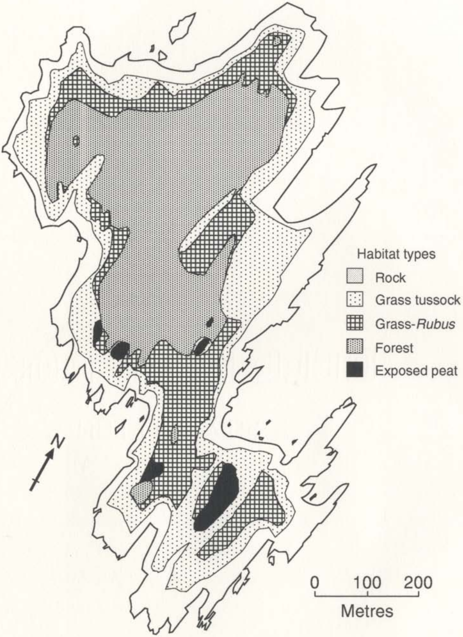

Figure 11: Distribution of habitat types on Great Island, Newfoundland, in 1994 (adapted from Rodway *et al.* 1996).

Chapter 4

DISCUSSION

The study design used in 1996, where study plots were chosen in areas of similar slope and aspect, proved to be difficult to work with statistically and may not have provided a good representation of the colony as a whole. However, the stratified random design used in 1997, likely provided an accurate representation of the entire colony, and allowed powerful statistical comparisons. The study was improved further in 1997, with fewer burrow interventions than in 1996, because storm-petrels may be susceptible to disturbance, particularly during the incubation period (Boersma *et al.* 1980, MacKinnon 1988). The general trends observed in 1996 were corroborated in 1997.

4.1. Forest and Open habitats

Clearly, there were distinct differences between forest and open habitats on Great Island. The forest had deeper peat and less compact soil than open habitat, and open habitat had a steeper slope than forest. Peat depth has been shown to be an important factor in habitat utilization in previous studies of Leach's Storm-Petrels (Harris 1974, Grimmer 1980, Watanuki 1985), and although soil compaction is thought to be extremely important in nest-site utilization in petrels (Harris 1974) it has rarely been considered (see MacKinnon 1988).

4.2. Reproduction in Forest and Open habitats

During the two years of this study, between 1.5 and 2 times as many burrows occurred in forested than in open habitat. All plots in forested habitat contained burrows, whereas 10 % of plots in open habitat contained no burrows at all. Besides showing a greater utilization of forest habitat, Leach's Storm-Petrels showed a preference for digging burrows on slopes in both forested and open habitats, with steeper sloping plots having greater burrow densities. Soil compaction may be related to slope, in that burrows dug in steeper slopes may provide better drainage.

Burrow activity was consistently higher in forested than in open habitat in both years and was positively related to burrow density. However, the proportion of active burrows may not provide a good indicator of the greatest habitat utilization, since many burrows showing signs of activity are not actually used for breeding (Hill *et al.* 1996, pers. obs.). Burrow occupancy was also consistently higher in forested than in open habitat in both years. The overall mean burrow occupancy rate was 65 %, consistent with occupancy rates previously recorded on Great Island, as well as in several other Atlantic colonies (Table 8). Burrow occupancy may provide the best indicator of habitat suitability, particularly continued occupancy over a series of breeding seasons, which is likely to reflect previous reproductive success in a given location. Occupancy rate had a positive relationship with both hatching and breeding success, which may suggest that sociality plays an important role in the breeding success of Leach's Storm-Petrels.

Virtually all occupied burrows in both habitats and in both years contained an egg. Consistent with the greater burrow density, forest habitat had a greater number of eggs laid per m^2 than open habitat. The high prevalence of eggs in occupied burrows in both habitats suggests that Leach's Storm-Petrels exhibit a constant reproductive effort

Table 8: Mean % occupancy and hatching success recorded at Leach's Storm-Petrel colonies in the northwest Atlantic.

Colony	Year(s)	% Occupancy	Hatching success	Source
Great Island, Newfoundland	1996-97	65	73	present study
	1982-84	65	68	Huntington *et al.* 1996
	1960	66	-	Huntington 1963
Gull Island, Newfoundland	1978	67	-	Grimmer 1980
Baccalieu Island, Newfoundland	1984	62	-	Sklepkovych & Montevecchi 1989
	1978	68	-	Grimmer 1980
Middle Lawn Isl., Newfoundland	1978	68	-	Grimmer 1980
Kent Island, New Brunswick	1955-95	-	76	Huntington *et al.* 1996
	1965	61	-	Wilbur 1969
Little Duck Island, Maine	1985-89	64	84	Huntington *et al.* 1996
Pearl Island, Nova Scotia	1975	63	-	Linton 1978

throughout their breeding life i.e. attempting to breed every year after breeding is initiated. Alternatively, birds that are not in suitable reproductive condition in any given year may simply not attend the colony. However, birds that are not in attendance are likely to lose their mate and/or their burrow, reducing their reproductive success in future years.

If egg breadth reflects age class differences in Leach's Storm-Petrels, as suggested by Grimmer (1980), the results of this study showed no evidence for age-biased occupancy of forest over open habitat.

Forest had more chicks per m^2 than open habitat, and was clearly the most productive habitat. Moreover, hatching success was also greater in forest than open habitat, suggesting that forest provides better, as well as more, breeding habitat for Leach's Storm-Petrels on Great Island. Overall mean hatching success on Great Island over both years was 73 %. This is similar to hatching success rates previously recorded in Atlantic colonies, which range from 68 % on Great Island in 1982-84, to 84 % on Little Duck Island, Maine, in 1985-1989 (Huntington *et al.* 1996).

Wing length is a reasonable index of chick age (Ricklefs & White 1975), and on average chicks in forest and open habitat were at similar developmental stages. In addition, chicks did not differ in mass, thus the results of this study showed no evidence for quality-biased occupancy of forest over open habitat. However, the timing of breeding was extremely variable in forest and open habitats in both years, with newly-hatched chicks appearing as others approached fledging i.e. there was no evidence of synchrony, at least on a colony-wide scale.

Breeding success was greater in forest than open habitat, supporting the hypothesis that forest provides better breeding habitat for Leach's Storm-Petrels on Great Island than open areas. Overall mean breeding success on Great Island over both years was 70 %. The difference between hatching success and breeding success was very slight, suggesting that the greatest mortality occurred during incubation rather than the nestling period.

Ideally, it would be useful to compare fledging dates for forest and open habitats, however, this proved to be impractical due to logistical and temporal constraints. The fledging period of Leach's Storm-Petrels is extended over many weeks, and investigation of fledging date is problematic due to the intense burrow exploration required. This may cause a high degree of disturbance, which is known to decrease growth rates and delay fledging in seabirds (Harris & Wanless 1984, Rodway 1994).

Under an ideal-free distribution, breeding success would be similar across habitats and breeding density would reflect qualitative differences between habitats. However, the higher breeding success observed in forest habitat in this study suggests that an ideal-free distribution is not operating on Great Island. Alternatively, if an ideal-despotic distribution was operating, breeding success would vary between habitats and breeding density would reflect both qualitative differences between habitats and dominance behaviour by individuals. This is more difficult to refute. Although there is an observed difference in breeding success between forest and open habitat in this study, little is known regarding the aggressive behaviour of Leach's Storm-Petrels, and the interaction between neighbouring individuals, at the breeding colony. Therefore, Fretwell & Lucas' (1970) assumption that habitat quality declines with density due to competition may or may not be appropriate in this situation. Given the advantages of breeding in forest over open habitat, the question of why Leach's Storm-Petrels breed in open habitat at all still remains.

4.3. Predation risk in Forest and Open habitats

Storm-petrels generally avoid mammalian predators by nesting on remote islands, however, avian predators are difficult to avoid and take their toll at colonies (Huntington *et al.* 1996). On Baccalieu Island, Newfoundland, a small native population of Red Foxes, *Vulpes vulpes*, depends largely on Leach's Storm-Petrels for survival (Sklepkovych 1986). However, the presence of foxes may in fact benefit the colony by preventing a potentially large number of gulls from nesting on the island (Montevecchi & Tuck 1987, Sklepkovych & Montevecchi 1989). Gull populations have increased steadily in the north Atlantic since the beginning of this century, particularly the Herring Gull (Kadlec & Drury 1968, Drury 1973, Howes & Montevecchi 1993, Chapdelaine & Rail 1997). The North Atlantic range expansion and population growth of these gulls has been supported and maintained by the increasing availability of human refuse and discarded fisheries waste (Kadlec & Drury 1968, Drury 1973, Furness *et al.* 1992). Since the eastern Canadian ground-fishery moratorium, introduced in the northwest Atlantic in 1992, massive quantities of fishery waste and discards from plants and vessels have no longer been available. Thus, the anthropogenically elevated gull populations have been forced to seek alternative food sources, and predatory pressures on other seabirds have increased considerably during the 1990s (Russell & Montevecchi 1996, Regehr & Montevecchi 1997). These events, in conjunction with centurially anomalous cold water temperatures in the early 1990s (Drinkwater 1996) that delayed the inshore movements of spawning Capelin, *Mallotus villosus*, by 4 weeks or more (Nakashima 1996) have intensified food stress on gulls (Montevecchi 1996, Regehr & Montevecchi 1997).

Pierotti and Annett (1991) found that Herring Gulls specializing in predation on Leach's Storm-Petrels nested significantly more often in open habitat than expected. In the present study, gull nests were over 2.5 times as likely to be found within 25 m of an open plot than a forest plot. In addition, forest plots that did have gull nests within 25 m of them tended to be near the forest edge or a clearing within the forest, suggesting that gulls nested near forest edges but not in densely forested areas (pers. obs.). In view of the close proximity of gull nests, the specialist predatory tendencies of these individuals, and a lower storm-petrel density in open habitat, there is likely to be greater predation risk for Leach's Storm-Petrels nesting in open habitat than for those nesting in forest.

Based on observations on Kent Island, New Brunswick, Grubb (1974) speculated that predation on Leach's Storm-Petrel by gulls was almost entirely confined to open terrain, and suggested that gull predation exerted a selection pressure for forest nesting. Predation levels in the present study, however, did not differ between forest and open habitats.

Predation was much higher in both habitats in 1997 than in 1996. In both years predation was high in May and June, lowest in July, and increased slightly in August. In a study of Leach's Storm-Petrels on Daikoku Island, Japan, Watanuki (1986) concluded that predation varied with gull energy requirements and the availability of storm-petrels. However, predation decreased dramatically on Great Island at a time when Leach's Storm-Petrels remained widely available and gull energy requirements were high.

The sudden decrease in predation during the last week of June in 1996 and during the first week of July in 1997 coincided with the inshore movement of spawning Capelin i.e. with the appearance of Capelin in the diet of both Common Murres, *Uria* *aalge*, and Atlantic Puffins on Great Island (C. Walsh & S. Wilhelm, pers. comm.). A switch in primary sources in the diet of Herring Gulls, from Leach's Storm-Petrels, Blue Mussels, *Mytilus edulis*, and garbage to Capelin and Short-finned Squid, *Illex illecebrosus*, was observed immediately after gull chicks hatched in early- to mid-June on Great Island in the late 1970s (Pierotti 1983, Pierotti & Annett 1987). However, the current dietary switch in Herring Gulls, observed indirectly through storm-petrel predation in this study, suggests that the hatching of gull chicks and/or the availability of alternate prey (i.e. the inshore movement of Capelin) is approximately three weeks later than in the late 1970s.

Capelin have spawned later in successive years in the 1990s (Nakashima 1994), and consequently the period of high predation on storm-petrels has likely been prolonged. In addition, with a move to offshore spawning in Capelin, also seen in the 1990s (Shackell *et al.* 1994), gulls may rely more heavily on storm-petrels as a prey source throughout the breeding season.

Gull predation at storm-petrel colonies is considered to consist largely of non-breeding storm-petrels (Morse & Buccheister 1977, Huntington *et al.* 1996). However, banding studies have shown that non-breeding storm-petrels tend to visit colonies mainly later in the season, in July and August (Scott 1970, Furness & Baillie 1981), when there is the greatest potential to use the success of breeders as a gauge of breeding habitat quality. In addition, if non-breeding Leach's Storm-Petrels mainly visit the Great Island colony late in the season, as suggested by observations of increased activity in late July (pers. obs., C. Walsh, pers. comm.), they may experience reduced predation risk at this time due to the dietary switches by gulls. In visiting the colony late in the season, prospecting birds may also increase their chances of identifying an existing suitable burrow which is unoccupied, thereby saving the time and energy, and avoiding risks, involved in digging their own burrow.

4.4 Habitat changes

Forest is optimal breeding habitat for Leach's Storm-Petrels. Forest habitat on small coastal islands is also dynamic, and changes in forest distribution may take place over a few decades. Since the late 1960s, the area of forest habitat on Great Island has decreased considerably, while open habitat has expanded. These habitat changes are thought to be caused by the actions of other nesting seabirds. Puffins are known to affect terrestrial habitats (Harris 1980), and on Great Island they disturb and damage tree roots by burrowing at forest edges. Gulls on Great Island roost on trees, particularly at the forest edge. The foliage of these trees is destroyed by the uric acid effects of the gull's guano. Areas where gulls are highly concentrated have many dead snags (pers. obs.). The observed pattern of habitat change may have been occurring on Great Island over a much longer period and is likely to have been intensified by increasing gull and Puffin populations (Montevecchi & Tuck 1987, Rodway *et al.* 1996). The long-term increase in gull populations has likely had a negative effect on the Leach's Storm-Petrel population, through the combined effects of habitat loss and increased predation pressure. The situation seems to have been further exacerbated by the indirect effects of fishery activities and later spawning in Capelin.

The Newfoundland colonies represent the largest breeding concentration of Leach's Storm-Petrels in the world, and together constitute over half the world population (Huntington *et al.* 1996). Given the sheer scale of these colonies, and the difficulties involved in accurately assessing numbers, investigations of habitat utilization, predation pressure and habitat changes are needed to improve understanding of the population dynamics and long-term protection of Leach's Storm-Petrels.

4.5. Summary

Leach's Storm-Petrels exhibit greater utilization of forest than open habitat on Great Island, Newfoundland. Overall the forest provides a consistently better breeding habitat, where hatching and breeding success are higher. It is speculated that this is largely due to lower soil compaction in the forest, which may allow easier digging. Leach's Storm-Petrels breeding in forest are less likely to be in close proximity to nesting gulls. Due to elevated gull populations that exploit human refuse and discards, indirect effects of the eastern Canadian ground-fishery moratorium that resulted in the cessation of massive tonnages of fishery discards in the northwest Atlantic, predation on Leach's Storm-Petrels has likely intensified during the 1990s. Predation on Leach's Storm-Petrels is greatly reduced following the inshore movement of Capelin. However, predation pressure may have been prolonged by the delayed inshore and the apparently increased offshore spawning in Capelin in the 1990s. Forest habitat is clearly more productive than open habitat. Forest coverage has decreased on Great Island over the last 25 years, while open habitat has increased. The combination of a loss in preferred habitat and an increase in predation pressure could have considerable negative effects on the productivity and population of Leach's Storm-Petrels on Great Island and potentially elsewhere.

Chapter 5

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