

Model of burrow selection predicts pattern of burrow switching by Leach's Storm-Petrels

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Received 8 July 2015; accepted 1 September 2015

ABSTRACT. Patterns of nest site selection exhibited at the scale of a population should result from initial preferences of individuals occupying nest sites as well as preferences exhibited by individuals moving between nest sites. We tested whether nest-site preferences measured at the population scale were predictive of patterns of burrow switching by Leach's Storm-Petrels (*Oceanodroma leucorhoa*), a long-lived seabird that nests in underground burrows. Breeding pairs generally choose from the pool of available existing burrows rather than constructing new burrows, and a portion of the burrows in a colony remains unused in any breeding season. We quantified burrow preference at a colony on Kent Island, New Brunswick, over four breeding seasons. We used a classification and regression tree analysis to build a predictive model of nest-site selection. Preferentially occupied burrows were drier, longer, had larger nest chambers, and were in areas of higher burrow density. To measure preferences during burrow switching, we tracked individuals that switched burrows, comparing characteristics of the burrows in which these birds were originally found to those they inhabited at the end of the study period. Characteristics preferred by switching individuals were a subset of those observed at the scale of the population; individuals moved to burrows that were drier, longer, and had larger nest chambers. Our results show how preferences of individuals that move between nest sites contribute to nest site preferences exhibited at the population scales commonly tested.

RESUMEN. Modelo de la selección de cavidades permite predecir el patrón de cambio de estas en *Oceanodroma leucorhoa*

El patrón de selección del lugar en donde anidar, exhibido a escala de una población, debe ser el resultado de preferencias individuales de organismos que ocupan lugares para anidar, e igualmente de preferencias exhibidas por individuos que cambian de lugar para anidar. Pusimos a prueba si las preferencias, medidas a escala de población, podían ser utilizadas para predecir el patrón de cambio de cavidades de parte de *Oceanodroma leucorhoa*, que es un ave marina que anida en cavidades bajo tierra. Las parejas usualmente seleccionan entre un grupo de cavidades disponibles, en vez de estos construir la propia, y una porción de las cavidades permanecen sin ser utilizadas a lo largo de la época de reproducción. Cuantificamos la preferencia de uso de cavidades en una colonia localizada en la Isla Kent, New Brunswick, durante cuatro temporadas reproductivas. Utilizamos una clasificación y un análisis de regresión para construir un modelo de predicción para la selección de lugar de anidar. Los lugares ocupados, con preferencia, se mantenían secos, eran largos, de mayor tamaño y se encontraban en lugares con alta densidad de cavidades. Para determinar las preferencias en el cambio de uso de cavidades, seguimos a individuos que cambiaron de cavidad, y comparamos las características del lugar utilizado originalmente, con aquellas cavidades siendo utilizadas al final del estudio. Las características preferidas, por individuos que cambiaron de cavidad, eran un subconjunto de aquellas observadas a nivel poblacional. Las aves se movieron a cavidades más secas, más largas y con una cámara de anidamiento más amplia. Nuestros resultados muestran como las preferencias individuales, de aves que se mueven a otras cavidades para anidar, contribuyen a las preferencias del lugar de anidamiento exhibido a escala poblacional.

Key words: burrow nesting, classification and regression tree, nest-site selection, *Oceanodroma leucorhoa*, seabirds

Nest-site characteristics can have fitness consequences, and birds are thought to exhibit preferences for habitat characteristics that improve fitness (Martin 1998). Studies of avian nest-site selection examine the hierarchical processes of behavioral responses that lead birds to occupy certain nest-sites over others (Jones 2001), and these studies can thus reveal aspects of breeding

habitat that are ecologically relevant for breeding success. Studies of nest-site selection based on habitat characteristics generally examine preferences by comparing used sites to the pool of available sites (Johnson 1980, Jones 2001). However, such tests somewhat obscure how the behavior of individuals gives rise to the pattern observed at the population scale. Observed nest-site preferences likely result from preferential movement by individuals between nest sites with

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differing characteristics, rather than from initial preferences of first-time breeders alone. We compare preferences exhibited at the population scale and preferences of individuals switching between nests in a long-lived burrow-nesting pelagic seabird, Leach's Storm-Petrel (*Oceanodroma leucorhoa*).

For burrow-nesting birds, characteristics of nest-sites can affect thermoregulatory costs and predation risk (Nilsson 1984, Rendell and Robertson 1994, Wiebe 2001, Paclík and Weidinger 2007, Ke and Lu 2009). Burrow characteristics can strongly predict reproductive success in other procellariiform seabirds (Ramos et al. 1997). Leach's Storm-Petrels generally breed once per year and do not switch burrows within years (Huntington et al. 1996). The underground burrows of Leach's Storm-Petrels at our study site on Kent Island, New Brunswick, maintain relatively constant temperatures (Ricklefs et al. 1980), and provide protection against predators such as gulls, hawks, owls, and corvids (Gross 1935). Leach's Storm-Petrels are thought to be a good example of a species where microhabitat characteristics shape burrow preferences (Huntington et al. 1996), although no one to date has examined such preferences.

To assess microhabitat preferences, nest-site selection studies must compare sites that are used with sites that are both accessible and procurable (Johnson 1980, Jones 2001). At the beginning of the breeding season, Leach's Storm-Petrels on Kent Island occupy an existing burrow from the pool of available burrows and rarely construct new burrows (R. Mauck, unpubl. data). Therefore, this species provides an appropriate system in which to examine preferred characteristics of existing nest-sites that are accessible and procurable. If burrows vary in the fitness benefits they provide, Leach's Storm-Petrels should preferentially occupy burrows with beneficial microhabitat characteristics.

Previous studies of breeding habitat use by Leach's Storm-Petrels have been conducted at broader scales, analyzing habitat correlates of burrow density, with slope of the ground, soil depth and penetrability, density of horizontal logs and roots, and distance to gull nests positively correlated with burrow density (Harris 1974, Grimmer 1980, Watanuki 1986, MacKinnon 1988, Sklepkovych and Montevecchi 1989). These results suggest that when Leach's Storm-Petrels do construct burrows,

they do so in areas that physically allow burrow construction. However, preferences between existing burrows in a colony are likely to be based on factors that differ from those used to select sites for constructing new burrows. Indeed, the nest-site characteristics identified as important often vary depending on the spatial scale of the analysis (Martin and Roper 1988, Brandt et al. 1995, Saab 1999, Chalfoun and Martin 2007). Leach's Storm-Petrel burrows have entrances that are often sheltered by trees, roots, or logs, have passages that can be straight or winding, and have nest chambers (NCs) of varying sizes. Non-breeding individuals are thought to choose or construct a burrow one or more years prior to breeding (Wilbur 1969, Huntington et al. 1996). Once burrows are established, there is little evidence for further excavation, and their characteristics remain consistent over many years (Huntington, pers. comm.).

Birds employ experience-based choices to avoid repeated nesting in low-quality sites (Bollinger and Gavin 1989, Haas 1998, Hoover 2003). Leach's Storm-Petrels generally exhibit a high degree of fidelity to burrows and may retain the same mate for many breeding seasons; site fidelity—rather than mate fidelity—appears to drive this socially and genetically monogamous pair bond (Wilbur 1969, Morse and Kress 1984, Mauck and Grubb 1995). Still, adults may switch burrows, especially after one or more years of reproductive failure (Huntington et al. 1996), but rarely nest in burrows further than 20 m from the previous burrow (Morse and Buchheister 1979).

Fretwell and Lucas (1969) argued that nest-sites are occupied in order of decreasing "suitability"; higher quality sites will be occupied before less suitable ones. Therefore, individual Leach's Storm-Petrel burrows with preferable microhabitat characteristics are expected to have higher rates of occupancy over time than less suitable ones. To create a predictive model of nest-site selection for Leach's Storm-Petrels, we measured a host of habitat characteristics for each burrow in a study site on Kent Island, New Brunswick, Canada, an island in the Grand Manan archipelago in the Bay of Fundy. By comparing these characteristics to rates of burrow occupancy and instances of burrow switching derived from a long-term study of this population, we examined the preferences of Leach's Storm-Petrels for habitat characteristics

including burrow morphology, characteristics of the surrounding landscape, and proximity to other burrows.

We used a classification and regression tree (CART) analysis to build a predictive model of nest-site selection. To describe preferences of switching individuals, we compared micro-habitat characteristics of burrows occupied at the beginning of the study period to burrows occupied at the end of the study period.

METHODS

Our study was conducted at the Bowdoin Scientific Station on Kent Island, New Brunswick, Canada (44°35' N, 66°45' W), a 100-ha island near the mouth of the Bay of Fundy. Leach's Storm-Petrel population on Kent Island has been estimated at 18,000 pairs (R. Mauck, unpubl. data). About one-third of the island is covered by forest, which is concentrated on the island's northern end. Most breeding pairs nest in this northern part of the island in burrows excavated in soft soil. There are no other species on the island that compete for burrows. The mixed forest comprises white spruce (*Picea glauca*), balsam fir (*Abies balsamea*), mountain ash (*Sorbus americana*), and heart-leaved birch (*Betula cordifolia*), with a forest floor of hummock ridges covered by ferns during the summer. Wind during severe weather events comes predominantly from the north and east. Kent Island receives a mean monthly precipitation during June, July, and August of 8.1 cm (R. C. Cunningham, unpubl. data).

Longitudinal burrow occupancy data.

Each burrow in the study area was marked with a unique tag and monitored during each breeding season. Starting in late May before egg-laying occurs, burrows were checked using established protocols to determine lay date and the identity of both individually banded adults. Yearly sweeps of the study area ensured that newly constructed burrows were tagged and monitored. Occupancy of a burrow was defined by the presence of an egg in that burrow any time during the breeding season. We do not have complete data on reproductive success because the protracted, asynchronous fledging period extends well after our field season.

We calculated an occupancy rate for each burrow to serve as a response variable, using data from the breeding seasons 2006 through

2009. Although occupancy data were recorded starting in 2003 (R. Mauck, unpubl. data), the study site expanded from 2003 to 2006. Thus, we only used data from burrows that were continuously monitored from 2006 to 2009 to ensure consistency. Burrows that were blocked or obliterated (i.e., uninhabitable) during the study were excluded. Occupancy rate was calculated as [number of seasons in which the burrow was occupied]/[4 seasons].

Habitat characteristics. We measured 28 characteristics of each burrow in the study site during 2009 (Table 1); most characteristics were measured during June and July. However, because the presence of a nestling or adult bird may alter the moisture environment inside a burrow, soil moisture was measured after young fledged. Burrow characteristics were measured quantitatively if measurements could be taken with minimal risk to the burrow's structural integrity, and were otherwise taken as categorical indices. We summarize how these characteristics were measured in Table 1.

Burrow switching. We determined the burrow occupancy history from 2006 to 2009 for each Leach's Storm-Petrel found in the study site in 2009. We identified the burrow that each individual initially occupied during the study period (hereafter, the initial burrow) and compared its characteristics with those of the burrow that the individual occupied in 2009 (hereafter, the final burrow). Any Leach's Storm-Petrels that occupied the same burrow throughout this time period were not included in our analysis of burrow switching. We identified 87 individuals that switched burrows.

Data analysis. Multicollinearity of independent variables can bias models even with levels of collinearity as low as $r = 0.28$ (Graham 2003). We thus used a correlation matrix to identify groups of collinear ($r \geq 0.28$) habitat variables and retained for further analysis the single variable from each group that best correlated with occupancy (MacNally 2000, Graham 2003). To assess which habitat variables best predicted occupancy, we used general linear mixed models with a binomial error distribution in the R package lme4 (Bates et al. 2013, R Development Core Team 2014). For each habitat variable, we used a binomial generalized linear mixed effects model (GLMM) with occupancy as the response variable, the habitat variable as the fixed effect, and burrow ID as the

Table 1. List of physical characteristics and measurement procedure.

Characteristic	Method of measurement
Soil depth at burrow entrance	Measured as vertical distance to rock. Three measurements were taken 10 cm in front, left, and right of the center of the burrow passage.
Slope at burrow entrance	Measured using a 1-m long inclinometer. The inclinometer was oriented to measure maximum incline, with the instrument's mid-point situated directly over the center of the burrow entrance.
Canopy density	A 12-cm diameter cylinder was oriented vertically up from 30 cm above the burrow entrance; measured in increments of 10% by sighting through the cylinder.
Thickness of soil above nest chamber	Measured as vertical distance between highest point of nest chamber and the surface above.
Length of burrow	Measured as the total length from the furthest extent of the burrow along the passage to the burrow entrance.
Number of turns in passage	Number of turns greater than 30° within 30 cm along the bottom of the passage.
Total degrees of passage turns	Total number of degrees turned in increments of 30°.
Nest chamber size index	Each nest chamber was assigned a categorical value of nest-chamber size from 1 to 5, with 1 being smallest (~15 cm in diameter) and 5 largest (over ~40 cm in diameter)
Nest chamber height	Measured as distance between highest point of nest chamber and the bottom of the nest chamber vertically below.
Nest chamber elevation index	The vertical location of the nest chamber relative to burrow entrance was categorically ranked, with -2 indicating that the nest chamber was lowest compared to the entrance, 0 being approximately level, and +2 being highest.
Burrow orientation	Measured by aligning a straight-edge out from the burrow passage along the burrow's first 10 cm and recording the bearing that the burrow passage faced.
Distance to nearest burrow	Measured the distance to entrance of nearest burrow.
Number of burrows within 1, 3, and 5 m	Number of burrows with entrances within 1, 3, and 5 m of the center of the focal burrow's entrance.
Presence of physical objects	Physical objects (tree, small root 3–7 cm diameter, large root diameter >7 cm, or fallen log) were recorded when directly contacting to the burrow entrance, passage, or nest chamber.
Nest chamber soil moisture	A 15–20 g soil sample was taken from each burrow's nest chamber from the top 5 cm of soil under the loose material that comprises the nest itself. Samples were weighed, dried at 70°C to a constant weight, and weighed again to determine gravimetric soil moisture.

random effect. We used likelihood ratio tests against a null model to test significance. Mean burrow orientation (0–360°) was analyzed using Rayleigh's test, and the orientations of burrows that were occupied and unoccupied in 2009 were compared using the Watson-Williams test (Zar 1999).

We used a CART analysis (Breiman et al. 1984, Clark and Pregibon 1992, Ripley 1996) to create a predictive model of burrow occupancy. CART models have been applied extensively in studies of resource selection (e.g., Rejwan et al. 1999, De'ath and Fabricius 2000, Eby

and Crowder 2002, Bourg et al. 2005, Friedlaender et al. 2006) because they (1) are well suited for modeling complex ecological data sets that contain nonlinear relationships, higher-order interactions, and missing values (De'ath and Fabricius 2000), (2) can identify critical threshold values of explanatory variables, and (3) do not assume an *a priori* relationship between the response variable and predictor variables (Guisan and Zimmerman 2000, Redfern et al. 2006). CART models resolve relationships between a single response variable (categorical or numeric) and one or more explanatory

variables (categorical and/or numeric) by recursively partitioning the data into two mutually exclusive subsets, each of which is as homogeneous as possible (Breiman et al. 1984, De'ath and Fabricius 2000, Urban 2002). The variables that were not excluded due to collinearity were used as predictor variables, and the 2006–2009 occupancy rate was used as the response variable. The circularly distributed burrow orientation data were not included in this analysis. CART analysis was performed using the unbiased recursive partitioning R package party (Hothorn et al. 2006) in the statistical software R (R Development Core Team 2014). Splitting and stopping were based on internal hypothesis testing criterion and Bonferroni adjusted P -values were associated with splits in the conditional inference tree (Hothorn et al. 2006).

To determine if individuals moved to burrows with characteristics identified by our population-level model, we compared the characteristics of the initial and final burrows of individuals that switched burrows during the study period. Habitat characteristics used in this analysis were those retained for analysis after identifying collinear variables. Such an analysis could overestimate the effect of habitat characteristics on switching behavior if individuals occupying burrows with unfavorable characteristics are more likely to move to a different burrow. Assuming the average quality of burrows is higher than those that individuals switch from, random burrow switching could result in the appearance of habitat preferences when in fact movement was random. For our analysis of burrow switching, we therefore used a randomization approach (Manly 1997). We paired each initial burrow with a random burrow sampled from all existing burrows, and calculated the mean difference in characteristics between the initial and random burrows. After 50,000 iterations of this approach, we calculated the probability that the mean differences between initial and randomly occupied "final" burrows would be greater than or equal to observed differences; this gives the probability that the observed differences could be due to chance.

RESULTS

Habitat characteristics and occupancy. Of 274 burrows measured, 255 had been mon-

itored during each breeding season of our study period. Burrow occupancy data for those seasons were included in the calculation of occupancy rate. Means of each habitat characteristic, except binomially distributed characteristics, are presented in Table 2. In this set of habitat characteristics, burrow length, NC elevation index, NC size index, and number of turns were positively related to occupancy rate, whereas NC soil moisture was negatively related to occupancy (Table 2).

We also recorded the presence or absence of tree, root, and log features. The most commonly occurring objects were trees at the entrance and roots in the passage and NC (Table 3). No difference in the frequency of these features existed between occupied and unoccupied burrows (Table 3). Mean orientation of all burrows was south (mean = 172° ; Rayleigh's $z = 6.1$, $P < 0.005$; Fig. 1). Burrows occupied in 2009 had a mean orientation of 178° and unoccupied burrows had a mean orientation of 166° (Watson-Williams test, $F_{1,273} = 0.5$, $P = 0.49$).

CART model of nest-site selection. The moisture content of soil taken from the floor of the NC was the primary predictor of occupancy; burrows with soil moisture ≤ 3.302 g H₂O/g dry soil had higher rates of occupancy (Fig. 2, CART, $P < 0.001$). NC size was a secondary determinant of occupancy for burrows that had greater NC soil moisture content. In these relatively wetter burrows, NCs with size indices > 1 had higher rates of occupancy (Fig. 2, CART, $P = 0.027$). For burrows with soil moisture content ≤ 3.302 g H₂O/g dry soil, burrows longer than 46 cm had higher rates of occupancy (Fig. 2, CART, $P = 0.028$). Analysis revealed a tertiary split in the pool of drier, longer burrows that indicated higher occupancy for sites with two or more burrows within 3 m (Fig. 2, CART, $P = 0.046$). Because soil moisture was a primary determinant of occupancy, we examined how burrow length and NC size index related to soil moisture content. Length was not related to the moisture content of NCs (Pearson's $r = 0.01$, $P = 0.44$), but larger NCs had a lower soil moisture content (Pearson's $r = -0.13$, $P = 0.023$).

Preferences in burrow-switching events. To test for individual-scale nest-site selection based on habitat characteristics, we analyzed 87 instances of burrow switching, examining differences between the characteristics of the initial

Table 2. Mean values (\pm SD) of 16 habitat variables associated with nest burrows of Leach's Storm-Petrels ($N = 255$) and individual binomial GLMMs of each habitat variable with 2006–2009 occupancy rate.

Collinear group	Habitat variable ^a	Mean \pm SD	Binomial GLMM	
			Estimate \pm SE	P^b
I	Burrows within 1 m	0.6 \pm 0.8	0.01 \pm 0.15	0.96
I	Burrows within 3 m	4.7 \pm 2.5	0.08 \pm 0.04	0.10†
I	Burrows within 5 m	11.4 \pm 4.3	0.04 \pm 0.03	0.13
I	Distance to nearest burrow (m)	1.29 \pm 0.75	-0.15 \pm 0.15	0.32
II	Canopy density (%)	57 \pm 21	0.02 \pm 0.05	0.72†
II	Soil depth (cm)	40 \pm 11	-0.002 \pm 0.010	0.83
III	Length (cm)	63 \pm 18	0.03 \pm 0.01	<0.001*†
III	Turns—number	0.8 \pm 0.8	0.41 \pm 0.16	0.013
III	Turns—total degrees (°)	56 \pm 62	0.002 \pm 0.002	0.35
IV	NC elevation index	2.4 \pm 0.8	0.35 \pm 0.14	0.017†
IV	Soil slope (°)	15 \pm 7	0.02 \pm 0.02	0.20
IV	Soil thickness above NC (cm)	13.6 \pm 5.4	-0.02 \pm 0.02	0.46
V	NC height (cm)	9.1 \pm 1.8	0.10 \pm 0.06	0.13
V	NC size Index	2.9 \pm 0.9	0.53 \pm 0.12	<0.001*†
VI	Soil moisture (g H ₂ O/g dry mass)	3.37 \pm 0.75	-1.00 \pm 0.15	<0.001*†
VII	Southern exposure	0.16 \pm 0.71	-0.25 \pm 0.16	0.14†

^aNC, nest chamber.

^bIn each collinear group, the habitat variable with the lowest P -value (marked with †) was retained for further analysis; other collinear variables were dropped. Asterisks indicate a statistically significant result after Bonferroni adjustment ($\alpha = 0.0033$).

Table 3. Frequency of trees, roots, and logs located at entrance, passage, and nest chambers of burrows occupied by Leach's Storm-Petrels or not occupied ($N = 255$; reported here only for 2009).

Collinear group	Feature	Location	Occupied	Unoccupied	Binomial GLMM	
					Estimate \pm SE	P^a
VIII	Tree	Entrance	22% (28)	18% (26)	0.33 \pm 0.28	0.26†
IX	Log	Entrance	4% (5)	10% (8)	-0.31 \pm 0.52	0.56†
X	Small root	Entrance	16% (20)	11% (17)	-0.07 \pm 0.34	0.85†
XI	Small root	Passage	50% (63)	44% (65)	0.32 \pm 0.23	0.17†
XII	Small root	Nest chamber	42% (53)	35% (51)	0.32 \pm 0.23	0.18†
XIII	Large root	Entrance	3% (4)	13% (19)	-1.05 \pm 0.39	0.010†
XIII	Large root	Passage	14% (18)	22% (33)	-0.33 \pm 0.30	0.28
XIII	Large root	Nest chamber	15% (19)	22% (33)	-0.45 \pm 0.28	0.13

Parenthetical values are observed number of occupied or unoccupied burrows with the feature at that location. The binomial GLMM analyses used binary occupancy data from 2006 to 2009.

^aIn each collinear group, the habitat variable with the lowest P -value (marked with †) was retained for further analysis; other collinear variables were dropped.

and final burrows of each switching individual. Just as soil moisture was the primary predictor of occupancy at the population scale, Leach's Storm-Petrels switched to burrows that were drier than their initial burrows (randomization test, $P < 0.0001$; Table 3). The final burrows were also longer than their initial burrows (randomization test, $P = 0.0001$; Table 3) and had larger NCs (randomization test, $P = 0.0005$;

Table 4), as predicted by the population-scale model (Fig. 2). These observed patterns were not due to random movements to available burrows from burrows of below-average characteristics (Table 4). Although the population-scale model found that burrow density was a predictor of occupancy, individuals did not switch to sites of higher burrow density (randomization test, $P = 0.22$; Table 4).

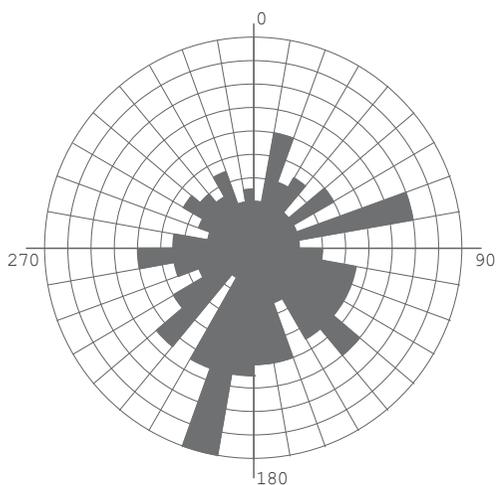


Fig. 1. Circular histogram of the compass bearings of entrances of nest burrows of Leach's Storm-Petrels. Burrow entrances had a statistically significant mean orientation of 172° (Rayleigh's test, $z = 6.1$, $P < 0.005$, $N = 274$).

DISCUSSION

We found that Leach's Storm-Petrels occupied burrows non-randomly, with habitat characteristics being strong predictors of nest-site selection. Microhabitat preferences assessed by comparing occupancy of burrows largely mirrored preferences assessed by comparing the burrows of individuals that switched nest sites over the study period. Drier and longer burrows with larger nest chambers (NCs) were preferred. Although burrows with greater nearby burrow density had higher occupancy rates, individuals moving between burrows did not switch to burrows in areas of higher density. Nest-site selection is commonly tested by comparing characteristics of used and available nest sites within a population (Jones 2001), and our data show that preferences exhibited by individuals that switch nest sites contribute to patterns of nest-site selection observed at the population scale. We found preferences for microhabitat characteristics that likely minimize energetic costs while perhaps decreasing predation pressure.

The cool, wet climate of the Bay of Fundy may drive preferences for burrow characteristics that minimize energetic costs. The incubation period is energetically costly for adults; after a 3-d incubation bout, adult Leach's Storm-Petrels

lose ~40% of their total metabolizable energy (Ricklefs et al. 1986). Breeding failure is more likely to occur during the incubation period (hatching success of 76%; Huntington et al. 1996) than during the nestling period (fledging success of 93%; Huntington et al. 1996, Mauck et al. 2004). Leach's Storm-Petrel chick mortality on Kent Island occurs most frequently after storms with heavy rains (Huntington et al. 1996, R. Mauck, unpubl. data), as is also true for other procellariiform seabirds (Boersma et al. 1980, Thompson and Furness 1991). When energetic costs were experimentally increased for adult Leach's Storm-Petrels, parents responded with a reduction in reproductive effort (Mauck and Grubb 1995), showing that this species is particularly sensitive to energetic costs during reproduction. Leach's Storm-Petrels are therefore expected to exhibit preferences for burrows with microhabitat characteristics that reduce energetic costs. Leach's Storm-Petrels chose burrows based on the soil moisture of the NC, a characteristic that likely affects thermoregulation. Because burrows are warmed relative to ambient temperatures, an energetic cost is associated with raising the temperature in the NC (Shenbrot et al. 2002, Ke and Lu 2009). Due to the high specific heat of water, burrows with higher soil moisture may incur a higher metabolic cost to warm the NC, making wetter burrows less thermally favorable.

Of the wetter burrows, larger NCs were preferred. This secondary preference for large NCs suggests that, if having a dry burrow does not satisfy this type of microclimate regulation criterion, Leach's Storm-Petrels exhibit preferences based on NC size, a characteristic that may confer microclimatic benefits (Smith and Belthoff 2001). Large chambers have more area in which to locate a relatively dry microsite for the nest itself. In support of this, we found that samples taken from directly below nest material were drier in larger NCs. Further, although smaller NCs can warm more quickly, larger NCs with lower surface-to-volume ratios generally maintain warmth longer (Ke and Lu 2009). Adult Leach's Storm-Petrels undergo long, energetically demanding incubation bouts and homeothermic chicks expend large amounts of energy for thermoregulation (Ricklefs et al. 1986). Large burrows presumably decrease the negative impact of high moisture content in wetter burrows via the insulating advantages

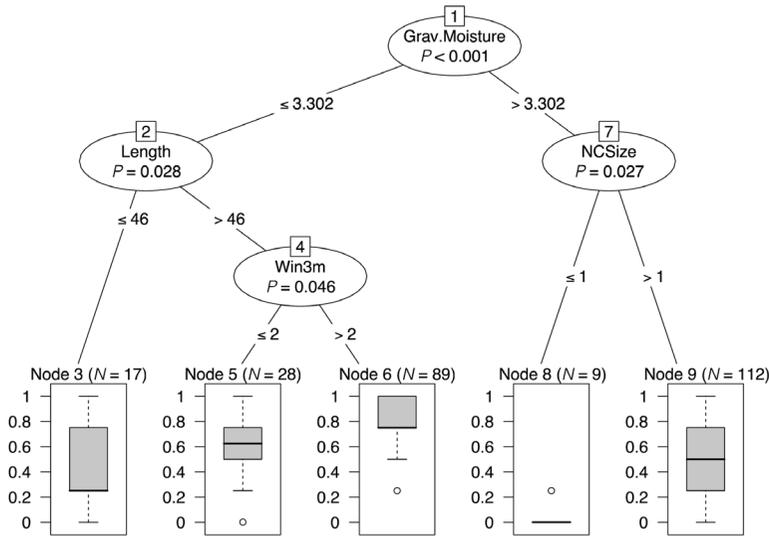


Fig. 2. Classification and regression tree between occupancy rate (dependent variable) and characteristics of burrows of Leach's Storm-Petrels (independent variables; $N = 255$, with box plots showing occupancy rates for each terminal node group. Dark bars indicate median occupancy rate for each node. Split and terminal nodes are identified as Node 1–9. *Abbreviations:* Grav.Moisture, gravimetric soil moisture; Length, burrow length; NCSize, nest chamber size index; Win3m, number of burrows within 3 m. Characteristics included in the analysis, but not shown because they were not significant predictors, were canopy density, nest chamber elevation index, southern exposure, tree, log, small root, large root at entrance, and small root at entrance, passage, and nest chamber.

Table 4. Mean values (\pm SD) of habitat variables for initial and final burrows in burrow-switching events ($N = 87$) by Leach's Storm-Petrels.

Habitat variable	Initial	Final	P^a
Soil moisture (g H ₂ O/g dry mass)	3.46 \pm 0.54	3.08 \pm 0.47	<0.0001*
Length (cm)	61 \pm 20	69 \pm 17	0.0001*
NC size index	2.9 \pm 0.9	3.2 \pm 0.9	0.0005*
NC elevation	-0.8 \pm 0.8	-0.6 \pm 0.9	0.12
Canopy density (%)	54 \pm 23	56 \pm 21	0.67
Burrows within 3 m	5 \pm 2	5 \pm 2	0.22

The randomization test calculates the probability that the mean differences between individual and final burrows would be observed if individuals switched randomly.

^aAsterisks indicate a statistically significant result after Bonferroni adjustment ($\alpha = 0.0083$).

of a low ratio of cool, wet soil surface area to air volume. Of the drier burrows, burrow length was a secondary predictor of burrow occupancy. Longer burrows did not have drier NCs, but may be preferred because they either decrease convective heat loss from NCs or aid in predator exclusion. Similarly, the preferred southerly orientation of burrow entrances may shield occupants from wind and rain that generally come from the north and

east, and may also result in greater incident solar radiation.

Predation within colonies is considered an important cause of mortality in Leach's Storm-Petrels (Huntington et al. 1996). Breeding adults nest on offshore islands, reducing encounters with non-avian predators (Huntington et al. 1996). Adults avoid avian predation at the colony by confining activity to the night and may also escape avian predation through

flight synchronization on moonlit nights (Harris 1974, Watanuki 1986). Longer, turning burrows may better exclude potential predators. For longer, drier burrows, we found greater burrow occupancy in areas of higher burrow density. This was a tertiary predictor of occupancy in our model and is expected to play a less significant role in nest-site selection, and could result from spatial heterogeneity in soil characteristics rather than preferences for density itself. Still, this finding is consistent with well-documented observations of greater breeding success at the dense center of colonies relative to the edges (Coulson 1968, Minias and Kaczmarek 2013).

When switching burrows, Leach's Storm-Petrels did so in a manner largely predicted by our CART model, moving to burrows that had lower soil moisture, longer burrow lengths, and larger NCs. Leach's Storm-Petrels appear to switch to burrows with characteristics preferred at the population scale. Improvement in nesting habitat with age by this mechanism is consistent with the hypothesis that experience increases reproductive success (Forslund and Pärt 1995) and observations that breeding success of younger individuals is low on Kent Island (Mauck et al. 2012). Still, the difference between the two scales of analysis in preferred characteristics underscores the relevance of scale in nest-site selection (Orians and Wittenberger 1991). Specifically, although burrows in areas of greater burrow density were more frequently occupied, individuals did not move to nest-sites surrounded by more burrows.

Importantly, the main predictors of nest-site selection we observed differ from those previously reported for Leach's Storm-Petrel breeding habitat use at larger spatial scales (Harris 1974, Grimmer 1980, MacKinnon 1988, Sklepkovych and Montevecchi 1989). By examining finer scales of selection—between existing burrows within a colony rather than for sites to construct new burrows—our results suggest that different sets of preferences are exhibited at these distinct scales. For example, higher slope, a characteristic that may be assessed prior to construction, is correlated with burrow density (MacKinnon 1988), but did not influence selection among existing burrows in this study. Preferred characteristics may be those that are more difficult or impossible to assess prior to construction.

The behavior of individuals gives rise to the microhabitat preferences observed in nest site selection studies, which typically examine preferences at the scale of a population by comparing used and available sites (Johnson 1980, Jones 2001). Our results show that burrow switching between years contributes to preferences observed at the scale they are typically measured. The existence of differences between these scales of analysis may elucidate how initial microhabitat preferences lead to reproductive success and how nest-site switching improves reproductive success with age.

ACKNOWLEDGMENTS

We thank J. Zangmeister, J. Cerchiara, J. Glazer, C. Mauck, and L. Harn for field work prior to 2009. J. Gannon assisted with the analysis. G. Ritchison and two anonymous reviewers provided helpful comments on the manuscript. This research was supported by the Kenyon College Summer Science Scholars Program, the Bowdoin Scientific Station, and a grant to RAM from the National Science Foundation (#0516784). This is contribution number 253 from the Bowdoin Scientific Station.

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