HABITAT SELECTION OF LEACH'S STORM PETREL (OCEANODROMA LEUCORHOA) IN THREE NEWFOUNDLAND COLONIES

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HABITAT SELECTION OF LEACH'S STORM PETREL (Oceanodroma leucorhoa) IN THREE NEWFOUNDLAND COLONIES

by

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ABSTRACT

Habitat selection of Leach's Storm Petrel (Oceanodroma leucorhoa) was studied in three Newfoundland colonies of this species. Habitat preferences as inferred by petrel burrow densities were examined and quantified (Study 1 and 2). Of habitat parameters studied, peat depth, tall vegetation and fern type vegetation were positively related to increasing petrel burrow density. Habitat preferences as a function of burrow density varied between colonies.

Burrow architecture was examined in one colony of petrels. Physical characteristics of the burrow may affect the internal microclimate of the burrow. Several burrow configurations were described which may serve to moderate internal burrow microclimates, maintaining a cool, stable environment in the burrow. The necessity for a cool, stable internal burrow environment is related to aspects of Leach's Storm Petrel life history which include early onset of nestling thermoregulation.

Eggs, hatching data and chick weights in a high burrow density (HD) area of one colony were compared with these measures taken in a low burrow density (LD) area of the same colony (Study 4). Non-significant differences in egg size were found between the two areas. No differences were found between the two areas in probability of hatching. HD area chicks were heavier and were more likely to be alone in the burrow on a given date than were LD area chicks.

A comparison of egg measurements from previous breeding seasons with the 1978 data suggests that egg dimensions (breadth and egg size) increase slightly with increased breeding experience of the female.

The ontogeny of habitat preferences was studied. The assumption that habitat preferences are mediated by habitat imprinting was tested (Study 5). Chicks from homogeneous biomes were allowed to choose between samples of their natal biome and a novel biome in a maze. Four age groups were tested. The test results were inconclusive, as chicks chose biome types randomly. Possible reasons for the experimental failure are discussed.

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INTRODUCTION

This thesis examines aspects of habitat selection by Leach's Storm Petrel (Oceanodroma leucorhoa) in Newfoundland. A study of this nature has not yet been systematically carried out in Newfoundland colonies of this species of bird. To this end, features of habitats differentially exploited by Leach's Storm Petrel were quantified, and ecological factors affecting burrow architecture, burrow status and breeding success were examined.

The literature review discusses: 1) general aspects of habitat selection by birds, 2) the habitat selection and preferences of Hydrobatidae and some of the Procellariidae throughout their Pacific, Atlantic and Antarctic distribution and, 3) relevant aspects of the breeding biology of Leach's Storm Petrel.

Habitat Selection by Birds

Although animals may be restricted to characteristic habitats because of behavioural and physiological responses to the environment (Wecker, 1963; 1964; Hilden, 1965; Klopfer & Hailman, 1965; Klopfer, 1969), a more parsimonious explanation is that the distribution of birds is representative of locations in the environment where breeding success is likely to be highest (Orians, 1971; Grant & Nettleship, 1972; Alcock, 1975). This implies that birds will evolve to be most receptive to suitable habitats (Orians, 1971) but do not necessarily select these habitats only on the basis of factors directly related to survival within the habitat (Svardson, 1949).

Habitat preferences of birds are frequently discussed as being governed by genetically mediated (innate) components or as the function of the experience of the individual (learned) or as some combination of genetic mediation and experience with the environment (Klopfer & Hailman, 1965; Hilden, 1965; Klopfer, 1969).

The degree to which habitat preferences of a species are influenced by one or the other components is a function of several aspects of the biology of a species (Klopfer, 1969). These influences include: 1) the peripheral and central neurophysiological capabilities of the bird which limit its perceptual world (Klopfer, 1969), and 2) the physical constraints and learning capabilities of the species which enable it to function most efficiently in certain habitats (Hilden, 1965; Klopfer, 1969). In some species of birds, rapid learning and attachment to habitat termed "habitat imprinting" occurs (Thorpe, 1944; 1945; Serventy, 1966). Imprinting here is defined as the development of stable preferences as a consequence of an exposure to a given set of stimuli at a particular developmental state (Klopfer, 1969). Although this type of effect is particularly relevant to precocial birds (Klopfer, 1969), it has been suggested (Serventy, 1966) that one species of procellariiform (Puffinus tenuirostris) and other species of altricial birds (Klinghammer & Hess, 1962) form attachments to habitats and environments in this way (Taylor & Taylor, 1964). Acquired habitat preferences may also be a function of a) socially guided learning whereby conspecifics guide or attract others to a nesting area (Klopfer & Hailman, 1965; Burger & Lesser, 1978) and/or b) site tenacity, which is the return to a particular breeding site for several or all of the breeding seasons of an individual (Hilden, 1965). This is known to be particularly strong in procellariiforms including Leach's Storm Petrel (Lien _et al._, 1977; Morse & Buchheister, 1979). A third major influence derives from the mode of development of a species. Altricial, nidicolous species of birds, being dependent on their parents, remain in the area of the nesting habitat and become accustomed to it. Precocial and nidifugous young are not physically constrained to remain with their parents and habitat preferences must be assured independent of habituation effects through habitat imprinting or genetically mediated preferences (Klopfer, 1969).

Habitat Preferences of Hydrobatids

The Hydrobatids, or the Storm Petrels, are a family of morphologically similar pelagic species distributed over most of the pelagic waters of the earch (Wilbur, 1969; Crossin, 1974; Ainley, Morrell & Lewis, 1976) which come to land only to breed. Although spending long periods of time at breeding colonies due to extended incubation and time to fledging of young (Gross, 1935; Huntington in Palmer, 1962), relatively little time is spent at the colony once the egg has hatched. They are with one exception (_O. tethys_ reported in

Harris, 1969), nocturnal on land (Ainley, et al., 1976).

There are several qualitative reports of the nesting habitats of hydrobatids in the Pacific Ocean along the coast of the United States (Harris, 1974; Ainley et al., 1976; Ainley, Lewis & Morrell, 1976), the Galapagos Islands (Harris, 1969) and other islands of the Atlantic and Pacific (Allan, 1962; Harris, 1969; Crossin, 1974).

Leach's Storm Petrel and the Ashy Storm Petrel (O. homochroa) have been reported breeding on North and South Farralon Islands off California since 1854 (Ainley & Lewis, 1974). Both species concentrate their nesting on the southeast quarter of South Island, under rocks in a south-facing talus slope (Ainley, Morrell & Lewis, 1976). This is an area of few or no nesting gulls. Predation by gulls has been implicated in the similar nesting habitats and times of the two species on the Farralons (Ainley, Morrell & Lewis, 1976).

Off the Northwestern coast of California, Ashy Storm Petrels, Leach's Storm Petrels and Fork-tailed Petrels (O. furcata) have been currently reported breeding on Little River Rock, and were previously known to nest on other small islands. Soil erosion caused by human intervention and the removal of vegetation, and the introduction of terrestrial mammalian predators caused the reduction and failure of Ashy Petrel colonies. On Little River Rock, Leach's Storm Petrels were only limited by the availability of soil in which to dig burrows, but preferred areas of nesting (as inferred from burrow densities of 1.2 burrows per square foot) where characterized by low brush vegetation and loose, easily excavated soils. Rock depressions were avoided. Burrows in grass sod (0.8 burrows per square foot) were less subject to collapse but more difficult to excavate. Extremely low burrow densities (0.3 burrows per square foot) reflected a lack of soil development around succulent vegetation. Fork-tailed Petrels were also flexible in burrow location, nesting in rock crevices and cavities, but preferring edges of banks and at northerly portions of their range, burrowing in soil (Harris, 1974). Gulls were common during the nesting season of the petrels and were a major source of predation on them. It was that author's opinion that the northern limit to petrel distribution (unless there were no diurnal predators) was created by the lack of nightfall in northern latitudes as the Pacific limit for Leach's Storm Petrels was St. Lazaria Island in Alaska, and southern Greenland, Iceland and the Faeroe Islands in the Atlantic Ocean.

Two species of storm petrels, the Madeiran Storm Petrel (O. castro) and the Galapagos Storm Petrel (O. tethys) are known to breed on the Galapagos Islands (Allan, 1962; Harris, 1969). The breeding habitats of these two species do not overlap although the breeding ranges do. The Madeiran Petrel is wide-spread in subtropical parts of the Atlantic and Pacific, on islands. Preferred nest sites on the Galapagos Islands were holes in cliffs or under boulders deep enough to hide the bird but not exclude light. A few burrows were located in soil or guano.

The Galapagos Storm Petrel concentrated its nesting on cliffs and lava fields in fissures between lava sections. Despite avian predation by the Galapagos Owl (*Asio galapagoensis*) it is diurnal on land.

The Madeiran Storm Petrel breeds on the smaller islands within archipelagos throughout the northern tropics and subtropics. The preference for smaller islands is attributed to the absence of terrestrial predation on these uninhabitable islands in a chain. Preferred habitats on islands were deep crevices in cliffs and burrows dug from under loose boulders. These sites were characterized by easy excavation and conspicuous boulders which could easily be identified by the occupants. Burrows were preferred to crevices and very steep cliffs were avoided. No preferences for leeward or windward sections of the island were noted despite the windward sides of the island being superior for hovering over the nest.

Off the coast of west central Baja California a subspecies of Leach's Storm Petrel, Chapman's Storm Petrel (*O. leucorhoa chapmani*), occupies every suitable habitat for nesting on the San Benitos Islands. The preferred areas were talus slopes and rocky areas. In these areas, they compete with the Black Storm Petrel (*O. melania*) and the Least Storm Petrel (*Halocyptena microsoma*) for nest sites under boulders and in cavities between rocks.

On Islote Negre, in the Guadelupe Islands, *O.l. socorroensis*, another subspecies of Leach's Storm Petrel, concentrated burrowing where large masses of volcanic rocks were present. These areas were favoured over the hard packed soil under the dense mats of plant material, although burrows excavated by Black-vented Shearwaters (P. puffinus opisthomelas) were sometimes occupied by petrels (Harris, 1974).

On the Phoenix Islands in the central Pacific, the White-throated Storm Petrel (Nesofregatta albigularis) preferred areas of bunch grass, large clumps of weeds or loose rocks. Rocky coral slabs without vegetation, or having only a short cover of vegetation, were avoided by these petrels.

Several species of Storm Petrels breed in the Antarctic (Maher, 1962; Beck & Brown, 1971; 1972). The breeding of the Blackbellied Storm Petrel (Fregatta tropica) is circumpolar but limited to islands near the Antarctic convergence. On Signy Island, they are restricted to the snow-free coastal zone of the island in areas of stable, lichen-covered scree. The nests themselves were well hidden cavities beneath boulders. Wilson's Storm Petrel (Oceanites oceanicus) also breed on Signy Island but have a broader range of habitats and nest in a wide variety of holes and crevices on talus slopes (Beck & Brown, 1971; 1972). Skuas preyed upon both species nocturnally. Snow Petrels (Pelagodroma nivea) breed in rocky areas on the perimeter of Antarctica and well inland. They locate in rock crevices which are fairly inaccessible to humans (Maher, 1962).

Reports of the nesting habitat of Leach's Storm Petrels in the Atlantic Ocean are general and lack quantitative details of habitat (see Gross, 1935; Ainslie & Atkinson, 1937; Palmer, 1962; Wilbur, 1969; Grubb, 1971; Drury, 1973; Morse & Buchheister, 1977; 1979). Generally restricted to islands because of vulnerability to terrestrial predation, and nocturnal because of diurnal predation by gulls (Larus marinus and L. argentatus) (Gross, 1935), Leach's Storm Petrels are reported to breed in burrows in grass islands (Drury, 1973) and in well-drained portions of rock-strewn meadows (Morse & Buchheister, 1979) and in spruce-fir forests on islands (Grubb, 1971).

The habitat preferences of the family Hydrobatidae are similar; however, the actual habitat selected varies between islands. For example, Leach's Storm Petrel is reported to prefer talus slopes on South Farralon Island (Ainley, Morrell & Lewis, 1974) because of the dearth of nesting gulls in this location. On Little River Rock, off the northern coast of California, the same species preferred habitat which was flat ground with low brush vegetation and loose soil. Harris (1974) felt that the availability of soil in which to burrow, and the ease with which a burrow could be excavated, were the prime determinants of optimal habitat for the petrels on that island.

Interspecific competition for nest sites has been reported between sympatrically nesting hydrobatids only on the San Benitos Islands (Crossin, 1974). Other sympatric hydrobatids avoid direct competition for nest sites by having flexible or slightly different preferred habitats and nest sites (Allan, 1962; Maher, 1962; Harris, 1969; Beck & Brown, 1971; 1972; Harris, 1974). Intraspecific competition for nest sites has not been demonstrated in hydrobatids in the Pacific or Antarctic species (Crossin, 1974) and Huntington (1963) presented evidence that nest site availability was not a limiting factor to populations of Leach's Storm Petrels, even in Newfoundland's largest and most crowded colony on Gull Island in Witless Bay.

Other factors influencing nest site selection by hydrobatids appear island dependent. Terrestrial predation and interference by domestic animals and rodents have been implicated in the decrease (Drury, 1973) and disappearance of storm petrels (Harris, 1974) from islands accessible to man. Avian predation both at the nest site and on the wing by gull and other birds (Gross, 1935; Harris, 1969; Harris, 1974) has resulted in burrow nesting or crevice nesting and nocturnality (Spencer, 1978). Ease of excavation of soil, conspicuousness of boulders marking burrows (Allan, 1962) and the availability of adequate (Harris, 1974) well-drained soil (Morse & Buchheister, 1979; Threlfall & Haycock, unpub. MS.) determined nesting habitat selection in Pacific and Atlantic storm petrel colonies. Surface vegetation plays an important role in burrow architecture, providing support for burrows but at the expense of facility of burrow excavation (Harris, 1974). Other effects of vegetation such as predator protection or insulation for burrows and conspicuousness have never been systematically examined.

Habitat Preferences of Burrowing Seabirds

Other species of seabirds (eg., some penguins and alcids, most of the Procellariidae and the Pelecanoididae) breed in burrows.

Puffins (Fratercula arctica) are colonial seabirds which burrow on islands. Habitat preferences of puffins in Iceland were quantified by assessing the environmental variables with which burrow density and breeding success were related (Grant & Nettleship, 1972). Factors which were negatively correlated with burrow density were vertical cliffs and soil cover of less than 20cm. Deeper soil and dense plant growth were positively correlated with burrow density, as was the presence of boulders. High burrow densities were advantageous because excavation of burrows was easier there and the landmark effect of the burrows decreased travelling time from sea to burrow and thus reduced predation by gulls and skuas. However, the distribution of burrows was neither uniform nor random, but strongly aggregated in assocation with certain habitat features, including boulders, vegetation and soil depth (Grant & Nettleship, 1972).

Crested Auklets (Aethia cristatella), Least Auklets (A. pusilla), and Parakeet Auklets (Cyclorrhynchus psittacula) nest sympatrically on St. Lawrence Island in Alaska (Bedard, 1969). The nesting habitat preferences of the three species were determined by correlating the density of birds of each species with aspects of their common habitat. A species's density in a given habitat was found to be under the structural control of the habitat substrate. The size of rock particles comprising substrate was critical to the numbers of individuals of each species because it regulated the number and size of interstices available as nest sites. For the Parakeet Auklet, food availability rather than the nest site options limited its numbers on the island. The Crested and Least Auklets' numbers were limited by the presence and abundance of suitable nest sites.

Shearwaters, like storm petrels, are burrow nesting procellariiforms which breed colonially on islands. They are pelagic when not at their breeding grounds (Rowan, 1952; Harris, 1966; 1969). Rowan (1952) described the Greater Shearwater (P. gravis) at its breeding grounds on Tristan da Cunha. On an island uninhabited by man at the time, the shearwaters burrowed in all habitats such as meadows, woods, tussock slopes, from the edges of low cliffs to the summit of a low plateau. The tussock-covered slopes were preferred habitat and the birds avoided pond areas where the soil was too waterlogged to support a burrow and also avoided burrowing in the penguin rookeries.

On Santa Cruz Island in the Galapagos, Audubon's Shearwater (P. l'hermenieri) nested in holes and recesses in the cliffs, among boulders, at the base of cliffs, and in a very few holes inland from the cliff tops (Harris, 1969).

In the British Isles, Manx Shearwaters occur on scattered islands off the western seaboard (Harris, 1966). The best known of these islands are Skokholm and Skomer where they burrow in the peat soil of grass meadows (Lockley, 1942).

Breeding Biology of Leach's Storm Petrel

Discussions of the breeding biology of Leach's Storm Petrel may be found in Gross (1935), Ainslie and Atkinson (1937), Palmer (1962), Wilbur (1969), Grubb (1971), Crossin (1974), Ainley, Morrell and Lewis (1976), and Morse and Buchheister (1977; 1979).

Leach's Storm Petrel range in adult body weight from 30-54 gm depending on the population (Spencer, 1978). It breeds colonially on islands in the North Atlantic and North Pacific from late April to October (Crossin, 1974; Morse & Buchheister, 1979).

When not at the breeding colony, the birds are solitary and pelagic and migrate to equatorial regions of the Atlantic and Pacific Oceans (Palmer, 1962; Crossin, 1974). Leach's Storm Petrels breed on distant and inaccessible islands where they are nocturnally active on land (Ainley, Morrel & Lewis, 1976). During the breeding season they forage offshore for small fish, cephalopods, siphonophores (Ainley, Morrell & Lewis, 1976) and euphausiid crustaceans (Linton, 1978).

In the North Atlantic, return to the breeding colonies begins in late April. Returning birds show extremely high fidelity to previous successful breeding sites (Lien, Grimmer & Spencer, 1977; Morse & Buchheister, 1979).

A single white egg comprising 20 percent of the female's body weight is laid in the nest chamber of the burrow between June and mid-July. Renesting after egg loss is rare. Incubation lasts

41-42 days and may be extended by temporary desertion during the incubation period. Incubation is shared by both members of a pair in average shifts of 2.7 days (1-5 day range) (Wilbur, 1969). Brooding of the nestling lasts from 1-3 days (Wilbur, 1969), and young Leach's Storm Petrels maintain body temperatures from at least the first week in life (Harris, 1974). Other species of procellariiforms (P. tenuirostris) (Farner & Serventy, 1959), have been reported to thermoregulate in burrows at hatching or within 1-2 hours of hatching. Adult body temperatures throughout the order are low and this is considered indicative of a low rate of basal metabolism (Warham, 1971).

Feeding of the nestling takes place at night in the burrow. The frequency of the feeding visits drops off grandually over time, until the chick is abandoned 1-3 days prior to fledging. Chicks fledge 62-70 days posthatch. Associated with the decrease in parental feeding is a decline in weight of the nestlings, completion of feather growth, and sojourns outside the burrow for wing exercise (Gross, 1935; Huntington, 1962; Ainley, Morrell & Lewis, 1976).

Procellariiforms typically experience deferred maturity and longevity. Most young birds do not visit the breeding colony until the age of three years, while breeding for the majority beings at five (Huntington & Burtt, 1972). There are reports of birds surviving for 16 years after initial banding (Huntington & Burtt, 1972) and in some populations, breeding birds have a minimum mean annual survival rate of at least 78.9 percent (Morse & Buchheister, 1977).

This thesis proposes to examine: 1) the habitat preferences of Leach's Storm Petrels on islands off the south and east coast of Newfoundland;

2) the environmental variables affecting habitat preferences and burrow architecture in one colony of Leach's Storm Petrel;

3) individual differences between petrels from high density areas and low density areas of this colony; and

4) the ontogeny of habitat recognition and preferences in nestlings of this species.

Study 1

Habitat Preferences of Leach's Storm Petrels

Introduction

Leach's Storm Petrel is known to breed at a number of sites in the Northwestern Atlantic, between northern New England and southern Labrador. The centre of the distribution is in eastern Newfoundland (Brown et al., 1975). The breeding habitat of Leach's Storm Petrel has never been systematically described although the literature contains reports of the breeding biology of this bird.

Study 1 attempted to assess the breeding habitat preferences of Leach's Storm Petrels nesting on the Lawn Islands, and quantify other variables affecting breeding on Middle Lawn Island.

Methods

The Study Area

The Lawn Islands (46° 55'N, 55° 36'W) are four small coastal islands off the Burin Peninsula (Figure 1). They are treeless islands, and the vegetation is primarily mixed grasses, ferns (*Dryopteris spinulosa*) and iris (*Iris versicolor*), underlain by peat. Middle Lawn Island, (350m by 400m; 61m in height), supports 26,000 pairs of Leach's Storm Petrels, which is by far the largest population of petrels on all four islands. As well, 4-5 pairs of Black Guillemots (*Cepphus grylle*) and one pair of Great Black-backed Gulls breed on the island. In the summer of 1977, Manx Shearwaters (*P. puffinus*) were first recorded breeding on the island (Lien & Grimmer, 1978). Offer Island (250m by 630m; 31m in height) supported a colony of approximately 200 pairs of Leach's Storm Petrels, 25 pairs of Great Black-backed Gulls, 900 pairs of Herring Gulls and numerous pairs of Blacklegged Kittiwakes (*Rissa tridactyla*). Columbier Island, (172m by 253m; 61m in height), supports approximately 100-150 pairs of petrels as well as large numbers of Herring Gulls and Kittiwakes. Swale Island (166m by 180m; 20m in height), supported no petrels in 1977 and about 75 pairs of Herring Gulls. On Middle Lawn Island, the population of Leach's Storm Petrels is increasing but

Figure 1. The Lawn Islands. Sample transects of 1978. Also shown is the location of the Lawn Islands in relation to Newfoundland. (After Johnson, 1978).

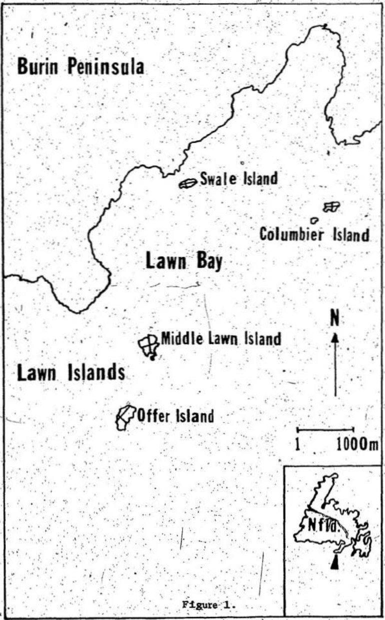
Burin Peninsula
Swale Island
Columbier Island
Lawn Bay
N
Middle Lawn Island
Lawn Islands
Offer Island
1
1000m
Nfld.

Figure 1.

on Columbier Island and Offer Island, the populations have decreased. No petrels were found nesting on Swale Island in 1977 or 1978.

Procedure

Habitat on each island was sampled by running two transects at oblique angles to each other across the four study islands. At 10 meter intervals along each transect, a m^2 quadrat was sampled for seven variables; (1) the number of burrows in the quadrat; (2) the number of burrows in each quadrat which had a bird with an egg, a bird with a chick or a chick in the nest chamber (a burrow which met one of these criteria was judged to be occupied); (3) the distance between the midpoint of the lower lip of each burrow entrance and the same point on every other burrow in the quadrat; (4) the depth of the soil in four places inside the quadrat and at the entrance of burrows if any occurred inside the quadrat; (5) slope; (6) the number of species of plants within the quadrat; (7) the percentage of cover afforded by grass, fern, iris, or infrequent species of vegetation. Variables two to seven were regressed on variable one, along with seven additional variables, which coded for the effects on burrow density of location on a particular island, location on a particular compass orientation and the interactions between island location and compass orientation (Kerlinger & Pedhazur, 1973). The simple multiple regression analysis was carried out using the Statistical Package for Social Sciences' subprogram Regression (Nie *et al.*, 1975).

Data collection took place on the following dates: Middle

Lawn Island, 15 June - 17 September; Columbier Island, 1 August - 5 August; Swale Island, 1 September; and Offer Island, 2 July - 5 July, 1977.

Slope was measured with a Brunton compass which was unavailable for use on Columbier Island and Swale Island. Slope was measured in all quadrats on Middle Lawn Island only, and analyzed in a simple multiple regression which included slope, pH, soil humidity, and other habitat variables measured there. Soil pH and humidity were measured with a hand-held commercial soil meter which was unavailable for use on Offer Island. Available soil pH data were analyzed in a 3 (island) by 3 (status of quadrat; ie. occupied burrow in quadrat, unoccupied burrow in quadrat, or no burrow in quadrat) analysis of variance. Past depths as a function of burrow occupancy and burrow preference in a quadrat was analyzed using a 2 (island) by 3 (status of quadrat) analysis of variance.

On five locations on Middle Lawn Island, the North slope, the East slope, the South slope, the West slope and at the highest point on the island, minimum-maximum thermometers were placed inside 0.5m sections of white p.v.c. drainage pipe ventilated with several 1 cm diameter holes and secured upright in the soil. Thermometers were read and reset daily, from 15 June to 1 September, 1977. Wind velocity was measured at the North slope thermometer from 15 June to 7 September, using a hand-held wind meter and compass.

In nine areas of Middle Lawn Island, 15 burrows in each area were assessed (total N=135) three or four times during the period between 15 June to 31 August, 1977. Burrows were included in the study on the basis of homogeneous biome, location on the island, and were all active with a bird and an egg when initially entered and staked. Chick weights were measured on 30-31 July and 29-31 August, and were analyzed in a 2 (biome type) by 2 (degree of slope of area) analysis of variance. The effects of this intensive interference in burrows were inferred from hatching success, (the number of eggs which hatched by 29-31 August/the initial number of eggs) x 100, and the number of abandoned burrows. Various burrow architecture parameters, (the length of the burrow, the number of turns in it, soil depth and humidity, soil pH and the mean distance to three nearest burrows), were regressed on chick weights.

Results

Habitat data: The direct multiple regression of the habitat variables on the number of burrows per quadrat yielded an overall $F_{13,132}=8.16$ (p.<01). Percent occupancy accounted for the greatest proportion of variance (31%); no other variables accounted for significant proportions of variance. Mean values for independent measures on all Lawn Islands are reported in Table 1.

Significant correlations occurred between the number of burrows per quadrat and each of the following: the percentage of occupied burrows ($r= .56, p<.01$), the percentage of ground cover by ferns ($r= .38, p<.01$) and a factor coding for Middle Lawn Island ($r= .46, p<.01$). Significant negative correlations occurred between the number of burrows per quadrat and a factor coding for Offer Island ($re = -.25, p<.01$). A factor coding for Columbier Island approached significance ($r= -15, p<.05$), as did peat depth in the quadrat ($r= .19, p<.05$). The percentage of occupied burrows was significantly correlated with the percentage of fern cover ($r=.35, p<.01$), and a factor coding for Middle Lawn Island ($r= .43, p<.01$).

The simple multiple regression of the habitat variables on Middle Lawn Island on the number of burrows per quadrat yielded an overall $F_{19,43}=6.81 (p<.01)$. Percent occupancy accounted for a significant proportion (16%) of variance in the regression. Significant positive correlations occurred between the number of burrows per quadrat and both the percent cover of fern ($r= .38, p<.01$), and the mean peat depth ($r= .22, p<.05$). Significant negative correlations occurred between the number of burrows per quadrat and the soil pH ($r= -.22, p<.05$), soil humidity ($r= -.28, p<.05$), and percent cover by grass ($r= -.25, p<.05$). Slope and peat depth were significantly negatively correlated ($r= -.41, p<.01$). Percent occupancy was significantly correlated with mean distance to neighbouring burrows ($r= .47, p<.01$) and the soil humidity ($r= -38, p<.01$).

On Middle Lawn Island, Columbier Island and Swale Island, there were no significant differences in the soil pH of occupied

TABLE 1

Mean (S.D.) of Habitat Parameters from Study 1

Parameter	Lawn Islands (n=145 quadrats)	Middle Lawn Island (n=55 quadrats)
No. of burrows/ m^2 quadrat	0.56(1.2)	1.23(1.57)
Percent occupancy	7.83(21.2)	20.4(32.3)
Mean peat depth (cm)	22.6(14.3)	26.3(10.5)
Percent cover		
fern	5.3(17.6)	12.2(23.9)
grass	43.3(32.5)	49.0(33.2)
iris	8.4(18.0)	12.9(22.5)
other	36.2(33.6)	26.0(28.1)
Plant species diversity (no. species /m^2 quadrat)	3.5(0.93)	3.5(0.74)
pH	---	5.8(0.4)
Mean distance to neighbouring burrows (m)	---	0.19(0.30)
Percent soil humidity	---	89.57(12.6)
Slope (°)	---	19.25(12.9)

burrows or unoccupied burrows, nor were there significant differences among islands regardless of burrow occurrence in a quadrat.

Peat depths on the quadrats on Middle Lawn Island and Offer Island showed no significant differences as a function of burrow occupancy or burrow occurrence in the quadrat. There was a significant difference between peat depths on Middle Lawn Island (mean=27.2cm) and Offer Island (mean=18.3cm), $F_{1,143}=4.37$ ($p < .05$). The average minimum-maximum temperatures for the give sites on Middle Lawn Island are presented in Table 2. There were no significant differences between the sites. Mean wind velocity is presented in Table 2. Mean wind speed was 15.2km per hour and prevailing winds were from a southwesterly direction. On stormy days, the winds were primarily from a north-northeast direction.

Chick weights and success: An anlysis of variance which compared the weights of chicks as a function of biome and slope yielded a non-significant $F_{1,91}=.01$. Chicks from sloped areas of the island were not significantly heavier than chicks from level areas of the island nor were chicks from fern biomes heavier than chicks from grass biomes. However, a significant interaction ($F_{1,91}=5.72, p < .05$) indicated that chicks from sloped, grassy areas were the heaviest in the sample.

The initial sample of occupied burrows was 135 on 18-26 June. Two other interventions in all study burrows were completed on 10-12 July and 25-27 July, and chicks weighed 25-27 July. On

TABLE 2

Mean Monthly Minimum and Maximum Temperatures (^oC) on Middle Lawn Island during June, July and August, 1977

Location	June min-max	July min-max	August min-max
North	8.2-15.0	9.6-19.6	11.4-20.3
South	6.5-16.5	9.6-19.6	11.6-20.2
Summit	8.2-16.0	10.4-19.4	12.6-19.3
West	7.7-18.2	8.9-21.3	11.5-21.1
East	8.3-18.6	10.2-20.3	11.9-19.2

Mean Monthly Wind Velocity on Middle Lawn Island during June, July and August, 1977

June		July		August	
Wind speed (km/hr)	Direction	Wind speed (km/hr)	Direction	Wind speed (km/hr)	Direction
32.7	SE 175°	12.6	SW 227°	11.8	SW 208°

29-30 July, the burrows were again entered and the chicks were weighed (with the exception of 11 burrows). At this time, 107 of the original burrows (79.3%) were still occupied. A fourth intervention on 24-28 September, 1977, relocated 106 of these 107 chicks (99%). These chicks were either fully feathered or the burrow was empty with no signs of predation mortality at the burrow. Some burrows were entered four times and some burrows were entered only three times. The number of interventions was negatively ($r = -.46$) but not significantly correlated with the number of chicks fledged per habitat area. No area fledged a significantly greater number of chicks and the rate of burrow abandonment was similarly uniform.

Burrow architecture parameters were regressed on the chick weights of 29-31 August. The simple multiple regression yielded a nonsignificant $F_{5,89}=1.27$. No variable correlated significantly with any other variable.

Discussion

The results were highly variable between all the islands when considered together and on Middle Lawn Island. Certain species of vegetation were positively related to the number of burrows per quadrat on all the islands. Variables related to island location or burrow location were not related to burrow density except on Middle Lawn Island where there was a higher mean density of burrows overall and a larger proportion of these burrows were occupied.

Comparing means of variables on all the Lawn Islands to means on Middle Lawn Island demonstrated that burrows on Middle Lawn Island were closer together, in deeper soil and were more likely to be occupied. The single variable that accounted for significant proportions of variance consistently on all islands was percent occupancy. Variables on Middle Lawn Island which accounted for relatively large amounts of variance did not account for similar proportions of variance when all the islands were considered together. This was taken to indicate that the petrels may be opportunistic in their breeding habitat selection on these islands. Furthermore, since the petrel population on Middle Lawn Island is increasing and the petrel populations on the other three islands are decreasing, it is suspected that petrels on Middle Lawn Island are beginning to utilize a broader range of habitats.

Although restricted to islands because of vulnerability to predation, once a colony is located on an island the habitat preferences of the petrels on the island may be influenced more by the nature of the available habitat rather than predetermined preferences.

Other data analyzed separately did not present a clear-cut picture either. For example, the pH of the soil, despite a significant negative correlation with the number of burrows per quadrat on Middle Lawn Island, was not significantly different in occupied burrows when compared to unoccupied burrows on Middle Lawn Island, Columbier Island or Swale Island. On Middle Lawn Island, occupied burrows had significantly lower soil pH's than the soil pH's of quadrats with no burrows in them. When unoccupied burrows on Middle Lawn Island, Swale Island and Columbier Islands were compared to quadrats with no burrows in them on the same islands, there were no significant differences in the soil pH's of either the islands or the burrows or quadrats. The biological significance of these findings may be negligible as Scott (pers. comm.) has expressed doubt that petrels change soil pH in and around their nesting colonies to an extent that the vegetation in the colonies would be affected. Furthermore, due to the small sample size of data collected on both Swale Island and Columbier Island, these results are to be interpreted cautiously.

Mean peat depth was significantly deeper on Middle Lawn Island than on Offer Island, when these two islands were compared, but was not different in quadrats with no burrows located in them, nor at unoccupied burrows or occupied burrows. In general, the caveat about small sample sizes holds for the data from these two islands as well, but on Middle Lawn Island alone, the mean peat depth in quadrats supporting burrows exceeded that of quadrats which supported no burrows.

Chick weights as a function of natal biome or slope were not significantly different, although chicks from flat, fern areas were significantly heavier (64.7 gm) than chicks from grassy, level areas (57 gm), grass slopes (60.1 gm) or fern slopes (53.2 gm).

There was no difference among these areas on the number of chicks presumed fledged by 24 September. The greatest mortality occurred during incubation of the egg. However, the mean percentage of eggs hatching from the initial sample was 85 percent (73-88% range) and all but one of these chicks survived to fledge. These rates of success compare with other studies of the breeding success of Leach's Storm Petrels which report success rates of 66-82 percent, from egg laying to fledging (Wilbur, 1969; Morse & Buchheister, 1979).

The negative correlation of the number of interventions with success does indicate the deleterious effects of entering a burrow.

The burrow architecture parameters could not be related to chick weights in any way.

The high degree of inter-island variability in habitat preferences of the petrels and the differences in the size of the petrel populations on the three islands which supported petrels made the results of this study inconclusive. The study of habitat preferences was therefore extended to two other islands which support much larger populations of Leach's Storm Petrels and a different sampling technique was employed.

Study 2

Habitat Preferences of Leach's Storm Petrel

Introduction

Study 2 was carried out in three large colonies of Leach's

Storm Petrels around Newfoundland. Field methods and statistical procedures were altered considerably. Sampling off a transect assured randomness (Smith, 1974) but habitat supporting no burrows was over-represented in the data. Furthermore, the range of the dependent measure (the number of burrows per quadrat) was from zero to a maximum of five. An alternative method of sampling which incorporated randomness and equal representation of preferred and nonpreferred habitat was achieved by sampling to a density criterion. The criteria used in Study 2 were arrived at by dividing the single continuous dependent measure of Study 1 into four dependent measures. A representative sample of petrel habitat on three islands was collected in 1978 and analyzed using a multivariate technique, discriminant analysis (Ferguson, 1971; Kerling & Pedhazur, 1973; Tatsuoka, 1975).

The Study Area

Gull Island (47° 15'N, 52° 46'W) lies off the east coast of the Avalon Peninsula (Figure 2). It is approximately 1600m long and 800m wide at its widest points. Eastward-facing exposures are of smooth cliffs, western cliffs are broken, overhanging cliffs with numerous ledges, north and south coastlines are indented with long, narrow coves. Maximum summer temperatures are about 27°C. Prevailing wind speed is 24.75 km/hour (Threlfall & Haycock, unpub. MS.). Vegetation above the rocky coastal slopes is grasses (_Festuca rubra_, _Deschampia flexuosa_), near sheltering vegetation such as dead trees or shrubs, red raspberry (_Rubus idaeus_) occurs. A forest of mixed species of trees

Figure 2a. Gull Island. Sample areas for Groups 1-4. (map of Gull Island after Threlfall & Haycock, unpub. MS.).

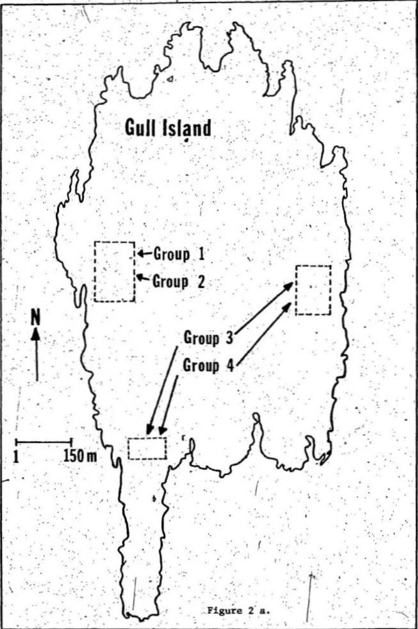

Figure 2 a.

Figure 2b. Gull Island in relation to the Avalon Peninsula and Newfoundland. (After Threlfall & Haycock, unpub. MS.).

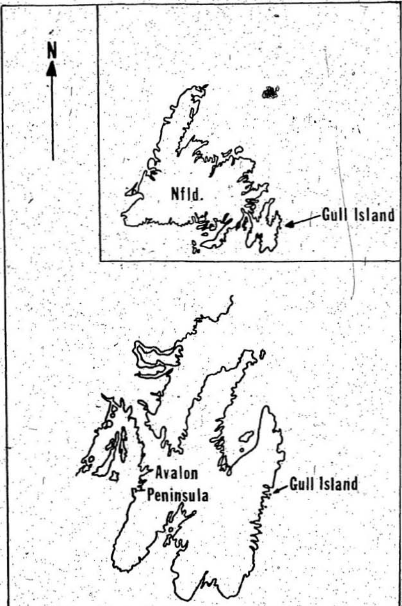

Figure 2 b.

covers the largest area of the island. The most abundant tree species is balsam fir (*Abies balsamea*) on the east and south sides of the island; on the south end, white spruce (*Picea glauca*) is common. Understory in the less dense forested areas is predominated by wood fern (*Dryopteris spinulosa*), shrubs and the seedling of the deciduous trees. Puffins, (50,000 pairs), Herring Gulls, (2,663 nests), Blacklegged Kittiwakes, (approximately 10,000 pairs), Razorbilled Auks (*Alca torda*, 37 pairs), Murres (*Uria aalge*, 316 pairs), and Black Guillemots, (14 pairs), were reported to breed on Gull Island in 1972. Petrels burrow everywhere that there is organic soil with the exception of wet areas and washouts (after Threlfall & Haycock, unpub. MS.).

Baccalieu Island, (48° 07'N, 52° 47'W) lies off the northwestern tip of Conception Bay (Figure 3). It is approximately 6km long and 1.3 km wide at its broadest points and rises to a maximum height of 122m. Vertical cliff faces of 50-75m punctuate the eastern and northwestern coastline of the island. Prevailing winds during the summer are from the south, with occasional winds from the north.

Coniferous forests of balsam fir and white spruce cover most of the northeastern and northwestern portions of the island. In some areas of the island the dense forest excludes light and there is no understory of shrubs and ferns. The edges of the forests, particularly in Group 3 and 4 areas are characterized by a thick understory of ferns, shrubs and mixed grasses. Areas not covered by forests are punctuated with rock outcropping covered with peat moss, grasses and ferns. In some of these areas there is little soil

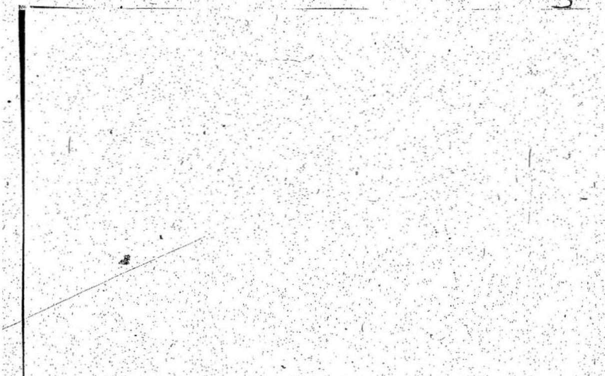

Figure 3. Baccalieu Island. Sample Areas for Groups 1-4. Location of Baccalieu Island in relation to Newfoundland. (After Montevecchi, Harvey, Kirkham & Purchase, in press).

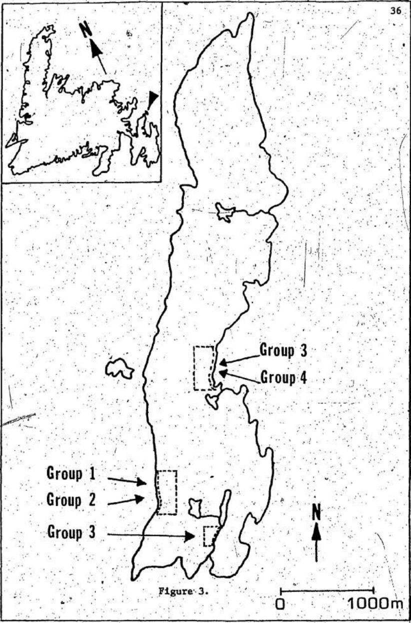

Figure 3.

deposition.

Several species of cliff-dwelling seabirds occur on the cliffs: North Atlantic Gannets (Morus bassanus), murres (Uria aalge and U. lomvia), Blacklegged Kittiwakes, Puffins, and Leach's Storm Petrels burrow in the soil (Montevecchi, Harvey, Kirkham & Purchase, in press).

The only mammalian predators on the island are red foxes and domestic animals (dogs). The foxes have been documented taking the eggs of all the species listed above and prey on the young and adult petrels which they dig out of their burrows (Montevecchi et al., in press).

Middle Lawn Island. (See Study 1 and Figure 4 for a description of this study area.)

Methods

Field methods: On each island, 40 m^2 quadrats were sampled in areas of the petrel colony which differed in visually estimated petrel burrow density. The areas are indicated on maps of the islands (Figure 1-3). Four groups were sampled with ten quadrats in each group; the total sample from each island was 40 quadrats. Quadrats were randomly placed in the study areas and then included in a group on the basis of burrow density within the quadrat; quadrats with zero burrows were assigned to Group 1, quadrats with 1-2 burrows were assigned to Group 2, quadrats with 3-4 burrows were assigned to Group 3 and quadrats with 5 or more burrows were assigned

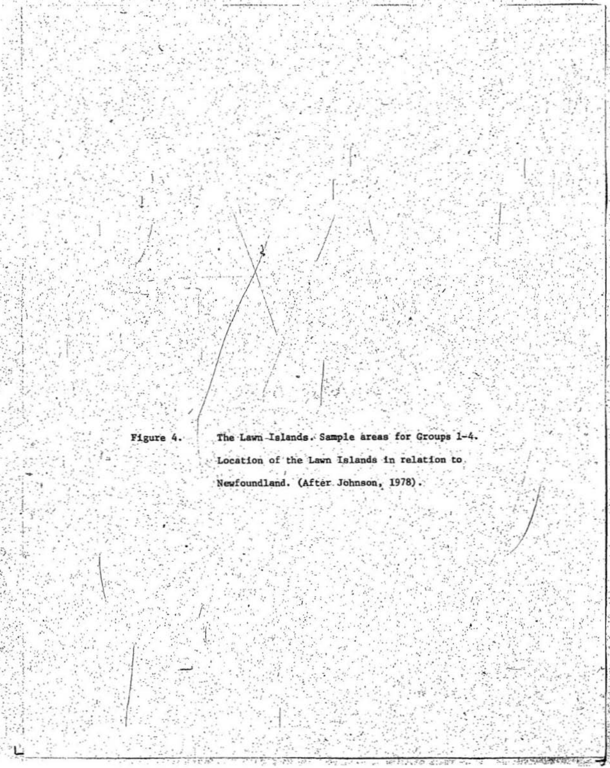

Figure 4. The Lawn Islands. Sample areas for Groups 1-4. Location of the Lawn Islands in relation to Newfoundland. (After Johnson, 1978).

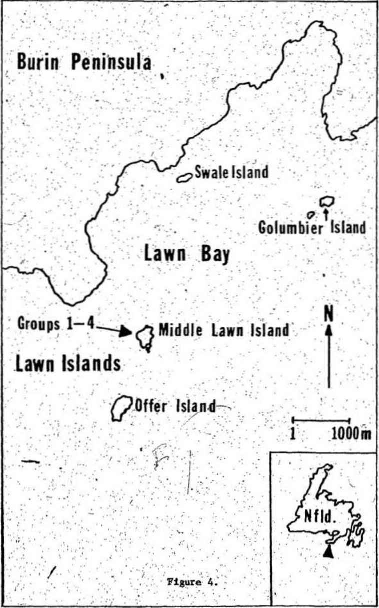
Burin Peninsula
Swale Island
Golumbier Island
Lawn Bay
N
Groups 1–4
Middle Lawn Island
Lawn Islands
Offer Island
1 1000m
Nfld.

Figure 4.

to Group 4. Occupied burrows (burrows with a bird and egg or chick, or a solitary chick, were considered occupied) and included in the sample.

Five measures were taken within each quadrat: (1) depth of soil in four places; (2) percent ground cover by plant species (estimated by assessing vegetation cover a 20 spots within the quadrat in a 4 x 5 matrix); (3) the number of species of plants; (4) the number of trees; (5) vegetation height from the surface of the ground to the top of the vegetation, excluding trees, in four places. From these five field measures, nine predictor variables were calculated. These nine predictor variables were then employed within the discriminant analysis. The nine predictor variables used were: (1) mean depth of the soil in the quadrat; (2) percent ground cover afforded by fern vegetation; (3) percent ground cover by grass species; (4) percent ground cover by moss species; (5) percent surface area which lacked vegetation; (6) percent ground cover by infrequent species of vegetation; (7) the total number of plant species or plant species diversity; (8) the total number of trees, both living and dead; and, (9) mean vegetation height.

The data sets from each island were analyzed separately. The similar scale of the predictor variables between islands rendered inter-island comparisons valid. Within each quadrat, the number of burrows and the status of all the burrows were recorded.

Statistical methods: Data was analyzed using a multivariate technique (see: James, 1971; Rice, 1978), discriminant analysis.

In general, multivariate analysis is concerned with several data groups which possess values on two or more predictor variables. Statistically significant group differences are sought on the basis of the interrelations among the predictor variables (Nie <u>et al.</u>, 1975; Tatsuoka, 1975). The dimensions along which group differences occur are linear combinations of the predictor variables and at the same time, geometric axes in space. Discriminant analysis is a statistical tool for determining a linear combination of the predictor variables that shows large differences in group means (Tatsuoka, 1975). Although conceptually analogous to multiple regression, with discriminant analysis the dependent variable is always group membership (Kerlinger & Pedhazur, 1973). To distinguish between groups of cases, predictor variables measuring characteristics on which the groups are expected to differ are sampled (Nie <u>et al.</u>, 1975). With three or more groups, a linear combination is sought that will maximize group differences between the groups relative to the differences within the groups (Kerlinger & Pedhazur, 1973). The subprogram Discriminant of the Statistical Package for the Social Sciences (Nie <u>et al</u>, 1975) was employed for the discriminant analysis.

In combining and weighing predictor variables, such that the groups are statistically as distinct as possible, one or more linear combinations of the form of:

$$D_i=d_{i1}z_1+d_{i2}z_2+\ldots d_{ip}z_p$$

are created. D_i is the score of each quadrat in a group on the discriminant function i, d is the weighting coefficient associated with a given predictor variable, z is the standardized value of the p predictor variables in the analysis. The discriminant scores are standardized ($\bar{x} = 1, s=0$), so each score represents the number of standard deviations that a quadrat is away from the mean for all quadrats on that discriminant function.

The mean of scores for the quadrats within a particular group is the group mean of that function. For each group, the mean on all functions is the group centroid. It is the most typical location of a quadrat from that group in the discriminant function space. Functions calculated by the program are arranged in order of decreasing importance (Nie et al, 1975) because each function is calculated from residual variance unaccounted for by preceeding functions (Kerling & Pedhazur, 1973). The location of group means along a particular function may be compared, keeping in mind that as residual variance decreases, group differences similarly decrease in significance. Differences on the first function are more meaningful than similar sized differences on later functions.

The Discriminant subprogram provided other analytic guides. The discriminant function coefficients (d_i) are analogous to beta weights of multiple regression. Calculated on standarized data, the absolute value of the coefficient represents the relative contribution to the function of its associated predictor variables. The sign denotes whether the variable makes a positive or negative contribution to the function. Coefficients may be used to name the function because they identify the dominant characteristics of a function (Nie et al., 1975).

Eigenvalues are also of analytic use. Each eigenvalue is a measure of the total variance existing in the discriminating variables explained by a given function. The relative importance of the associated function is indicated by the percentage of the total sum of the eigenvalues that a particular eigenvalue accounts for. The number of functions or the dimensionality of the discriminant space is determined by the number of eigenvalues associated with an analysis. It is the smaller of two numbers, either (K-1), where K is the number of groups, or p which is the number of predictor variables. The number of statistically significant functions may be even smaller because not all of the discriminant functions may represent dimensions along which statistically significant differences exist (Nie et al, 1975).

Canonical correlation in general is the correlation between two linear composites, one each for the dependent and independent variables. It is symbolized as R_c. In the discriminant subprogram, it is used as a means of judging the importance of a discriminant function. R_c measures the degree of association between the function and the set of (K-1) dummy variables which code group membership. It is indicative of how closely the function and the group variables are related. When the canonical correlation is squared, the value R_c^2 equals the amount of variance in the discriminant function explained by the groups.

The number of discriminant functions is mathematically limited to (K-1) or p. Either of these two values may exceed the number of functions needed to distinguish between groups. Wilk's lambda is a test of the significance of the difference between groups and the significance of the contribution to group differentiation of a function (Tatsuoka, 1975). By testing for the significance of discriminating information not already accounted for by earlier functions, it becomes a criterion for the elimination of superfluous functions. As lambda's value increases, it is an indication that there is less information remaining in subsequent functions. It may be transformed into a Chi square statistic for testing the difference between group centroids. The null hypothesis, that group differences after removal of the first discriminant function are due to sampling error, is rejected if the Chi square is significant. Otherwise, group differences are assumed to be the result of sampling error and no subsequent functions will be significant, if derived. Non-significant functions need not be derived for mathematical or analytical purposes if discrimination has been attained by previous functions (Nie et al., 1975; Tatsuoka, 1975).

Results

Gull Island

One function of the three possible functions, was statistically significant (Wilk's lambda= 0.06,$p<.01$). It accounted for 92 percent of the variance associated with the predictor variables. The discriminant coefficients of Function 1 are presented in Table 3. Mean vegetation height provided the best criterion on which to discriminate the four groups. The distribution of the group centroids is presented in Table 3. Groups 1 and 2 were close on Function 1, while 3 and 4 were separate from each other and the first two groups. The classification routine of the Discriminant program verified the group overlap between Group 1 and Group 2 by showing that statistically half the Group 2 quadrats were Group 1 quadrats despite the differences in petrel burrow densities between the groups. Overall, 67.5 percent of the quadrats were correctly classified.

Middle Lawn Island

Two of the possible three functions were significant. Those functions accounted for 90.8 percent and 9.1 percent of the variance associated with the predictor variables. Wilk's lambdas, canonical correlations and discriminant function coefficients associated with the functions are presented in Table 4. Coefficients of less than 0.1 are not reported. In both functions, the percentage of ground cover by fern is the best criterion on which to separate the groups. Group centroids on the two functions are presented in Table 4. Groups 1 and 2 scored highly along Function 1 and were characterized by a small percentage of fern cover, shallow soil, and low percentage cover by either grass or infrequent species of vegetation. Group 1 quadrats scored highly along Function 2 and were discriminated from the other groups primarily on the basis of having low vegetation. This function was interpreted cautiously as it

TABLE 3

Discriminant analysis on Gull Island

Function	Wilk's lambda	Canonical correlation
1	0.061	0.934
2	0.056	0.571
3	0.825	0.418

Predictor variable	Standardized coefficient
Mean vegetation height	0.766
mean peat depth	0.175
% ground cover by moss	0.172
% exposed ground	-0.148
% cover by ferns	-0.027
number of trees in quadrat	-0.014

Group centroids on the significant function

Group	Centroid on Function 1
1	-0.937
2	-0.887
3	0.643
4	1.181

TABLE 4

Discriminant analysis on Middle Lawn Island

Function	Wilk's lambda	Canonical correlation
1	0.004	0.989
2	0.176	0.903
3	0.956	0.210

Predictor variable	Standardized coefficient
Function 1	
% ground cover by fern	-1.097
% ground cover by grass	-0.248
mean peat depth	-0.149
% ground cover by infrequent species	-0.149
Function 2	
% ground cover by fern	5.991
% ground cover by grass	4.175
% ground cover by infrequent species	3.252
mean vegetation height	-0.999

TABLE 4 (cont'd)

Group centroids on significant Functions

Group	Function 1	Function 2
1	1.125	1.152
2	0.810	-1.355
3	-0.880	0.097
4	-1.056	0.106

accounted for a small proportion of variance. The classification subroutine indicated that 77.5 percent of the quadrats on Middle Lawn Island were statistically correctly classified.

Baccalieu Island

Three, of the three possible functions, were statistically significant. Wilk's lambda, canonical correlations and discriminant function coefficients are reported in Table 5. Function 1 accounted for 50.3 percent of the variance associated with the predictor variables, Function 2 accounted for 30.2 percent of the variance, and Function 3 accounted for 19.5 percent. The interpretations of the functions were weighted accordingly. Highly variable predictors were eliminated from the interpretation of the results (Tatsuoka, 1975).

Function 1 discriminates between Groups 1 and 3 on the basis of percentage ground cover by moss, grass and infrequent species of vegetation, the number of trees in the quadrats and peat depth. Group 3 quadrats scored highly along this function and were characterized by a low percentage of cover by moss, grass or infrequent vegetation, the deepest soil and the greatest number of trees of any area on the island. Function 2 best discriminated between Group 4 and the other three groups on the basis of plant species diversity, percentage of exposed ground, species and height of vegetation cover and peat depth. Group 4 quadrats were character-

TABLE 5

Discriminant analysis on Baccalieu Island

Function	Wilk's lambda	Canonical correlation
1	0.047	0.850
2	0.179	0.791
3	0.480	0.721

Predictor variable	Standardized coefficient
Function 1	
% ground cover by moss	-1.155
% ground cover by grass	-0.993
% ground cover by infrequent species	-0.931
number of trees	0.323
mean depth of soil	0.204
Function 2	
plant species diversity	0.903
% exposed ground	0.828
mean vegetation height	0.731
mean peat depth	-0.497
% ground cover by ferns	0.430

TABLE 5 (cont'd)

Predictor variable	Standardized coeffeicient
Function 3	
% ground cover by moss	-1.487
% ground cover by infrequent species	-0.945
% exposed ground	-0.758
% ground cover by grass	-0.465
% gound cover by ferns	-0.444

Group centroids on significant functions

Group	Function 1	Function 2	Function 3
1	-1.059	-0.451	-0.747
2	-0.332	-0.313	1.166
3	1.274	-0.579	-0.307
4	0.117	1.034	-0.112

ized by tall, diverse vegetation and the predominance of ferns. Function 3 discriminated between Group 2 and Group 3. Group 2 quadrats were characterized by very small percentage cover by moss, infrequent species of vegetation and exposed ground, and larget percentage cover by grass and some ferns. Eighty-six percent of the quadrats were correctly classified by the analysis. This is in part due to the power of the predictors and the number of significant functions (Tatsuoka, 1975).

Burrow occupancy rates and mean group values on the predictor variables are presented in Tables 6 and 7.

Discussion

Breeding habitat selection by the petrels on the three islands in the study was variable. This was similar to the results found in Study 1.

On Gull Island, high burrow density habitat was characterized by tall vegetation, deep peat, and trees. The low burrow density quadrats, and quadrats with no burrows in them fell close together on the single significant function. This habitat had shallow soil, trees, and short, sparse understory of moss vegetation. It is possible that most of the best habitat has been occupied on Gull Island and now petrels are beginning to cultivate marginal (Groups 1-2) habitat.

TABLE 6

Rates of Burrow Occupancy

Island	No. of burrows entered	Percent inaccessible	Percent occupied	Percent unoccupied
Gull Island	99	15.2% (15/99)	66.7% (56/84)	33.3% (28/84)
Middle Lawn Island	96	22.2% (22/96)	67.7% (50/74)	32.4% (24/74)
Baccalieu Island	99	26.3% (26/99)	68.5% (50/73)	31.5% (23/73)

Rates of Burrow occupancy on each Island by Group

Island	Group 2	Group 3	Group 4	Overall rate
Gull Island	50%	75%	66.6%	66.7%
Middle Lawn Island	75%	78.3%	56.4%	67.7%
Baccalieu Island	60%	72%	66.7%	68.5%

TABLE 7

Mean Group Scores on Predictor Variables on Middle Lawn Island, Gull Island and Baccalieu Island in 1978

Predictor variable	Group 1	Group 2	Group 3	Group 4
Middle Lawn Island				
mean peat depth(cm)	21.8	31.1	44.3	44.3
% fern cover	0	5.0	86.0	96.0
% grass cover	63.5	40.5	8.0	2.0
% moss cover	1.5	0.0	0.0	0.0
% exposed ground	5.5	0.0	0.0	0.0
% infrequent species	29.9	54.0	5.5	1.5
species diversity	3.8	3.6	3.4	3.1
number of trees	0	0	0	0
mean vegetation height(cm)	10.0	33.2	33.1	34.4

TABLE 7 (cont'd)

Gull Island				
Predictor variable	Group 1	Group 2	Group 3	Group 4
mean peat depth(cm)	27.6	28.3	44.7	55.0
% fern cover	0.0	0.0	56.0	59.0
% grass cover	0.0	0.0	0.0	0.0
% moss cover	10.8	17.5	10.5	6.5
% exposed ground	86.5	81.5	23.0	33.0
% infrequent species	3.0	1.0	10.5	1.5
species diversity	2.6	2.8	3.1	2.6
number of trees	0.1	0.6	0.2	0.0
mean vegetation height(cm)	4.8	2.8	42.0	59.9

TABLE 7 (cont'd)

	Baccalieu Island			
Predictor variable	Group 1	Group 2	Group 3	Group 4
mean peat depth(cm)	34.1	37.6	66.2	45.1
% fern cover	0.0	3.5	26.5	18.1
% grass cover	20.0	72.5	14.0	28.5
% moss cover	49.0	9.0	18.1	6.5
% exposed ground	0.0	2.0	33.5	16.5
% infrequent species	30.0	11.5	5.5	30.0
species diversity	4.4	5.2	3.1	5.1
number of trees	0.2	0.0	0.5	0.3
mean vegetation height(cm)	18.0	16.1	20.0	30.0

On Middle Lawn Island, the high petrel burrow density and moderate density (Groups 3-4) were close together on both significant functions, while Groups 1 and 2 were widely separated from each other and the other two groups. Groups 3 and 4 habitat had a large percentage of ground cover by ferns and deep soil. The location of Group 3 and 4 on both functions suggests that there is little qualitative difference between these habitats. Some good habitat is available to birds breeding for the first time. The divergent location of the Groups 1 and 2 suggested that if good habitat was not available, the alternative choice was different habitat from the habitat where no birds burrowed. This was unlike the results from Gull Island where Group 1 and 2 habitats were similar, which indicated that alternative habitat was the same as habitat where no birds located burrows. Non-utilized areas of Middle Lawn Island had shallow soil and low vegetation.

Baccalieu Island habitat, with a sparse, tall understory of ferns, and moderately deep soil and trees, was highly utilized by the petrels. Group 1 quadrats, in contrast, had no trees, few plants, and shallow soil.

The significance of burrow location strategies may be related to the survival value of such strategies and the nature of available habitat on an island. In this study, 67.7 percent of the accessible burrows on Middle Lawn Island were occupied when the burrow was entered, 67.7 percent of the accessible burrows on Gull Island were active, and 68.5 percent of accessible burrows were occupied on

Baccalieu Island. If the rate of occupancy is broken down by group (see Table 6), the largest numbers of occupied burrows occurred in Group 3 habitat. Although this might be a result of the intrinsic value of the habitat being reduced as the number of conspecifics in it increases (Orians, 1971), the occurrence of empty burrows argues against this. Huntington (1963) found that there appeared to be room for more birds even in areas of high petrel burrow density as 75 percent of the burrows entered on Gull Island were occupied and 66 percent of the burrows were occupied on adjacent Great Island.

The present data may reflect a change in breeding habitat selection by the petrels on these islands. Petrels may not be returning to Group 4 type habitats but are colonizing Group 3 habitats on the same island or leaving the colony. This is speculation which could be tested by consistent banding of adults and young over many years.

Factors other than nest site availability appear to be affecting the numbers of petrels in each area. The factors could be predation or habitat changes which render the burrows uninhabitable (eg. see Threlfall & Haycock, unpub. MS.) or emmigration of birds reared in Newfoundland colonies, (Huntington, 1963; 1973). Huntington (1963) has suggested that the Newfoundland colonies of Leach's Storm Petrels have a tremendous influence on other Atlantic colonies of petrels through the interchange of individuals.

Other species of burrowing birds (eg. puffins and auklets) are limited in location by the availability and depth of suitable soil

(Bedard, 1961; Grant & Nettleship, 1972). On all three islands in this study, the greatest number of petrel burrows occurred in the areas of deep peat soil. Possibly there is a minimum peat depth required for support of the burrows and this minimum may increase as the number of burrows increases. Peat could also serve to insulate and keep burrows dry. Habitat variables which were correlated with deep soil were tall vegetation and fern vegetation, and trees were also good indicators of peat depth when they occurred with tall understory such as on Baccalieu Island. Conceivably, petrels are guided to nest sites by vegetational characteristics which signal other necessary factors such as peat depth. Grant & Nettleship (1972) speculated that puffins return most rapidly to burrows which have a landmark feature beside them and that a rapid return to cover of a burrow increases the chances of survival. Other petrels (Allan, 1962) rely on conspicuous boulders to mark burrows. Tall vegetation or trees may serve a similar purpose for Leach's Storm Petrels on these island which requently experience avian predation by gulls (Ainslie & Atkinson, 1937).

Study 3

Burrow Architecture Characteristics

Introduction

Certain advantages are accrued by birds which burrow or live in crevices. These include the avoidance of predation (Morse & Buchheister, 1979), the avoidance of environmental fluctuations (White et al., 1978), and energy conservation (Kendeigh, 1960).

Leach's Storm Petrels burrow in peat soil on islands. Burrows consist of a straight or curved tunnel, terminating in a spherical nest chamber. Nesting material lines the bottom of the nest chamber where the single egg is laid. Incubation of the egg, brooding and feeding of the chick takes place in the nest chamber. Previous studies of the burrows on Middle Lawn Island (Lien, 1976; Lien & Clements, 1977; Spencer, 1978) demonstrated that turns in the tunnel are frequently the result of impediments to burrowing directly into the soil, such as root or rocks. However, there may be other functions served by the turns in the tunnels such as regulation of the burrows' internal climate. Burrow configuration affects acoustical properties such as standing waves generated by the burrow and attenuation of different sound frequencies. Both are features of the burrow which modify petrel vocalizations and their meaning (Lien, 1976). Physically, the burrows change with age as a result of the digging back of the nest chamber by each season's occupants (Lien, pers. comm.; Morse & Buchheister, 1979).

This study relates the physical characteristics of the petrel burrows on Middle Lawn Island to the daytime internal microclimate of the burrow and the status of the burrow.

Methods

During July and August, 1978, thirty burrows on the northeast exposure of the island, and twenty burrows on the southwest exposure were entered and marked with numbered stakes. These burrows were chosen at random within each area.

In each area, half the burrows were occupied at the time of the intervention, and half were unoccupied. All burrows judged occupied had birds with eggs or birds with chicks in them.

Interventions into the burrows were carried out during the day to minimize the disruption of the birds. The following measures were taken at each burrow: (1) slope, (2) direction of exposure on the island, (3) ambient air temperature, (4) surface air temperature below the vegetation, (5) air temperature in the tunnel, (6) nest chamber air temperature, (7) peat depth to bedrock at burrow entrance, (8) peat depth to the tunnel, (9) peat depth to the nest chamber, (10) distance to the five nearest neighbouring burrows, (11) percent ground cover by fern, grass, or infrequent species of vegetation, (12) the total length of the burrow, (13) the shape index of the burrow.

Peat depth at the burrow was measured by pushing a graduated metal rod into the ground and recording the depth that it penetrated. Peat depth from the ground surface to the tunnel floor and nest chamber floor was measured by dropping the rod into the tunnel or nest chamber and measuring the distance from the surface to the bottom of the tunnel or nest chamber.

On the surface of the ground, an arbitrary grid was placed over the burrow. The first set of (x,y) co-ordinates relative to the grid was at the burrow entrance. A turn in the tunnel or 25 cm from the burrow entrance was the location of the second set of co-ordinates. The third set of co-ordinates was taken in the nest chamber. From the co-ordinates and peat depths a surface map and a depth profile of the burrow was obtained.

Temperatures were taken in each burrow with a mercury thermometer dropped into the soil or suspended inside the burrow at the two locations where the metal rod had been used to measure peat depths.

Total length of the burrow was calculated by considering the distance between the co-ordinates as the hypotenuses of right-angled triangles, using the formula $a^2+b^2=c^2$. The value of c was taken to be the length between the first and second set of co-ordinates or the second and third set of co-ordinates as described above.

Once the distance between the burrow entrance and the tunnel and the distance between the tunnel and the nest chamber were obtained, these two values were summed to give the total length from the burrow entrance to the chamber. The ratio of the length from the entrance to the tunnel turn over the length from the tunnel turn to the nest chamber was calculated and this variable was termed the shape index of the burrows. The range of the index is from 0-2. A burrow with an index of one, for example, was interpreted as penetrating the soil vertically a distance equal to its length from the turn to the nest chamber. An index of two indicated that the burrow was deeper than it was long from the turn to the nest chamber.

The data were analyzed using a simple multiple regression, with the independent measures regressed on the dependent measure of burrow occupancy which was coded with zero for an unoccupied burrow and one for an occupied burrow (Kerling & Pedhazur, 1973).

Results

Significant correlations between variables are presented in Table 8. Means and standard deviations of independent measures appear in Table 9. The regression yielded an overall $F_{17,32}=5.52(p<.01)$. Frequency distributions of modal values of the variables are presented in Appendix A.

The burrows sampled were located on sloped ground on the island as this was characteristic burrow location (see Table 1). The data from study 1 indicated that slope and peat depth were negatively correlated on Middle Lawn Island, thus the mean peat depth of the soil in this study is 10cm less than the overall mean on the island.

The status of the burrow was not significantly correlated with any of the independent variables related to the habitat. Nest chamber air and soil temperature and tunnel soil temperature were significantly correlated with the burrow being occupied.

TABLE 8

Summary of Independent Measures from Study 3

Measure	Mean (s.d.)
slope	25.2 (13.0)
ambient air temperature (^0C)	22.2 (4.1)
surface air temperature (^0C)	19.7 (3.3)
tunnel air temperature (^0C)	15.5 (5.4)
tunnel soil temperature (^0C)	13.2 (4.6)
nest chamber air temperature (^0C)	17.1 (1.9)
nest chamber soil temperature (^0C)	15.2 (1.7)
mean distance to nearest neighbouring burrows (cm)	111.1 (42.5)
% fern cover	36.6 (45.1)
% grass cover	57.2 (43.1)
% other species cover	6.1 (6.4)
soil depth to tunnel (cm)	20.6 (8.2)
soil depth to nest chamber (cm)	23.2 (6.3)
overall soil depth (cm)	30.4 (12.7)
total length of burrow (cm)	40.8 (10.0)
shape index of burrow	2.0 (3.3)

TABLE 9

Summary of Significant Correlations between Variables in Study 3

Variable	Variable	r	p
nest chamber soil temperature	nest chamber air temp.	.71	.01
	surface air temp.	.40	.05
	tunnel air temp.	.36	.05
	nest chamber peat depth	-.41	.05
	% fern cover	-.30	.05
nest chamber air temperature	nest chamber soil temp.	.71	.01
	ambient air temp.	.55	.01
	surface air temp.	.53	.01
	tunnel air temp.	.36	.05
	tunnel soil temp.	.43	.05
	% grass cover	.32	.05
	overall peat depth	-.38	.05
tunnel air temperature	tunnel soil temp.	.96	.01
	soil depth to tunnel	.96	.01
	nest chamber soil temp.	.36	.05
	ambient air temp.	.33	.05
	surface air temp.	.29	.05
total burrow length	tunnel soil depth	.37	.05

TABLE 9 (cont'd)

Variable	Variable	r	p
total burrow length	tunnel soil temp.	.30	.05
surface air temperature	% cover grass	.28	.05
	% cover fern	.30	.05

Although the compass orientation of a burrow on the island was significantly correlated with ambient air and surface temperatures, this is an artifact of sampling the burrows located on the southwest area on warm parts of the day. Data summarized in Study 1 demonstrated that no exposure on the island was significantly warmer than any other although the rates of daily temperature change in these areas were not measured.

Soil temperature inside the nest chamber was correlated with nest chamber air temperature ($r=.71, p<.01$), surface air temperature ($r=.40, p<.05$), and tunnel air temperature ($r=.36, p<.05$) and negatively correlated with the nest chamber peat depth ($r=-.41, p<.05$) and the percent of cover by fern ($r=-.30, p<.05$).

Mean air temperatures in the tunnels and nest chambers of occupied and unoccupied burrows exceeded soil temperatures in the same spot by 2°C but were cooler than either ambient or surface air temperatures by 5-7°C.

Tunnel peat depth averaged 3cm less than peat depth to the nest chamber but nest chambers overall were warmer than tunnels. This may be due to the presence of a bird or a chick in the nest chamber. The temperature profile of the burrow during the day showed warm air outside the burrow, warm air inside the nest chamber and cool air in the tunnel.

Air temperature in the nest chambers was significantly correlated with nest chamber soil temperature ($r=.71, p<.01$), ambient air temperature ($r=.55, p<.01$), surface air temperature ($r=.53, p<.01$), tunnel air temperature ($r=.36, p<.05$), soil temperature in the tunnel ($r=.34, p<.05$), and percent cover of grass ($r=.32, p<.05$) and negatively correlated with peat depth at the burrow ($r=-.38, p<.05$).

The total length of the burrow was positively correlated with the depth of the soil over the tunnel ($r=.37, p<.05$), and the soil temperature in the tunnel ($r=.30, p<.05$). The correlation of total burrow length and overall peat depth approached significance ($r=.22, p<.05$).

Surface air temperature was 2.5°C lower than the ambient air temperature. Surface temperatures were positively correlated with percent ground cover by grass ($r=.28, p<.05$) and negatively correlated with percent cover by fern ($r=.30, p<.05$).

The frequency distribution of the burrow parameters as a function of burrow occupancy are presented in Appendix A and summarized in Table 10. The modal tunnel air temperature was the same (17°C) for occupied burrows as unoccupied burrows, but modal nest chamber temperature for occupied burrows (17°C) was two degrees warmer than in unoccupied burrows (15°C) . Similarly, the soil temperature of the tunnel (14°C) was not different in occupied and unoccupied burrows but nest chamber soil temperatures were higher in occupied burrows (16°, 17°C). The modal peat depth in occupied burrows to nest chamber was less (15-19 cm) than in unoccupied burrows (20-24 cm) but peat depth to the tunnels (20-24 cm) was not. Overall peat depth at the burrow entrance was 19.5 cm (average modal value) for unoccupied burrows, but for occupied burrows it was 24.5 cm. Occupied burrows were shorter than unoccupied burrows (35-39 cm compared to 45-49 cm). The burrow shape index was generally 2, indicating that the distance from burrow entrance to the turn was twice the length of the distance from the turn to the nest chamber in occupied burrows. This value was 1 in unoccupied burrows, indicating that the two distances were equal.

Discussion

Although previous studies of burrow structure on Middle Lawn Island were in general corroborated by this study, there were some differences. Lien & Clements (1976) found the northern and eastern exposures of the island to have colder soil temperatures than the southern and western exposures. This difference was attributed to the cooling effects of the wind and differential exposure to sun. In this study, no significant correlation was found between the direction of the exposure on the island and soil temperatures in the nest chamber or tunnel. Surface vegetation and peat depth over the burrow may affect internal soil temperature. Nest chamber soil temperature was negatively correlated with the percent cover of fern and the nest chamber peat depth. Occupied burrows had nest chambers which were closer to the surface than did unoccupied burrows and were warmer inside, although this may be in part due to the presence of a bird or chick. Lien & Clements data were collected in the early part of the breeding season before the vegetation growth was complete. This study on the other hand took place in August after

TABLE 10

Modal Values of Burrow Architecture Parameters as a Function of Burrow Occupancy

Burrow parameter	Occupied burrows	Unoccupied burrows
ambient air temp. (^0C)	21	18
surface air temp (^0C)	19	18,21
tunnel air temp. (^0C)	17	17
nest chamber air temp. (^0C)	17	15
tunnel soil temp. (^0C)	14	14
nest chamber soil temp. (^0C)	16,17	14
overall peat depth (cm)	20-24	20-24
mean distance to neighbouring burrows (cm)	70-79, 80-89	80-89
next chamber peat depth (cm)	15-19	20-24
tunnel peat depth (cm)	20-24	20-24
distance from entrance to turn (cm)	20-24	20-24
distance from turn to nest chamber	10-14	20-24
total length (cm)	35-39	45-49
shape index of burrow	2	1

such growth would be complete. It is possible that the ferns act as an insulator once they are grown because of their height and cover. This would explain the difference between the data, if the ferns negated the chilling effects of the wind on the soil in the breeding season.

No correlation was found between the shape of the burrow and the burrow orientation on the island. This is in contrast to Lien & Clements' data which showed that burrows located on the cold side of the island tended to turn sharply and burrows located on the warmer sites were straight, deep burrows. Seven of the 50 burrows were straight burrows and six of these seven were located on the northeast slope of the island. This difference may be because slope influences burrow shape to a greater extent than do other variables such as soil temperature or orientation on the island. This, also, is in contrast to the nesting of the Cactus Wrens (Campylorhynchus brunneicapillus), in which the direction of wind and ambient air temperatures significantly affect burrow orientation. Burrows are oriented to get maximum wind incidence as this has a cooling effect on the internal temperature of the burrow (Ricklefs & Hainsworth, 1969), which in turn increases the probability of nesting success in this species (Austin, 1974). On sloped ground, most burrows have turns in them probably because the shallowness of the peat in these areas prevents further digging. The average peat depth in the study areas was 30.4cm. Average modal overall peat depth of occupied burrows was 24.5cm, while that of unoccupied burrows was 19.5cm. Spencer (1978) demonstrated that, as peat soil compacted around a burrow, there was an increased probability of wetness inside the burrow. He concluded that peat soil depth was important to the drainage of the burrows. Threlfall & Haycock (unpub. MS) implicated burrow flooding in permanent burrow desertion by petrels on Gull Island. The data from this study are consistant with both of these findings. Occupied burrows were located in deeper peat soil than unoccupied burrows and may, therefore, have been better drained, drier burrows.

Other procellariiform nestlings, for example the Christmas Island Shearwater (P. nativitatis) thermoregulate better under cool conditions than under heat stress (Howell & Bartholemew, 1961). As well, thermoregulation in other species (P. tenuirostris)begins at hatching, or very shortly after, in the burrow. It has been suggested that Leach's Storm Petrel can thermoregulate within a week of hatching (Farner & Serventy, 1959). These aspects of the life history of other procellariiforms may be relevant to Leach's Storm Petrels, considering that the burrow seems to be constructed to maintain stable, cool temperatures inside. This is similar to the function of burrows built by other birds within the same order (Farner & Serventy, 1959).

The temperature profile of the burrow during the day would maintain air circulation in the burrow by convection alone, in the absence of wind. Although temperatures were never measured at night, it is assumed that ambient temperatures would be lower than temperatures inside the burrow and the differential would again serve to maintain air circulation. Night-time air movement would be facilitated by nocturnal visits of the adult birds whose movements along the tunnel would act as pistons to force air circulation (White et al., 1978). Petrels on inshore islands would rarely have to contend with windless days or nights (see Study 1) when air would have to be circulated by convection alone. Furthermore, air turnover inside the burrow is more rapid as the airspeed of the wind increases and is enhanced by a slightly flared burrow entrance or location on sloped ground, thus the petrels have several structural options open to them which create a functionally similar burrow. Indeed, with the high incidence of wind on the islands, it is conceivable that the tunnel turn serves to slow down air as it enters the burrow and thus reduces the cooling effect of wind. The importance of air circulation for the petrels is evidenced by the relative shortness of their burrows when compared to the burrows of other birds (eg. Merops apiaster) which averaged 100cm in length (White et al., 1978), compared to the average length of petrel burrow in this study, which was 40.8cm. As well, short petrel burrows generally have one entrance but long burrows may have two (Lien & Clements, 1977).

The nature of vegetation surrounding the burrow may have an indirect effect on the internal temperature of the burrow as surface temperatures in fern biomes were slightly cooler than in grass biomes, and the nest chamber air temperature was significantly positively correlated with the percentage of ground cover by grass. However, both were relatively small significant correlations.

The role of peat in drainage and insulation of the burrow was inferred from some of the data. Modal peat depths at burrow entrances of occupied burrows exceeded the overall modal peat depth of unoccupied burrows. This was related to drainage in the burrows and the possible reduced probability of wet, unoccupiable burrows.

If peat provides insulation for burrows, then the degree of the cooling effect of peat may be related to the peat depth over the nest chamber. In fact, although modal peat depths to the tunnels of occupied burrows and unoccupied burrows were the same, modal peat depths to nest chambers of occupied burrows was less than modal peat depth to nest chambers of unoccupied burrows. Considering the significant negative correlation between nest chamber soil temperature and nest chamber soil depth, burrows with less peat over nest chambers are likely warmer burrows, while still not being subject to daily temperature fluctuations. Again, this construction provides another alternative of burrow architecture which moderates internal burrow temperatures.

Study 4

Egg Measurements

Introduction

Differences in breeding success and clutch size as a function of nesting locations densities have been demonstrated in Ring-Billed gulls (L. delawarensis; Dexheimer & Southern, 1974; Somppi, 1978), Laughing Gulls (L. articilla, Montevecchi, 1978), puffins (F. arctica, Grant & Nettleship, 1972; Nettleship, 1972) and nesting density in Kittiwakes (R. tridactyla, White & Coulson, 1960; Coulson, 1968). These differences are frequently attributed to birds from dense central areas of a colony being older and breeding earlier than birds nesting in peripheral, less dense areas of the colony.

Egg size (breadth^2 x length) has been directly related to age of the adult bird in kittiwakes (Coulson, 1963; 1966), Short-tailed shearwaters (P. tenuirostris, Serventy, 1966), and Buller's mollymawk (Diomedea bulleri, Richdale & Warham, 1973). In this study, the size of eggs, probability of hatching, and weights of chicks from burrows located in high burrow density areas of Middle Lawn Island were compared to the same measures taken of eggs and chicks in low density areas of the island.

Davie (1889) and Reade and Hosking (1967) describe Leach's Storm Petrel eggs as being shaped much like a pigeon's egg. It is white in colour with a fine spattering of minute dots of reddish brown or pale lavender. Average size of 50 eggs is 3.57 cm by 2.70 cm in Davie's (1889) report.

Spencer (1978) found that the date of egg laying was inversely related to the breadth of the egg for petrels on Middle Lawn Island. Eggs laid later in the breeding season were narrower and longer than those laid early in the breeding season. This relationship is consistent with the hypothesis that breeding experience is associated with earlier laying and the production of shorter, wider eggs. In his studies on homing by Leach's Storm Petrels, Spencer also found a weak relationship between the ability to home and the breadth of an egg, presumably because older petrels are experienced navigators or more dedicated parents.

The predictions made here are that petrels from high burrow density areas of Middle Lawn Island produce larger eggs than birds from low density areas. Differences on these measures may be related to the age of the bird producing the egg, and the probability of the egg hatching.

Methods

Between 10-14 June, 1978, Leach's Storm Petrel burrows on Middle Lawn Island were examined to assess the status of the burrow. On the Northeast slope of the island, mean interburrow distance was 0.5m and this area was designated as a high burrow density area (HD). A total of 151 burrows were entered to obtain the sample of 50 eggs. Length and breadth at the maximum point on each egg were measured with calipers, to the nearest 0.01cm. Burrows entered were marked with numbered stakes. The same procedure was followed for a low burrow density area (LD) on the East and South sides of the same island where mean interburrow distance was 1.46m. A total of 153 burrows were entered to obtain a sample of 50 eggs. Eggs in burrows unoccupied by adults were included in the sample if they appeared white and semi-translucent, as petrels frequently desert fresh eggs for periods of up to one week (Wilbur, 1969; Pefaur, 1974). Egg size was calculated as length x maximum breadth^2 (Romanoff & Romanoff, 1949). The shape index was calculated as maximum breadth x 100/length (Coulson, 1963; Ryder, 1975).

On 31 July and 1 August, 1978, the status of the HD and LD area burrows was reassessed. The numbered stakes were relocated and the burrows entered. The chick, if present, was weighed with a 100gm pesola scale.

Data collected by Spencer on Middle Lawn Island in 1975 and 1976 are used, with his permission, to relate egg size to age of adult. Data on egg size and adult body dimensions collected on Baccalieu Island in 1978 are used with permission of Dr. W. Montevecchi.

Results

The results of the egg dimension study and the re-interventions are presented in Table 11. In all dimensions of egg size, the HD eggs exceeded the LD eggs but these differences were not statistically significant. Shape index data indicated a slightly shorter, broader egg from the HD areas of Middle Lawn Island.

Of the original 50 HD burrows, 42 were relocated and entered on 1 August (Table 11). Forty-seven of the 50 LD area burrows were relocated and entered on 1 August. Interventions into HD area burrows were carried out 29-31 July, one day sooner than LD area burrows, but there were fewer birds with eggs, no brooded chicks, and mean chick weight was 32.4gm. This was 3.7gm heavier than the LD mean chick weight of 28.7 gm. LD area burrows had a greater number

TABLE 11

Egg Dimensions from Middle Lawn Island in 1978

Dimension	High density area (n=50)	Low density area (n=50)
mean length(mm,s.d.)	32.89 (1.08)	32.76 (1.09)
mean breadth (mm,s.d.)	24.00 (0.74)	23.90 (0.66)
mean egg size (s.d.) (1 x b^2)	18.93 (1.34)	18.27 (1.32)
mean shape index (s.d.) (b x 100/1)	73.04 (0.24)	72.81 (2.55)

Results of Reintervention

Measure	High density area 31 July/78 (n=42)	Low density area 1 August/78 (n-47)
% birds with eggs	16.6	19.0
% birds with chicks	0.0	6.4
% sole chicks	71.4	68.0
% adults birds alone	1.9	1.8
% chicks 35 gm wt.	43.3	28.1
mean chick weight (gm)	32.4 (10.2)	28.7 (10.7)*
% empty burrows	7.1 (3/42)	4.8 (2/47)

* not significantly different

of birds with eggs, brooded chicks, and a smaller percentage of solo chicks. Although individual differences were not significant, this pattern clearly indicates earlier laying and older chicks in the HD area.

The larger percentage of empty burrows in the HD area is an unexpected result, although the actual number of empty burrows is not great. In HD areas, 3 of 42 burrows were empty.

During the summers of 1975 and 1976, Spencer collected data on egg size of the Petrels on Middle Lawn Island. Combined with data collected in 1978, it seems to indicate a direct, if weak, relationship between egg size and the age of the female in Leach's Storm Petrels. The data are presented in Table 12. Several trends are evident. Romanoff & Romanoff (1949) demonstrated that breadth and size are most sensitive to age effects in birds. Six of nine (67.7%) birds whose histories were available showed increases in the breadth of the egg laid in 1978 when compared to the breadth of the egg laid in 1975 or 1976. In this sample, five of nine eggs (56%) showed an increase in length with age. The overall mean egg size is 18.84cm^3; the combined mean for 1975 and 1976 is 18.54cm^3; and the 1978 mean is 19.15cm^3, indicating an increase of 0.61cm^3 over two years. The shape index also increased from 72.56 in 1975-76 to 73.81 in 1978, indicating that 1978 eggs were shorter and broader than the 1975-76 eggs associated with the same adult.

In addition, while intervening in burrows on the island

TABLE 12
Size Change in Leach's Storm Petrel Eggs as a Function of Age

Band no. (75/78 borrow)	75/76 dimensions (l x w,mm)	78 dimensions (l x w,mm)	△ l	△ w	△ Egg size (cm^3)	76 Shape Index	78 Shape Index	△Shape Index
791-59703 (1137/576)	31.1 x 24.14	34.0 x 24.0	+2.9	+1.86	+4.86	77.62	76.47	-1.15
761-59329 (726/726)	30.96 x 30.82*	30.9 x 25.6	-0.6	+1.78	+2.68	76.94	82.85	+5.91
761-59190 (710/710)	33.92 x 24.68*	33.4 x 24.0	-0.5	-0.68	-1.42	72.76	71.86	-0.90
791-32086 (681/681)	33.74 x 23.44	34.3 x 23.8	+0.56	+0.36	+0.88	69.47	69.39	-0.08
761-42945 (412/412)	32.16 x 23.28	32.2 x 23.3	+0.04	+0.02	+0.51	72.39	72.36	-0.03
761-59742 (658/658)	32.04 x 24.12	32.3 x 24.2	+0.26	+0.08	+0.28	75.28	74.92	-0.36
761-42923 (358/358)	32.64 x 23.92	32.1 x 23.1	+0.54	-0.82	-0.15	71.11	71.96	+0.85

* data from 1976 breeding season; all other data is from 1975 or 1976 as indicated.

TABLE 12 (cont'd).

Band no. (75/78 burrow)	75/76 dimensions (l x w,mm)	78 dimensions (l x w,mm)	Δl	Δw	Δ Egg size (cm^3)	76 Shape Index	78 Shape Index	ΔShape Index
761-59070 (520/520)	32.28 x 23.34	33.2 x 24.3	-1.08	+0.96	+ 0.93	68.09	73.19	+5.10
761-59174 (525/525)	33.74 x 23.42	32.4 x 23.1	-1.34	-0.32	-0.12	69.41	71.30	+1.89

TABLE 13

Egg Dimensions from August 1978

Dimension (n=17)	$\bar{x}$
mean length (mm,s.d.)	32.88 (1.29)
mean breadth(mm,s,d.)	23.88 (0.37)
mean size(l x b^2, s.d.)	18.77 (1.07)
mean shape index(s.d.)	72.67 (4.22)

during August, 1978, dimensions of any viable egg were taken (Table 13). Between 3 August and 9 August, seventeen eggs were found. All but one of these eggs were accompanied by incubating adult petrels and two were pipping eggs. These burrows had not been previously disturbed during 1978. Eggs encountered early in August were probably laid during the last week in June or early July, making them late eggs. The mean breadth of eggs encountered was 23.88 mm, mean length was 32.88 mm. Mean egg size was $18.77 cm^3$, and average shape index was 72.61. In all measures but mean length, the eggs measured from LD and HD areas on the island in June exceeded the measures of the eggs encountered in August. This finding supports Spencer's data. The shape index indicated that the August eggs were narrower, relative to their length, than those eggs measured earlier in the breeding season.

Discussion

Measures on eggs from burrows located in LD areas were slightly smaller than eggs from burrows located in HD areas on the same island. None of these differences was statistically significant, but to gain perspective on the magnitude of these differences, the differences in egg size described above were compared with differences reported in studies of other procellariiforms.

Leach's Storm Petrels begin to breed at the age of four to five years (Huntington & Burtt, 1970). Birds first banded while incubating an egg, in 1975, may have been about eight years old by 1978. Assuming two breeding seasons between 1975-76 to 1978, the average increase in breadth over the two years is 0.79mm for eggs which average (n=100) 32.83mm. This is an increase of 2.4 percent. Serventy (1966) examined egg size in relation to age in the short-tailed shearwater. The sample of breeding females had been studied for a minimum of ten breeding seasons. From Serventy's data for female shearwaters, aged five to eight years, the increase over two years in egg breadth was 1.2mm for eggs which average (n=100) 47.10mm, a 2 percent increase. Similarly, Buller's mollymawk showed average increases in breadth of 2.01mm for eggs which range between 67.5mm and 64.5mm in breadth. This is an increase of 3 percent over thirteen breeding seasons. The petrels seem to be experiencing an increase in egg breadth with age and breeding experience which is typical of the order.

Spencer (1978) presented data demonstrating an inverse relationship between egg size and date of egg laying in petrels. Larger eggs were laid earlier in the breeding season. This finding is supported by the present data. Eggs found in burrows during August were narrower and slightly shorter than eggs found during early June. It is suggested that older petrels laid slightly larger eggs sooner during the breeding season than did young or inexperienced birds which laid smaller eggs, later in the season. The effect of the small but consistent egg size differences on hatching was not clear in this study as there appeared to be no relationship between the two variables.

The HD area chicks weighed an average of 3.7gm more than the LD area chicks. It was suggested that this difference occurred because the HD chicks were older, as fewer HD chicks were being brooded at the time of the intervention. Data on Blacklegged Kittiwakes (Coulson & White, 1960), and puffins (Nettleship, 1972) supports this idea. More older chicks occurred in high density areas of kittiwake colonies on a given date than in low density areas of the colony. This difference was attributed to the earlier nesting of experienced birds (White & Coulson, 1968). Nettleship (1972) demonstrated that puffin chicks from sloped, high burrow density areas were heavier and fledged sooner than chicks from low density habitats. The difference in fledging dates between the two areas was related to the earlier date of egg laying by birds nesting in the sloped habitats.

Huntington (1962) suggested that Leach's Storm Petrels have occupied an ecological niche based on an inefficient feeding method which prevents it from threatening its own food supply. Age and experience of an adult would increase its ability to forage effectively and the ability to rear a chick (Lack, 1968). It is possible that the weight differences in chicks from the two areas was, in part, also due to differences in the age and experience of the parents and the improvement in parenting which is commensurate with experience of the adults.

Although a limited age-egg size relationship has been demonstrated, it may be that egg size covaries with body size only. Montevecchi's data from Baccalieu Island refute this hypothesis. Neither adult body length nor adult body weight was significantly correlated with egg breadth or egg size. Large Leach's Storm Petrels do not necessarily lay large eggs.

Study 5

Recognition of Vegetation by Chicks

Introduction

Young birds and animals form rapid attachments to habitat characteristics of their environments. This phenomenon is referred to as habitat imprinting (Thorpe, 1944; 1945, Wecker, 1963; Serventy, 1966). These early attachments influence subsequent habitat selection by adult organisms (eg. Peromyscus maniculatus, Wecker, 1963) or nesting locality (eg. P. tenuirostris), Serventy, 1966; L. atricilla, Bongiorno, 1970).

The timing of a sensitive period for habitat imprinting is influenced by the mode of development of the bird and the timing of the nestling's experience with the habitat. Serventy (1966) cross-fostered eggs and young of Short-tailed shearwaters and found the sensitive period for locality imprinting to be when the chicks first emerged from their burrows to exercise their wings. This coincided with the beginning of the desertion or starvation period for the chicks.

Leach's Storm Petrels, like Short-tailed shearwaters, experience slow growth rates post hatch and require 63 to 70 days to fledge (Huntington, 1962). As fledging approaches, the number of feeds of the chick by the adult and the amount of food per feed decrease. The nestling's weight declines coincidentally with the completion of feather growth and it begins to emerge from the burrow at night on exercise forays (Gross, 1935; Huntington, 1962). This may be the time of habitat imprinting by the petrels.

Olfactory tests of vegetation around an individual's burrow demonstrated that adult petrels could discriminate olfactorily between their own biome and vegetation not found around their burrow (Johnson, 1978).

Given that petrels which return to natal colonies occupy burrows close to the natal burrow (Huntington, 1963; Lien, pers. communication), it is conceivable that early experience of the habitat by the chick has influenced subsequent habitat preferences by the same chick as an adult. The importance of visual cues in mediating habitat preferences has never been tested.

The ontogeny of visual recognition of nest biome was examined in this experiment. If petrels become imprinted on visual habitat characteristics when exiting the burrow at night to exercise, then older fledging chicks would recognize their own biome but young chicks would not. Habitat recognition and preference just prior to fledging would support a habitat imprinting hypothesis.

Methods

Subjects were 240 nestling Leach's Storm Petrels from either fern or grass biomes on Middle Lawn Island. Subjects were recruited from burrows in homogeneous habitats (ie., within 50cm diameter of the burrow entrance was either all grass or all fern vegetation). Half the chicks were from fern biomes, and half were from grass biomes. Each burrow was marked with a numbered stake, if a suitable subject was found inside. The nestlings were weighed, banded and assigned to an age group on the basis of plumage development and weight (Table 14) after Wilbur (1969). Initially, three age groups of chicks were to be tested (Groups 2, 3, 4) but as testing of Group Two finished, it appeared that the nestlings might be discriminating habitat types at age 15-25 days, so another younger group (Group One) aged 8-15 days was included in the study. Half the chicks in each age group were naive individuals which had never been in the test box and half were individuals that had experienced the activity test box and/or the habitat test box as previous subjects in the apparatus. By the time Group One was instituted, on 20 August, small chicks were not readily available and only a naive group was run.

Previous experiments with adult and nestling Leach's Storm Petrels in a maze apparatus met with some lack of participation by the subjects (Grubb, 1973; 1974; Johnson, 1978). To reduce the number of nonresponding subjects among the chicks used as subjects, a pilot study on activity as a function of stimulation was run. The effects of tactile stimulation, auditory stimulation, or a combination of auditory and tactile stimulation was examined (and is presented in Appendix B). On the basis of this data on chick activity, a pretreatment of auditory and tactile stimulation for age Group One, Two and Three was instituted. The results of the chick activity study are reported in the Appendix.

Chicks which participated in the activity study were later used in the preference study.

All habitat preference testing was carried out during the day, between 1000 and 1900 hours, in a covered test box. The dates of testing by age group were: Group One, 20-26 August; Group Two, 20-29 August; Group Three, 28 August - 9 September; Group Four, 8-24 September. Downy chicks were run on sunny days to prevent chilling from dampening of the natal down. Temperatures during testing ranged from 16^{o}C on 25 August, to 5^{o}C on 8-9 September.

The test box was a wooden box 100 x 50 x 50cm. At each end were 30 x 40cm pieces of sod from fern or grass areas of the island. The box was modified for Group One chicks by resting a piece of four-inch pipe between the two sods. The pipe was cut in half to prevent the small nestlings from straying in the box. Chicks in other groups were tested with a plywood floor between the two ends of the box. Chicks were placed in the center of the pipe on the floor, after ten seconds of tactile stimulation, and the cover of the box was then drawn over it. Crow call vocalizations of Leach's Storm Petrels were then played to the chicks for the duration of the five minute test period. At the end of the trial, the tape recorder was stopped, the cover was removed from the box and the chick was located within the box. A preference was recorded on the basis of the chick's location in the box at this time. A chick was scored as having chosen one biome or the alternative if its head and a minimum of half its body was in the biome sample in the test box. All test days were

TABLE 14

Plumage Development and Age in Leach's Storm Petrels

(after Wilbur, 1969)

Group	Description	Weight (gm)	Age (days)
1	natal down covering body and head; mesoptile plumage emergent	40-50	8-15
2	natal down covering body and head; emergent primaries and secondary teleoptiles; restrices not emerged	60-70	15-25
3	some natal down on body; head partially covered by contour feathers; primaries and secondaries unsheathed; rectrices unsheathed	80-90	40-50
4	adult plumage on head, body, wings; downy brood patch; band identifies individual as a bird of the year	60-70	63-70

TABLE 15

Vegetation Preferences of Nestling Leach's Storm Petrels at Four Ages

Group	Experienced chicks		Naive chicks	
	choice		choice	
	own biome	other biome	own biome	other biome
1	/	/	12	12
2	26	10	10	10
3	15	18	13	22
4	22	18	18	19
Total	63	46	53	65

windy days but ~~the~~ test box had no directed air circulation within it because of the cover which excluded both light and wind.

Results

The results are presented in Table 15. Only Group Two non-naive chicks chose their own biome significantly more frequently than would be expected by chance alone (X^2=7.7, d.f.=1, $p<.01$). All other groups of chicks chose habitat types in the box in a random fashion. In all, 203 of the 240 (81.4%) of the nestlings responded in the box. Of these 203 responders, 104 chose their own biome type in the maze and 99 chose a biome that was not similar to their own (X^2=0.10,1d.f.=$p<.05$).

Discussion

The results of this study do not support, nor definitely refute, a habitat imprinting hypothesis. The single occasion of significance Group Two, non-naive was by chicks which could not have been outside the burrow prior to the time of testing. Furthermore, because the data were cut and analyzed several ways, the probability of attaining significance on one test is one in 12 (Neher, 1967) cited in Barber (1976), so this result is possibly due to chance alone. It was concluded that the nestlings never appeared to prefer their own biomes over a strange, alternative one.

Before dismissing habitat imprinting as the mechanism by which young petrels return to natal area burrows, two explanations for the experiment's failure should be discussed. The cues tested in box were of a visual and olfactory nature, provided by the samples of the biome in the box. Although vegetation characteristics may be salient cues, other species of seabirds, particularly larids, use landmarks to locate the nest site (Tinbergen, 1953). These types of cues were not tested in this experiment. Alternatively, even with fully feathered subjects in Group Four, it is not certain that the chicks had previously exited from the burrow. It is possible that habitat imprinting occurs on those last few nights before fledging and that the last group of chicks was not old enough to have been outside the burrow at the time they were tested. Moreover, the evidence of olfactory discrimination of vegetation by adult petrels (Johnson, 1978) indicates knowledge and recognition of the biome by the adult birds on an olfactory basis.

Procedural and/or apparatus difficulties are also sources of error. The covered test box reduced light from entering the box during the tests and although the birds were nocturnal on land as adults and exercise nocturnally as chicks, it is possible that not enough light was available to the chicks to make visual discrimination of the habitat. As well, testing the chicks was stressful to them and this might have resulted in chicks seeking shelter randomly inside the box rather than moving toward natal biomes, if recognized. This conjecture is partly supported by the tendency of chicks to go to tall vegetation which was evident when the data were partitioned and analyzed by a criterion of vegetation height (ie., low versus high vegetation) rather than by plant species.

The results of this experiment do not lend support to the hypothesis that petrels become imprinted on visual aspects of their biome prior to fledging. However, the results do not cast serious doubt on petrels use of the vegetation for visual navigation cues.

General Discussion

Breeding microhabitat features were highly variable between the islands studied; however, tall vegetation and deep or moderately deep peat soil were found to be good predictors of high petrel burrow density and high rates of burrow occupancy (Study 2). These relationships raise some interesting questions in terms of possible causal relationships between the variables. This is not to suggest that causal relationships may be inferred from what are as yet correlational relationships presented in the data, but that the observed relationships provide points of departure for speculation in this direction.

It has been demonstrated that Leach's Storm Petrels navigate olfactorily to their colony and burrow areas (Grubb, 1973; 1979) and that they discriminate preferentially the vegetation typical of the biome in which their burrow is located (Johnson, 1978). Conceivably, olfactory navigation to burrows is facilitated by the presence of familiar understory vegetation which has familiar olfactory cues. Tall vegetation, particularly ferns with durable roots, may act as a deterent to predators which attempt to dig petrels out of their burrows (Ainley, Morrell & Lewis, 1979; Lien pers. comm.; Montevecchi, Unpub. MS.). It seems doubtful that height or species of vegetation provides visual cues for navigation to burrows by adult petrels as habitat recognition by fully feathered chicks was not demonstrated. Thus it is possible that petrels on the islands studied burrowed in greatest numbers in tall vegetation because it was most likely ferns which protect the burrows from terrestrial predators and provided the adults with salient cues for navigation to the burrow. The advantages to a bird of rapid relocation of the nest site were discussed earlier with respect to avian predation on puffins (Grant & Nettleship, 1972).

Microhabitat preferences are probably initially a function of the strong nest site tenacity characteristic of Leach's Storm Petrels (Huntington, 1963; Wilbur, 1969; Morse & Buchheister, 1979) rather than habitat imprinting. This conjecture is presented despite the data of Study 5 which did not demonstrate habitat imprinting. Indeed, the most salient microhabitat characteristics for petrels may not be visual (Johnson, 1978).

Tall vegetation was frequently indicative of deep peat soil which may be necessary for both the support of burrows and for the maintenance of stable air and soil temperatures inside the burrow (Study 3).

On the islands of Study 2, it was demonstrated that the choice of habitat was not directly related to the density of conspecifics or nest site availability as habitats with high burrow densities had empty burrows in them. The reasons the burrows were empty at sampling were not determined in Study 2 and the possibility remains that sampling cross-sectioned a colony succession phenomenon. This is a possibility as Orians (1971) suggested that the intrinsic worth of a given habitat decreases as the number of conspecifics in that habitat increases. Although his model is primarily in terms of birds which forage on breeding territories or compete for nest sites, and petrels do neither of these, crowding alone may be a factor in their distribution on an island. This would explain why fewer burrows are occupied in dense burrow areas while higher rates of burrow occupancy are found in less dense burrow areas.

Burrow architecture on one island (Study 3) suggested that the maintenance of a cool (relative to external, daytime summer temperatures), stable, ventilated burrow environment was achieved by convection, burrow length, slope of the ground and flared or double entrance burrows in combination with wind movement. Given the constant wind which the islands are subject to, the structural features of burrows which maintain air circulation are to some extent redundant. There are several burrow designs which would maintain the same internal environment. This redundancy may operate to expand the range of suitable habitats available to petrels on an island because no one proximate feature of the habitat, eg. slope or surface vegetation, would determine the suitability of the habitat.

On one island, (Study 4), small differences in egg size were related to burrow densities within a colony. Small increases in egg breadth and size over two or three breeding seasons, in eggs associated with the same adult, were found by comparing data from Study 3 with Spencer's (1978) data. This relationship has been demonstrated in other procellariiforms.

Slightly larger eggs were found in high burrow density areas of the island although the differences in egg breadth and size between high and low petrel burrow density areas were not statistically significant. These differences hypothesized to be the result of older birds nesting in high burrow density areas of the colony. Petrels exhibit high nest site tenacity and generally do not permanently leave a burrow unless they die during the intervening winter or experience poor breeding success in that burrow during the breeding season. The initial prediction in this study was that the probability of an egg hatching would be higher in HD areas of the colony than in LD areas of the colony. This was not found in the study, but the HD area burrows consistently had heavier chicks, fewer incubated eggs and no brooded chicks during interventions than did LD area burrows. This is strong indication that HD area burrows held older chicks than did LD area burrows.

In Leach's Storm Petrel, and other species of seabirds, larger, older chicks fledge sooner in the breeding season and are more likely to survive than chicks which are comparitively smaller and younger on a given date in the breeding season (White & Coulson, 1960; Perrins, 1966; M. de L. Brooke, 1978; Morse & Buchheister, 1979).

It is possible that HD areas of the colony may be more successful in terms of fledged birds. This is probably because of earlier egg laying or better parenting by experienced birds, rather than the small differences in egg breadth or size.

There appears to be a hierarchy of factors exerting greater or lesser selection pressures on the habitat selection of Leach's Storm Petrels. Factors of great ultimate significance such as avian or terrestrial mammalian predation have resulted in relatively invariant habitat selection strategies such as nocturnality on breeding habitat (islands) and breeding in burrows on inaccessible islands (Gross, 1935; Palmer, 1962; Wilbur, 1969). Burrow architecture may serve to broaden the range of suitable microhabitats as a number of burrow designs appear to result in adequate ventilation and internal burrow temperature regulation.

In Study 2, peat depth was found to be a possible limiting factor to burrowing by petrels as was found previously in puffins (Grant & Nettleship, 1972). Breeding success (Study 4) and continued occupancy of a burrow (Study 3) are probably more directly related to burrow density than to microhabitat features other than peat depth. The nature of the success, occupancy and burrow density relationship invites further study.

Return to natal colony and subcolony by chicks in years subsequent to fledging is probably initially mediated by the high nest site tenacity characteristic of the species (Morse & Buchhester, 1979) not imprinted habitat preferences. The inconclusive nature of Study 5 invites further study, particularly with regard to determining whether adult petrels can visually discriminate the biome in which their burrows are located. The environmental conditions under which such a discrimination may be made (if one is made) also invites some study.

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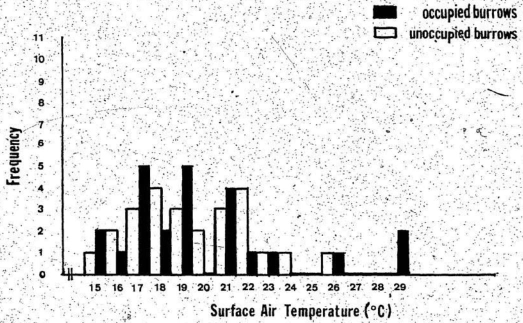
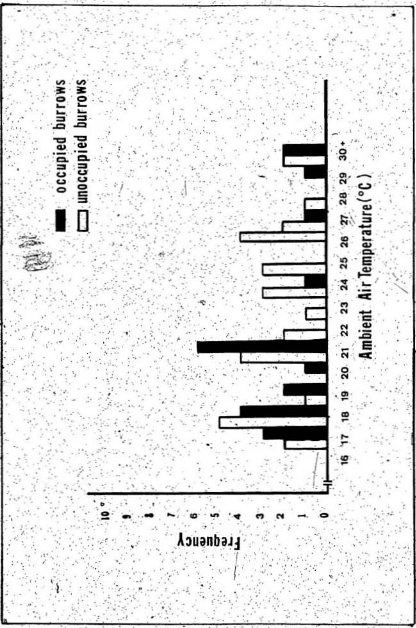
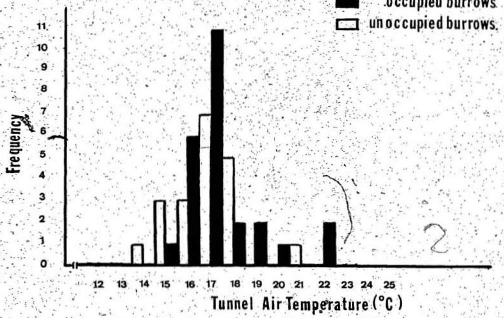
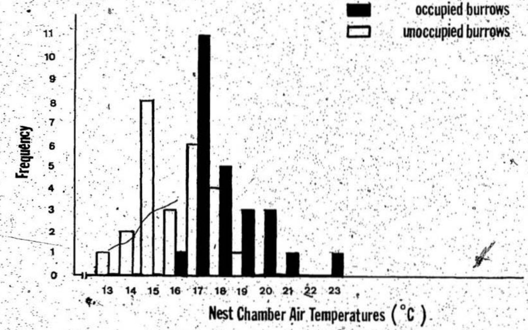
APPENDIX A

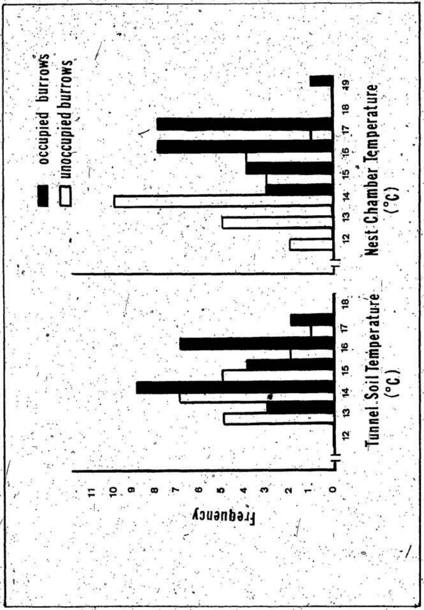
Frequency Distributions of Modal Values of Burrow Parameters as a Function of Burrow Occupancy

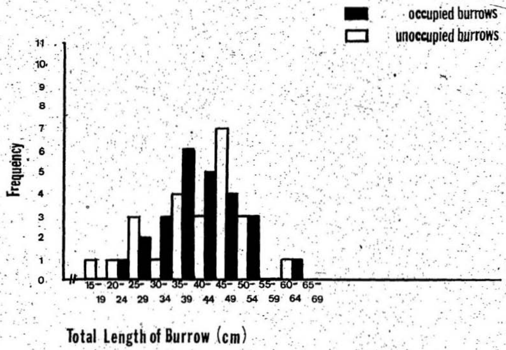

occupied burrows
unoccupied burrows
Frequency
0
1
2
3
4
5
6
7
8
9
10
11
15
16
17
18
19
20
21
22
23
24
25
26
27
28
29
Surface Air Temperature (°C)

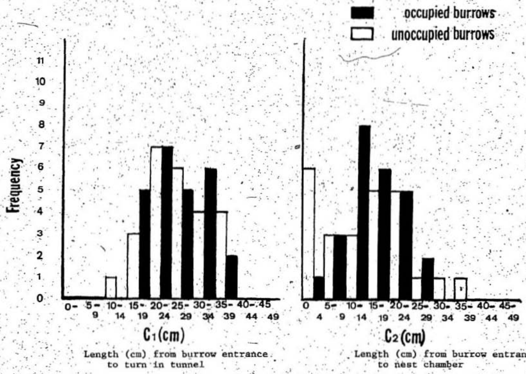

occupied burrows
unoccupied burrows
Frequency
0
1
2
3
4
5
6
7
8
9
10
16
17
18
19
20
21
22
23
24
25
26
27
28
29
30+
Ambient Air Temperature (°C)

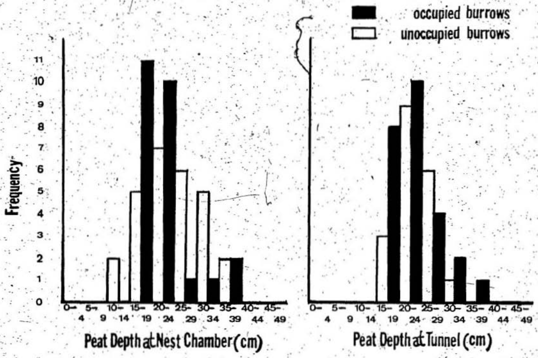

■ occupied burrows
□ unoccupied burrows.
Frequency
11
10
9
8
7
6
5
4
3
2
1
0
12
13
14
15
16
17
18
19
20
21
22
23
24
25
Tunnel Air Temperature (°C)
2

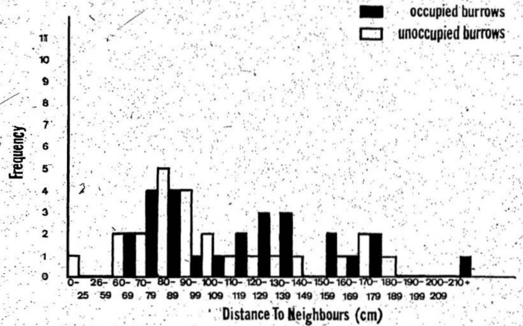

occupied burrows
unoccupied burrows
Frequency
0
1
2
3
4
5
6
7
8
9
10
11
13
14
15
16
17
18
19
20
21
22
23
Nest Chamber Air Temperatures (°C)

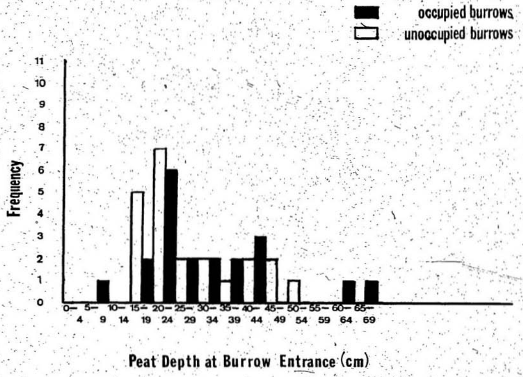

occupied burrows
unoccupied burrows
Frequency
0
1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
Tunnel Soil Temperature (°C)
12
13
14
15
16
17
18
19
Nest Chamber Temperature (°C)


■ occupied burrows
□ unoccupied burrows
Frequency
0
1
2
3
4
5
6
7
8
9
10
11
15-19
20-24
25-29
30-34
35-39
40-44
45-49
50-54
55-59
60-64
65-69
Total Length of Burrow (cm)


occupied burrows
unoccupied burrows
Frequency
0
1
2
3
4
5
6
7
8
9
10
11
0- 9
5- 9
10- 14
15- 19
20- 24
25- 29
30- 34
35- 39
40- 44
45 49
C1 (cm)
Length (cm) from burrow entrance to turn in tunnel
0 4
5- 9
10- 14
15- 19
20- 24
25- 29
30- 34
35- 39
40- 44
45- 49
C2 (cm)
Length (cm) from burrow entrance to nest chamber


occupied burrows
unoccupied burrows
Frequency
0
1
2
3
4
5
6
7
8
9
10
11
0–4
5–9
10–14
15–19
20–24
25–29
30–34
35–39
40–44
45–49
Peat Depth at Nest Chamber (cm)
Peat Depth at Tunnel (cm)


occupied burrows
unoccupied burrows
Frequency
0
1
2
3
4
5
6
7
8
9
10
11
0-25
26-59
60-69
70-79
80-89
90-99
100-109
110-119
120-129
130-139
140-149
150-159
160-169
170-179
180-189
190-199
200-209
210+
Distance To Neighbours (cm)


occupied burrows
unoccupied burrows
Frequency
0
1
2
3
4
5
6
7
8
9
10
11
0–4
5–9
10–14
15–19
20–24
25–29
30–34
35–39
40–44
45–49
50–54
55–59
60–64
65–69
Peat Depth at Burrow Entrance (cm)

APPENDIX B

Chick Activity Study

Chick Activity Study

Purposes: To determine the type of stimulation most effective in reducing the numbers of nonresponding subjects in the nestling habitat recognition study.

Subjects: Subjects were 42 nestling Leach's Storm Petrels taken from burrows on Middle Lawn Island between August 19 and August 29, 1978. The mean weight of the nestlings was 64.9gm (range 52-70gm). The subjects were judged to be from 20 to 25 days of age on the basis of feather development and weight. Individuals included in the study were covered with natal down but emergent primaries and secondaries were visible. No other teleoptiles were evident on the body, nor were rectrices emergent. Because of the large individual variance in weight, individuals were never excluded from the sample on this criterion alone. Plumage development was judged to be of primary importance for aging the nestlings.

Apparatus & Procedures: A wooden box 80cm long, 80cm wide, 50cm high, with three sides, was divided into 4 quadrats of 40cm by 40cm each, with surveyor's tape tacked to the floor of the box. A plywood lid approximately 85cm by 60cm covered the top of the box. The test box was always oriented with the back of the box to the wind. All testing took place outdoors, between the hours of 09:00 and 18:00. Weather conditions were clear, 14^{o}-16^{o}C with SW winds. I attempted to minimize the disruptive effect of testing by taking the nestlings from their burrows, weighing and banding them, testing responses to stimulation and returning them to their burrows in less than 30 minutes. During holding time, the chicks were kept in a large covered tin pot insulated for the purpose. Careful watch was kept to avoid either chilling or keeping the chicks overly warm. Chicks were tested individually in the test box. A UHER 4400 stereo tape recorder, placed directly in front of the box near the open side, played a recorded tape of an unfamiliar petrel crowing from inside a burrow. Each nestling received a 2 minute adaptation period (A) at the center of the test box, followed by a random sequence of the following conditions: 1) Control (C), no stimulation; 2) 'Adult 'crow' vocalization on tape (CR); 3) Tactile stimulation (T) consisting of gentle touching of the chick about the head and dorsal body surface; 4) Adult vocalizations and tactile stimulation (CR & T). Taped 'crow' vocalizations were presented throughout the 2 minute trials in (CR) and (CR & T) conditions; tactile stimulation was given for 10 seconds prior to putting Ss into the right front quadrant of the test box. Each condition trial was 2 minutes (120 seconds) during which Ss latency to first body movement and the number of crossings of quadrant lines was recorded by E, who sat quietly in front of the test box recording and timing trials with a stopwatch.

Results

Latency: A 1-way analysis on the latency data yielded a significant F. ($F_{4,210}$=11,61 $p < .01$). The mean latency in seconds for each condition was (A) 66.0, (CR) 25.1, (T) 16.2, (C) 30.7, (CR & T)

14.7 seconds, an effect that is significant. The (CR & T) condition was most effective in activating the chicks to move.

Activity: A 1-way analysis of variance on the number of bars crossed by a chick in that test condition yielded a $F_{4,219}=4.28$, p 0.01. The average number of bars crossed by chicks in each test condition was (A) 0.67, (C) 1.12, (CR) 1.3, (CR& T) 1.37, (T) 1.51. The (T) and (CR & T) condition seemed to be the most effective treatments for inducing nestlings to move, and keeping them active during the test period in the box. The means of these two groups were the highest of all conditions.

Discussion: From the results of the experiment, a pretreatment of 10 seconds of tactile stimulation prior to being placed in the habitat maze was instituted for Groups 1, 2 and 3. For the duration of the 5 minute test period in the habitat maze, these groups also heard a 5 minute recorded tape of an unfamiliar adult petrel crowing in a burrow.

It has been documented that upon return to the burrow containing a nestling, the adult bird crows and touches the nestling on the head. The nestling, in the absence of the adult, remains relatively quiet while in the burrow. The auditory stimulation of the crow vocalization, combined with the tactile stimulation of the adult's return, rouse the chick to feed.

I attempted to simulate the types of stimulation that an adult petrel would provide for the nestling upon return to the burrow.

From the latency data and activity data, these types of stimulation were effective in increasing activity of the chicks.