Habitat utilization and breeding success in Leach’s Storm-Petrel: the importance of sociality

Ian J. Stenhouse and William A. Montevecchi

Abstract: Models like “ideal-free distribution” that have been developed to predict the spatial distribution of animal populations typically assume that high densities will occur in preferred habitats. We investigated habitat utilization in Leach’s Storm-Petrels (Oceanodroma leucorhoa) at the centre of the species’ breeding range in the North Atlantic by comparing microhabitat features and breeding success in forest and open meadows on Great Island, Newfoundland. Leach’s Storm-Petrels utilized forest more than open habitat. Overall, forest provided consistently better breeding habitat, with burrow density and activity and occupancy rates higher than in open habitat. A strong positive relationship between occupancy and both hatching and breeding success suggests that sociality plays an important role in habitat utilization and reproduction in Leach’s Storm-Petrel.

Résumé : Les modèles tels celui de la répartition libre idéale qui ont été élaborés pour faciliter les prédictions sur la répartition des populations animales supposent ordinairement que c’est dans les habitats préférés que se trouvent les densités les plus élevées. Nous avons étudié l’utilisation de l’habitat chez l’Océanite cul-blanc (Oceanodroma leucorhoa) au centre du territoire de reproduction de l’espèce dans l’Atlantique-Nord, par comparaison des caractéristiques du micro-habitat et du succès de la reproduction en forêt et dans les prés ouverts sur Great Island, Terre-Neuve. Les oiseaux utilisent davantage la forêt que l’habitat ouvert. Dans l’ensemble, la forêt offre un meilleur habitat pour la reproduction puisqu’on y trouve une densité plus élevée de terriers et des taux d’activité et d’occupation supérieurs à ceux qui prévalent en habitat ouvert. Une forte corrélation positive entre l’occupation, le succès de l’éclosion et le succès de la reproduction indique que l’aspect social joue un rôle important dans l’utilisation de l’habitat et la reproduction chez l’Océanite cul-blanc.

Introduction

Based on the assumption that individuals act to maximize fitness, models have been developed to predict the spatial and temporal distributions of animal populations (Fretwell and Lucas 1970; Rosenzweig 1981; Holt 1987; Morris 1991; Rodway 1994). These models typically assume that population density is associated with resource abundance and that densities will be high in preferred habitats (Rosenzweig 1981). “Ideal-free” and “ideal-despotic” models (Fretwell and Lucas 1970) also assume density-dependent dampening, so habitat quality will eventually decline with increasing density, owing to such factors as increased predator activity and intraspecific competition.

In an ideal-free distribution, where individuals are assumed to have a complete knowledge of the environment and can move freely among habitats, populations should distribute themselves in such a way that individual fitness is similar across habitats. However, it is expected that individual fitness will differ across habitats where established individuals are despotic, i.e., can prevent others from accessing preferred habitat. Many studies have shown a positive correlation between density and breeding success, although this is often associated with predation risk (Nettleship 1972; Harris 1980; Hatchwell 1991). In burrow-nesting species such as storm-petrels, density may also be limited by qualities of the substrate (Harris 1974).

Leach’s Storm-Petrel (Oceanodroma leucorhoa) is the most widely distributed procellariiform in the northern hemisphere, breeding on small islands across the northern Atlantic and Pacific oceans. Recent estimates suggest a world population of more than 8 million breeding pairs (Huntington et al. 1996) plus an unknown number of non-breeders, mostly immature birds that remain at sea most of the year. Leach’s Storm-Petrel is the smallest and most abundant seabird to breed in the northwest Atlantic (Montevecchi et al. 1992). The species’ breeding range is centred on eastern Newfoundland, Canada, where over half of the world’s breeding population is found (Huntington et al. 1996), as well as the world’s largest colonies (Sklepkovych and Montevecchi 1989).

Leach’s Storm-Petrels nest in burrows and are strictly nocturnal at colonies (Wilbur 1969). In the northwest Atlantic they breed in a variety of island habitats that range from densely canopied coniferous forest to open meadow (Gross 1935; Sklepkovych 1986; Huntington et al. 1996). Within these habitats, nest-site selection may be determined by microhabitat features such as characteristics of soil, slope, and vegetation (Harris 1974; Grimmer 1980; Watanuki 1985; MacKinnon 1988; Vermeer et al. 1988; Sklepkovych and Montevecchi 1989; Huntington et al. 1996). In addition to environmental features, habitat selection may be influenced by indirect cues such as the presence and (or) repro-
ductive success of conspecifics in different habitats (Danchin and Wagner 1997).

We assessed the optimal breeding habitat of Leach's Storm-Petrels at the centre of the species' breeding range in the North Atlantic by comparing microhabitat features and breeding success in forest and open meadows. We predicted that (i) peat would be deeper and less compact (more penetrable) in forest habitat, (ii) average slope and aspect would not differ between habitats, (iii) more birds would burrow in areas of deep peat and low peat compaction, therefore density would be higher in forest habitat, (iv) individual fitness, measured as reproductive success, would be similar across habitats, i.e., Leach's Storm-Petrels would exhibit an ideal-free nesting distribution.

**Methods**

This study was conducted from 17 May to 14 September 1996 and from 16 May to 26 August 1997 on Great Island (47°11′N, 52°49′W) in the Witless Bay Ecological Seabird Reserve in Newfoundland. Great Island lies approximately 2.4 km off the southeast coast of Newfoundland (Fig. 1), is approximately 1200 m long (north–south), and ranges between 150 and 700 m in width (east–west). The island has a precipitous rocky shoreline topped by steep grassy slopes, levelling to gently sloping grass—shrub meadows and dense conifers, predominantly dwarfed balsam fir (Abies balsamea) and black spruce (Picea mariana). The forested area is considered to have contracted over the past 20–30 years, while the grass and meadow habitats have expanded (Rodway 1994). Nine seabird species breed on the island, including an estimated 270,000 pairs of Leach's Storm-Petrels (Stenhouse et al. 2000).

Two nesting habitat types were identified and characterized: forest habitat was an area of grass, shrub, or fern vegetation and (or) bare peat under a dense canopy of coniferous forest, and open habitat was an area of grass and shrub vegetation open to the sky (Stenhouse 1998). In 1996, burrow density and breeding success were recorded in two 10×10 m plot studies chosen in areas of similar slope and aspect in each of the habitat types. In 1997, a random-sampling method was used, with samples stratified by habitat. A transect grid running east–west at 100-m intervals (see Rodway et al. 1996) was used to establish random points (Fig. 2). For each point, a transect number, direction of travel, and two coordinates (at 10-m intervals) were randomly generated. The first coordinate represented the distance along the transect in the selected direction and the second represented the distance directly south of the transect (up to 90 m). Each random point was marked with a stake and constituted the southeast corner of a 2×2 m plot. Random points that did not fall in forest or open habitat were omitted. The process was repeated until 50 random plots were established in each habitat.

**Microhabitat features**

Aspect, slope, peat depth, and peat compaction were measured for each plot. Aspect, the direction of slope, was measured to the nearest 1° at the central point of each plot, using a Silva sighting compass. Slope and peat depth and compaction were measured at the transect number halfway between the centre and lower corner of the plot. Slope was measured to the nearest 1° over a 20-cm span using an MJP Mini-Gradometer (Michael Jay). Peat depth was estimated to the nearest 5 cm using an iron rod approximately 1 cm in diameter and marked at 10-cm intervals. Peat compaction was measured using a Lang penetrometer (James D. Lang, Alabama), which recorded the resistance of the peat to penetration; dense peat had high resistance and thus a high compaction score. Throughout the study, burrow intervention was minimized in an attempt to prevent disturbance (see Boersma et al. 1980; MacKinnon 1988), and nests chambers that could not be reached were not disturbed by digging hatches.

**Reproduction parameters**

In 1996, burrows were counted in each plot in open habitat on 17–18 May and in forest habitat on 25–26 May, and in four random 10×10 m plots in each habitat type on 16–18 August. In 1997, burrows were counted in all plots on 25–31 May. Activity at each burrow was assessed by placing a lattice of grasses over the entrance and examining it later for evidence of disturbance. In 1996, all burrow lattices were examined on each of 6 consecutive nights from 25 May to 1 June. In 1997, all burrow lattices were examined once, 7 nights after placement, between 25 May and 7 June.

The presence of adults and (or) eggs (i.e., reproduction attempts) was established by diurnal burrow exploration, with four visits to each burrow in 1996 (June, July, August, September) and three in 1997 (June, July, August). A burrow was considered to be occupied when two adults were found during the day on at least one occasion, a single adult was found during the day on more than one occasion, or an egg was found. The proportion of occupied burrows was calculated as the number of burrows in which birds attempted to breed divided by the total number of burrows in each plot.

In 1996, the length, breadth, and mass of eggs in each plot were recorded. Maximum egg length and breadth were measured with calipers to the nearest 0.1 mm and eggs were weighed with a 50-g Pesola scale to the nearest 0.5 g. An egg-shape index, ESI, was calculated using the formula $ESI = \frac{B}{L} \times 100$ (Coulsou 1963), where $L$ is egg breadth and $B$ is egg length, and egg volume, $V$, was calculated using the formula $V = 0.51 \times L \times B^2$ (Preston 1974; Hoyt 1979).

Hatching success was calculated as the number of eggs hatched divided by the number found in each plot. To obtain an index of growth, chicks were weighed with a 100-g Pesola scale to the nearest 0.5 g and the wing chord was measured to the nearest 1 mm. In 1996, chicks in open plots were weighed and measured once on 27–28 August and those in forested plots on 31 August – 1 September, and reweighed in both habitats on 12–13 September. In 1997, chicks in both habitats were weighed and measured once on 18–23 August. For the purposes of this study, breeding success was defined as the number of chicks surviving at the last burrow exploration divided by the number of eggs laid in each plot. Breeding success was determined on 12–14 September 1996 and between 18 and 23 August 1997, at which times surviving chicks were assumed to fledge.

**Statistical analyses**

In 1996, the effects of habitat variables were explored using the $G$ test of independence, employing Williams’ correction for a 2×2 table (Sokal and Rohlf 1995). In 1997, the effects of habitat variables were explored using the General Linear Model and relationships between variables were examined using ANOVA, analysis of covariance (ANCOVA), and simple and multiple regression (Data Desk 5.0, Data Description Inc., Ithaca, N.Y., U.S.A.). Error distributions were examined for homogeneity, normality, and independence of residuals. Where error distributions were deemed unacceptable, the sample size was low ($n < 30$) and $P$ was close to $0$. $P$ was recalculated using a randomization test ($n = 5000$; Minitab 10.2, Minitab Inc., State College, Pa., U.S.A.).

**Results**

**Forest and open habitats**

Mean slope was significantly less steep in forest than in open habitat, though aspect did not differ between the two...
habitats. Peat was deeper and less compact in forest than in open habitat (Table 1), and peat depth and compaction were negatively related, deeper peat being less compacted (Fig. 3). Peat depth was omitted from further statistical analysis because peat was deep enough in either habitat to support storm-petrel burrows (mean depth = 34 cm, SD = 9.4 cm, n = 100). Peat compaction was more variable and therefore considered to be a more important determinant of habitat suitability.

In 1996, the proportion of inaccessible nest chambers was significantly higher in forest than in open plots (Table 2) but in 1997 it was not (Table 3). The following results, other than overall burrow density and activity, pertain to statistical analysis of accessible burrows only.

Reproduction in forest and open habitats

In 1996 and 1997, mean burrow density was significantly higher in forest than in open plots (Tables 2 and 3). From 5 to 10% of the variance in burrow density was explained by a positive relationship with slope ($r^2 = 0.11, F_{[1,98]} = 12.8, P < 0.001$) and a negative relationship with peat compaction ($r^2 = 0.05, F_{[1,98]} = 5.6, P = 0.02$).

The density of active burrows was higher in forest than in open habitat in both years, and the proportion of active burrows was significantly higher in forest than open habitat in 1997 (Table 3). The proportion of active burrows was positively related to burrow density ($r^2 = 0.17, F_{[1,93]} = 20.0, P < 0.001$), whereas slope and aspect showed no significant effects on activity.

Overall mean burrow occupancy on Great Island in 1996–1997 was 65%, consistent with rates previously recorded on Great Island, 67% in 1960 (Huntington 1963) and 65% in 1982–1984 (Huntington et al. 1996), as well as in other Atlantic colonies, which range from 61% (Wilbur 1969) to 68% (Grimmer 1980). The density of occupied burrows was higher in forest than in open habitat in both years, and the proportion of occupied burrows was also significantly higher in forest than in open plots (Tables 2 and 3). There was no significant relationship between burrow density and occupancy, although there was a significant positive relationship between activity and occupancy ($r^2 = 0.11, F_{[1,91]} = 11.4, P = 0.001$).
While there was no significant difference between habitats in the number of eggs laid per occupied burrow, the number of eggs laid per square metre was higher in forest than open habitat in both years (Tables 2 and 3). Egg characteristics did not differ between habitats on Great Island in 1996 (Table 4).

Overall mean hatching success on Great Island in 1996–1997 was 73%, similar to rates recorded previously in Atlantic colonies, which ranged from 68% on Great Island in 1982–1984 to 84% on Little Duck Island, Maine, in 1985–1989 (Huntington et al. 1996). In 1996, the number of eggs hatched per square metre was higher in forest, although the difference in hatching success in forest and open habitat was not significant (Table 2). In contrast, in 1997, both the number of eggs hatched per square metre and hatching success were significantly higher in forest than open habitat (Table 3). Multiple-regression analysis indicated a significant positive relationship between occupancy and hatching success across the two habitats (Table 5).

A positive linear relationship between chick mass and wing length existed in both habitats in both years (Fig. 4), and the relationships did not differ in magnitude or in slope between habitats. In 1996, more chicks survived per square metre in forest than in open habitat, although the difference in the proportions of successful burrows in the two habitats was not significant (Table 2). In 1997, significantly more chicks survived per square metre in forest, where breeding success was significantly higher than in open habitat (Tab-
Table 3. Summary of means (±SD) and results of ANOVA of comparisons of variables in forest and open habitats on Great Island in 1997.

<table>
<thead>
<tr>
<th>Variable</th>
<th>Unit</th>
<th>Forest</th>
<th>Open habitat</th>
<th>F</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>Density</td>
<td>No. of burrows/m²</td>
<td>2.21±1.23</td>
<td>1.53±1.13</td>
<td>8.41</td>
<td>0.004</td>
</tr>
<tr>
<td>Activity</td>
<td>Proportion of burrows</td>
<td>0.95±0.09</td>
<td>0.71±0.31</td>
<td>13.7</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Occupancy</td>
<td>Proportion of burrows</td>
<td>0.70±0.25</td>
<td>0.56±0.24</td>
<td>6.82</td>
<td>0.01</td>
</tr>
<tr>
<td>Eggs</td>
<td>No. laid/occupied burrow</td>
<td>0.93±0.17</td>
<td>0.98±0.08</td>
<td>2.93</td>
<td>0.09</td>
</tr>
<tr>
<td>Hatching success</td>
<td>No. of eggs hatched/egg laid</td>
<td>0.72±0.31</td>
<td>0.52±0.44</td>
<td>4.26</td>
<td>0.04</td>
</tr>
<tr>
<td>Breeding success</td>
<td>No. of chicks surviving/egg laid</td>
<td>0.71±0.31</td>
<td>0.52±0.44</td>
<td>4.34</td>
<td>0.04</td>
</tr>
<tr>
<td>Inaccessible nests</td>
<td>Proportion of burrows</td>
<td>0.34±0.21</td>
<td>0.26±0.10</td>
<td>2.98</td>
<td>0.09</td>
</tr>
</tbody>
</table>

Table 4. Characteristics of Leach's Storm-Petrel eggs in forest (n = 93) and open habitats (n = 50) on Great Island in 1996, and results of ANOVA of comparisons between habitats.

<table>
<thead>
<tr>
<th>Characteristic</th>
<th>Habitat</th>
<th>Mean</th>
<th>SD</th>
<th>Range</th>
<th>F</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>Length (mm)</td>
<td>Forest</td>
<td>33.08</td>
<td>0.98</td>
<td>30.05–35.10</td>
<td>0.14</td>
<td>0.71</td>
</tr>
<tr>
<td></td>
<td>Open</td>
<td>33.02</td>
<td>1.07</td>
<td>30.68–35.35</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Breadth (mm)</td>
<td>Forest</td>
<td>23.79</td>
<td>0.60</td>
<td>22.20–25.25</td>
<td>0.89</td>
<td>0.35</td>
</tr>
<tr>
<td></td>
<td>Open</td>
<td>23.89</td>
<td>0.57</td>
<td>22.61–24.86</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Mass (g)</td>
<td>Forest</td>
<td>9.84</td>
<td>0.73</td>
<td>8.00–12.00</td>
<td>2.68</td>
<td>0.10</td>
</tr>
<tr>
<td></td>
<td>Open</td>
<td>10.04</td>
<td>0.68</td>
<td>8.75–12.00</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Volume (mL)</td>
<td>Forest</td>
<td>9.56</td>
<td>0.64</td>
<td>7.90–11.41</td>
<td>0.25</td>
<td>0.62</td>
</tr>
<tr>
<td></td>
<td>Open</td>
<td>9.61</td>
<td>0.56</td>
<td>8.56–10.95</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Shape index</td>
<td>Forest</td>
<td>71.95</td>
<td>2.22</td>
<td>66.44–78.51</td>
<td>1.19</td>
<td>0.28</td>
</tr>
<tr>
<td></td>
<td>Open</td>
<td>72.42</td>
<td>2.85</td>
<td>66.69–79.29</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Table 5. Summary of a multiple regression of habitat variables against hatching and breeding success on Great Island in 1997.

<table>
<thead>
<tr>
<th>Variable</th>
<th>$R^2$</th>
<th>F</th>
<th>t</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>Hatching success</td>
<td>0.39</td>
<td>2.93</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Habitat</td>
<td></td>
<td></td>
<td>-1.53</td>
<td>0.14</td>
</tr>
<tr>
<td>Density</td>
<td></td>
<td></td>
<td>1.50</td>
<td>0.14</td>
</tr>
<tr>
<td>Activity</td>
<td></td>
<td></td>
<td>0.58</td>
<td>0.57</td>
</tr>
<tr>
<td>Occupancy</td>
<td></td>
<td></td>
<td>3.39</td>
<td>0.002</td>
</tr>
<tr>
<td>Slope</td>
<td></td>
<td></td>
<td>-0.55</td>
<td>0.59</td>
</tr>
<tr>
<td>Soil compaction</td>
<td></td>
<td></td>
<td>0.69</td>
<td>0.50</td>
</tr>
<tr>
<td>Breeding success</td>
<td>0.37</td>
<td>2.82</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Habitat</td>
<td></td>
<td></td>
<td>-1.52</td>
<td>0.14</td>
</tr>
<tr>
<td>Density</td>
<td></td>
<td></td>
<td>1.50</td>
<td>0.14</td>
</tr>
<tr>
<td>Activity</td>
<td></td>
<td></td>
<td>0.22</td>
<td>0.83</td>
</tr>
<tr>
<td>Occupancy</td>
<td></td>
<td></td>
<td>3.57</td>
<td>0.001</td>
</tr>
<tr>
<td>Slope</td>
<td></td>
<td></td>
<td>-0.71</td>
<td>0.48</td>
</tr>
<tr>
<td>Soil compaction</td>
<td></td>
<td></td>
<td>0.57</td>
<td>0.57</td>
</tr>
</tbody>
</table>

Table 3). Multiple-regression analysis indicated a significant positive relationship between occupancy and breeding success across the two habitats (Table 5).

**Discussion**

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

On Great Island, there were 1.5–2 times as many burrows in forest than in open habitat. All plots in forest contained burrows, whereas 10% of plots in open habitat contained none. Besides utilizing forest habitat more, Leach’s Storm-Petrels showed a preference for digging burrows on slopes in both forested and open habitats, with steeper sloping plots having greater burrow densities. Soil compaction may be related to slope, in that burrows dug in steeper slopes may be better drained. Burrow activity was consistently higher in forest, although many burrows showing signs of activity are not actually used for breeding (Hill et al. 1996; I.J. Stenhouse and W.A. Montvecchi, personal observations). However, burrow occupancy was also consistently higher in forest than in open habitat. Burrow occupancy may provide the best indicator of habitat suitability, particularly continued occupancy over a series of breeding seasons, which is likely to reflect previous reproductive success in a given location.
Virtually all occupied burrows contained an egg, and owing to greater burrow density, forest contained more eggs and more chicks per square metre than open habitat and was clearly the more productive habitat. The greater hatching and breeding success indicates that forest provides better breeding habitat than open meadows for storm-petrels on Great Island. Moreover, the advantages of breeding in forest over open habitat are not linked to predation, as there was no difference between habitats in the number of storm-petrels killed per occupied burrow (see Stenhouse 1998; Stenhouse and Montevecchi 1999).

The positive relationship between burrow occupancy and both hatching and breeding success suggests that sociality plays an important role in habitat selection by and reproductive success of Leach’s Storm-Petrels. Social interaction and social stimulation can benefit colonial birds through enhancement of physiological activity (Darling 1938), facilitation of behavioural display and pair formation (Southern 1974; Gochfeld 1980; Burger and Gochfeld 1990), increased synchrony in reproductive activity (Darling 1938; Patterson 1965; Montevecchi et al. 1978; Gochfeld 1980), facilitation of effective antipredator responses (Kruuk 1964; Lack 1968; Montevecchi 1975), and enhancement of food-finding abilities (Ward and Zahavi 1973; Burger 1997). Boulinier and Danchin (1997) and Danchin et al. (1998) proposed that individuals use the reproductive success of conspecifics as a cue in selecting breeding habitat. In species, such as storm-petrels, that exhibit high nest-site tenacity and mate fidelity.
(Huntington et al. 1996), individuals usually select breeding habitat only at first recruitment, and thus their initial selection may affect their lifetime reproductive output. Performance-based conspecific attraction could provide information that is critical for habitat selection and overall breeding success for many species (Danchin and Wagner 1997). Although our results support this hypothesis, it is important to note that we did not directly test the effect of density on habitat attractiveness. However, such a test may be achieved by comparing breeder recruitment in areas with similar habitat features other than burrow densities and occupancy rates. Manipulation of apparent breeding densities in different plots may be possible with the introduction of decoys and (or) recorded vocalization playbacks, as well as the use of hand-dug burrows (see Podolsky and Kress 1989).

Some findings of this study were consistent with an ideal-free nesting distribution of storm-petrels. If, as suggested by Grimmer (1980), egg breadth reflects age-class in Leach’s Storm-Petrels, there was no evidence for age-biased occupancy of forest over open habitat. Moreover, chicks did not differ in body mass between habitats, providing no evidence for quality-biased occupancy of forest over open habitat. However, under an ideal-free distribution, breeding success would be similar across habitats and breeding density would reflect qualitative differences between habitats. The higher breeding success observed in forest habitat suggests that an ideal-free distribution is not operating on Great Island. Alternatively, if an ideal-despotic distribution was operating, breeding success would vary between habitats and breeding density would reflect both qualitative differences between habitats and dominance behaviour by individuals. This is more difficult to refute. Although a difference in breeding success between forest and open habitat was observed in this study, little is known regarding the aggressive behaviour of Leach’s Storm-Petrels, and the interaction between neighbouring individuals, at the breeding colony. Therefore, Fretwell and Lucas’s (1970) assumption that habitat quality declines with density because of competition may not be appropriate in this particular situation, though negative effects might be found at higher nesting densities.

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