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Avian Behavior, Ecology, and Evolution

Soil moisture associations with burrow occupancy and reproductive success of Leach's Storm-Petrels

Asociaciones de la humedad del suelo con la ocupación de cavidades y éxito reproductivo en *Hydrobates leucorhous*

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ABSTRACT. Parent birds are under selection to choose nest sites that protect themselves and their nestlings from threats. Burrow-nesting can provide protection from predators and buffer against inclement weather. Soil characteristics within and around burrows may determine suitability of sites for burrow-nesting, and parents may choose sites based on factors such as soil compaction, composition, and moisture. Leach's Storm-Petrels (*Hydrobates leucorhous*) nest in burrows on islands that likely reduce predation and provide thermoregulatory and humidity benefits. We tested for associations between volumetric water content (hereafter, soil moisture) and nest site selection, burrow occupancy, and nest success. Soil moisture readings were taken from inactive and active burrow entrances and comparison points on Bon Portage Island, Nova Scotia, Canada. Soil moisture was significantly higher at comparison points than at burrows in each year; however, there was no difference in soil moisture at inactive versus active burrows or between burrows that were deemed to have or not to have produced a fledgling. Lower moisture content may allow for easier excavation; however, Leach's Storm-Petrels often use the same burrow for many years, and soil moisture almost certainly changes over time, so measurements taken during our study may not be representative of conditions when sites were initially chosen. Nonetheless, burrowing will allow freer exchange of water vapor than burrow-free soil so that burrows are expected to have lower moisture than soil within the same microclimate. With climate change increasing the frequency of inclement weather, soil moisture data and use of weather stations may be useful for predicting which petrel burrows will be more susceptible to loss by flooding, thereby informing threat assessments during conservation planning.

RESUMEN. Las aves parentales están bajo selección para escoger sitios de anidación y protegerse y proteger a sus pichones de las amenazas. La anidación en cavidades en el suelo puede proveer protección de depredadores y amortiguar el clima inclemente. Las características del suelo dentro y alrededor de las cavidades pueden determinar la idoneidad de los sitios para la anidación en cavidades en el suelo, y los parentales pueden escoger sitios basados en factores como la compactación del suelo, su composición y su humedad. *Hydrobates leucorhous* anida en cavidades en islas que probablemente reducen la depredación y proveen beneficios termo-regulatorios y de humedad. Comprobamos la asociación entre el contenido volumétrico de agua (de aquí en Adelante, humedad del suelo) en la selección del nido, ocupación de la cavidad y éxito de los nidos. Las lecturas de la humedad del suelo fueron obtenidas de las entradas de cavidades inactivas y activas y en puntos comparativos en la isla de Bon Portage, Nueva Escocia, Canadá. La humedad del suelo fue significativamente mayor en los puntos comparativos que en las cavidades en cada año; sin embargo, no hubo diferencia en la humedad del suelo entre cavidades inactivas y activas o entre cavidades que produjeron o no volantones. Un contenido de humedad más bajo puede facilitar la excavación; sin embargo, *Hydrobates leucorhous* con frecuencia utiliza la misma cavidad por muchos años y la humedad del suelo con certeza cambia a través del tiempo, por lo tanto, las medidas tomadas durante nuestro estudio pueden no ser representativas de las condiciones cuando los sitios son inicialmente seleccionados. No obstante, la excavación puede permitir un intercambio de vapor de agua más libremente que el suelo libre de excavaciones por lo que se espera que las cavidades presenten un nivel de humedad del suelo más bajo que el suelo en el mismo microclima. A medida que el cambio climático incrementa la frecuencia del clima inclemente, los datos en la humedad del suelo y el uso de estaciones meteorológicas pueden ser útiles para predecir cuales cavidades de *Hydrobates leucorhous* son más susceptibles a perderse por inundación, informando las estimaciones de las amenazas para planes de conservación.

Key Words: *burrow-nesting; microclimate; seabird; soil moisture*

INTRODUCTION

Nest site choice can be critical to avian reproductive success (Martin 1988, Clark and Shutler 1999). Among factors that can affect success are weather events (Yorio and Boersma 1994, Boersma and Rebstock 2014, Anctil et al. 2014, Öberg et al. 2015). Thus, parents should choose nest sites that provide protection against such events for themselves and their offspring. Habitat around, and microclimate at, nests can provide shelter from wind, rain, and buffer against temperature changes (Yorio and Boersma 1994, Shutler et al. 1998, Fricke et al. 2015, Høyvik Hilde et al. 2016). High or low ambient temperatures may cause hyperthermia or hypothermia in nestlings, and exposure to heavy rainfall can reduce nestling survival (Anctil et al. 2014, Öberg et al. 2015). For example, Peregrine Falcon (*Falco peregrinus*) nestlings were more likely to survive if their parents used nest boxes versus natural sites because the former provided better shelter from rain (Anctil et al. 2014). It is also more costly for parents to incubate eggs in damp, cool, windy conditions. Accordingly, Common Eiders

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(*Somateria mollissima*) increased incubation effort with higher windspeed and lower ambient temperatures (Høyvik Hilde et al. 2016). In addition, higher windspeed counteracted incubation benefits of higher temperature (Høyvik Hilde et al. 2016).

Some birds nest in cavities or burrows, which may lower exposure to predators and wind and can provide improved insulation compared to open sites (Collias and Collias 1984, Nilsson 1984, Deeming and Reynolds 2015, Fricke et al. 2015). Burrowing birds can experience nest failure from heavy rainfall events that drown or cause hypothermia of eggs or nestlings, but burrows nonetheless often provide more protection than above-ground nests (Yorio and Boersma 1994, Boersma and Rebstock 2014). For example, of 2482 Magellanic Penguin (*Spheniscus magellanicus*) nestlings alive during storms in a 28-year study, 8% died due to rainfall (Boersma and Rebstock 2014). Moreover, of those lost, nestlings from bush nests (i.e., low cover) were three times as likely to die from exposure during storms as nestlings in burrows (Boersma and Rebstock 2014).

Soil structure and composition may be important to burrow site choice, affecting ease of excavation and drainage (McLaren et al. 2014, Charre et al. 2017). Accordingly, Russet-crowned Motmot (*Momotus mexicanus*) burrows in sandy soil were more likely to be lost to flooding, whereas burrows in loamy soil were more structurally sound (Charre et al. 2017). In contrast, Blue-tailed Bee-eaters (*Merops philippinus*) preferred burrowing in sandier soils versus clay, because the former substrate tends to be drier and have better drainage (McLaren et al. 2014). Drier, less compacted soils may also be easier to excavate (McLaren et al. 2014, Charre et al. 2017).

Leach's Storm-Petrels (*Hydrobates leucorhous*, hereafter, petrels) lay a single egg in burrow-nests on islands that likely decrease predation by birds and mammals and may provide thermoregulatory benefits (Ricklefs et al. 1980, Fricke et al. 2015, Pollet et al. 2020). Incubation lasts ~45 d and is shared by both parents. After a few days of brooding, chicks are fed by both parents for 50–60 d, at which point the former are left alone to fledge at about 65 days post-hatch. Thus, eggs and nestlings spend extended intervals within burrow microclimates. This led Warham (1990) to suggest that the breeding range of various burrow-nesting Procellariiformes may be limited to latitudes with appropriate soil moisture. Most petrel nest failures occur in the incubation stage, although nestlings may succumb to starvation, drowning, hypothermia, or predation (Fricke et al. 2015). Ricklefs et al. (1980) noted that temperature within occupied petrel burrows on Kent Island, New Brunswick, Canada, remained relatively constant at around 10-15°C during the nestling stage. Within 2–12 days of hatching, petrel nestlings are left alone in their burrow while parents forage for food, and although nestlings can thermoregulate at this point, burrow microclimate is still important to nestling survival (Pollet et al. 2020). Petrels may dig a new burrow, or choose an existing one for nesting, but once chosen, ~95% return to the same burrow in successive years (Fricke et al. 2015, Pollet et al. 2020). A minority may switch after one or more reproductive failures; however, a new burrow is typically ≤ 20 m away (Fricke et al. 2015). Fricke et al. (2015) quantified microclimate at petrel nests, including soil moisture, and found that if switching occurred, the new burrow tended to be drier than the original. This may be because higher metabolic costs are associated with heating a wetter nest chamber. However, Fricke et al. (2015) measured soil moisture within nest chambers after chicks fledged in fall, which may not reflect conditions when burrows were chosen. Unlike Fricke et al. (2015), D'Entremont et al. (2020) did not find an association between soil moisture and nest site selection, but noted that mature forest loss on Kent Island, due to an outbreak of bark beetles (*Dendroctonus* sp.) in 2008, may have increased soil moisture that is expected to decrease as forests regenerate.

In this study, we tested whether there was an association between soil moisture and nest site selection or nest success of petrels. We predicted that burrows would be drier than comparison points, and that inactive burrows would have higher moisture levels than active burrows. We also predicted that burrows producing a fledgling would be drier than those that did not.

METHODS

This study was conducted on Bon Portage Island (also referred to as Outer Island; 43°28′N, 65°44′W), Nova Scotia, Canada, in 2018 and 2019. Bon Portage has a maximum elevation of 7 m on the northern and southern ends of the island. Ends of the island are forested primarily with black spruce (*Picea mariana*) and balsam fir (*Abies balsamea*) interspersed with patchy areas of graminoids, moss, other woody vegetation, and snags. Burrows monitored in this study were in both forest and patchy areas on the southern end of the island, where the majority of the petrel population breeds (Pollet and Shutler 2018). The soil is characterized as sandy loam and is very stony and imperfectly drained with the water table always present at a depth of 100 cm (Canadian Soil Information Service 2023).

Annual monitoring of petrel survival and productivity has been conducted since 2010 in twelve 12- × 12-m study plots on Bon Portage (Pollet et al. 2014). Burrows that have been active at least once since 2010 are marked with a uniquely numbered tag. Half of these plots were monitored since 2016 to determine nestling growth and nest success (hereafter, productivity plots), whereas the other half were visited less frequently to evaluate costs of disturbance to adult survival (hereafter, survival plots). Prior to 2016, parts of some plots were used for other studies (Shutler 2023, honours theses listed at https://www.acadiau.ca/~dshutler/PRes)

Burrows in survival plots are only checked twice per year, approximately 5 d apart in Jul to identify returning adults and band new adults, so that occupancy is determined but not nest success. Productivity plots are checked ≥ 2 times per year to determine burrow occupancy (Jul), whether eggs have hatched or not (Jul–Aug), nestling growth (mid-late Aug; methods described in Pollet et al. 2019), and finally, whether nestlings were predicted to fledge (i.e., had reached a wing chord length of ≥ 120 mm) or not (mid-Sep). At the very least, occupancy and fledge checks occur each year in productivity plots. At the first visit in Jul, burrows were considered active if they contained one or both adults, an egg, an adult and egg, or a nestling, and were considered inactive if empty or destroyed (e.g., collapsed from disuse, trampled by white-tailed deer (*Odocoileus virginianus*), etc.). Burrows were considered successful if nestlings were predicted to fledge. Burrows with nestlings that had not reached a wing chord length of 120 mm (indicative of reaching at least 56 d of age; Pollet et al. 2019) by the final check in mid-Sep were considered failed. This cut-off is used across all petrel colonies in Atlantic Canada and is used to determine long-term reproductive success to inform conservation action (Pollet, unpublished manual). Active burrows that were empty after a first check were also considered failed. In 2019, a borescope (HOMIEE Digital Inspection Camera, Model: IC1003-99) was used to view burrow contents but could not be used to determine nestling wing chord length. However, this resulted in fewer burrows with unknown activity status than in 2018, and allowed us to confirm nest failures in burrows where the end could not be reached by hand.

Percent volumetric water content of the soil (hereafter, soil moisture) was measured at a depth of 12 cm at both active and inactive burrows within the 12 plots using a soil moisture meter. A Spectrum TDR 300 was used at the first sampling on 5 Jul 2018; however, the unit failed that day, and was replaced by a Spectrum TDR 150 for subsequent visits, beginning on 2 Aug 2018. Measurements were taken in all 12 plots in 2018. In 2019, because of logistical constraints, measurements were only taken in a subset of productivity plots where we determine both occupancy and reproductive success, versus survival plots where we only determine survival and occupancy due to long-term monitoring protocols. Measurements were taken immediately adjacent to burrow entrances at the bottom edge of the opening, or as close to entrances as possible. Comparison measurements were taken ~1 m north of each entrance which meant that there were trivial differences in vegetation between burrows and comparison points. In general, burrow tunnels were approximately parallel to the surface soil and often curved around rocks or roots. Length of burrows ranged from 27–76 cm on islands in Maine and Newfoundland (Pollet et al. 2020). On Bon Portage, mean distance between burrow entrances in study plots was 61.9 ± SD 36.8 cm (n = 306; D. Shutler, unpublished data).

Readings taken on the Spectrum TDR 300 were, on average, 18.5% higher than readings from the Spectrum TDR 150 in 2018. We do not know whether this difference was due to differences in timing of sampling, rainfall prior to sampling, or other factors. Because the Spectrum TDR 300 failed, it was not possible to test the two devices side-by-side to determine a correction factor, or whether one was needed. However, it seems likely that each device would deliver similar results given that they were designed to measure the same soil moisture metric and were produced by the same manufacturer. Nonetheless, to be conservative, soil moisture at burrows and comparison points was tested within TDR machines using Wilcoxon signed-rank tests to determine if results were consistent.

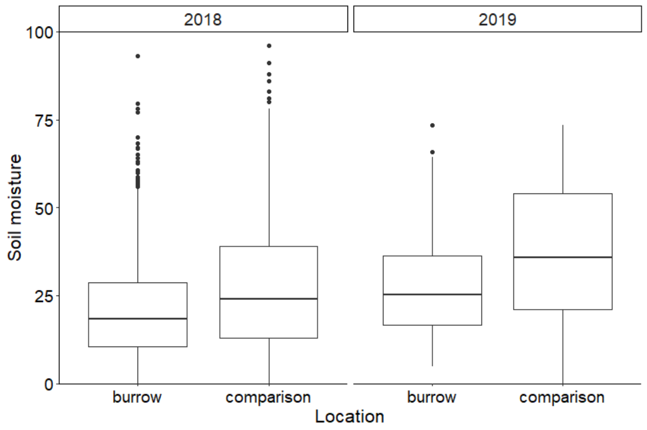
When analyzing moisture at burrows versus comparison points, raw moisture data were used because all these observations were paired; however, when analyzing moisture at active versus inactive, and successful versus failed burrows, median moisture at each burrow for that season was calculated. This was to account for occasions when different numbers or timings of visits to burrows occurred, and in some cases in 2019, burrows were only visited once. As an extra assessment, we also tested within sampling intervals to control for timing. Soil moisture data were not normally distributed (Shapiro-Wilk test, $W = 0.93$, $P < 0.0001$). Logarithmic and arcsine square root transformations did not improve normality, so Wilcoxon signed-rank tests were used to compare moisture levels at burrows versus comparison points, at active versus inactive, and at successful versus unsuccessful burrows. All statistical analyses were conducted in RStudio (R Core Team 2022, RStudio Team 2022).

RESULTS

In 2018, 1523 soil moisture readings were taken at burrows and 1523 at comparison points over 4 sampling periods (Table 1, $n_{burrows} = 481$). Because of logistical constraints, in 2019, soil moisture data were collected from a subset of burrows and their respective comparison points ($n_{burrows} = 91$). We restricted measurements to only burrows in productivity plots where both reproductive success and occupancy were determined. Thus, only 157 soil moisture readings were collected at burrows and comparison points each, over 3 sampling periods in 2019 (Table 1). In 2018 and 2019, 228 and 236 burrows, respectively, were included in productivity monitoring (Table 2, Table 3), and in 2019, only occupancy and productivity data from measured burrows are reported (Table 2, Table 3).

For data collected using the Spectrum TDR 300, soil moisture at burrows (median = 29.0%, range = 3.0 - 93.0%) was significantly lower than at comparison points (median = 45.0%, range = 10.0 - 96.0%; Wilcoxon signed-rank test, $W = 5780$, $P < 0.0001$). Similarly, for data collected using the Spectrum TDR 150, soil moisture at burrows (2018: median = 17.4%, range = 0.0 - 79.6%; 2019: median = 25.3%, range = 4.7 - 73.4%) was significantly lower than at comparison points (2018: median = 22.4%, range = 0.0 - 83.0%; 2019: median = 35.8%, range = 0.0 - 73.4%; $W = 967284$, $P < 0.0001$, Fig. 1).

Fig. 1. Boxplots of medians, quartiles, and outliers (black circles) of soil moisture (% volumetric water content) at Leach's Storm-Petrel (*Hydrobates leucorhous*) burrow entrances and comparison points on Bon Portage Island in 2018 and 2019.



Because both soil moisture meters gave similar results, data were pooled for these last analyses. There was no significant difference in moisture at active versus inactive burrows ($W = 4487.5$, $P = 0.62$, Fig. 2). Finally, there was no significant difference in moisture at failed versus successful burrows ($W = 1869.5$, $P = 0.64$, Fig. 3).

When testing within sampling periods, soil moisture at comparison points was significantly higher than at burrows, with the exception of samples collected on 22 Jun and 22 Jul 2019, when statistical significance was marginal (Table 1).

Table 1. Soil moisture sampling dates, Leach's Storm-Petrel (*Hydrobates leucorhous*) study plots sampled, number of burrows sampled, and reading unit used to measure soil moisture. In 2018, 1523 measurements were taken at burrows and 1523 at comparison points; the preceding measurements involved 481 different burrows and 481 different comparison points. In 2019, there were 157 measurements taken at burrows and 157 at comparison points; the preceding measurements involved 91 different burrows and 91 different comparison points. Wilcoxon signed-rank tests were used to compare soil moisture at burrows and comparison points within dates.

Year	Sampling interval	Plot numbers sampled	N burrows sampled	Spectrum TDR meter used	*W*	*P*
2018	5 July	1, 2, 3, 4, 5	135	300	5780.0	< 0.0001
	2-3 Aug	1, 2, 3, 4, 5, 6, 9, 10, 11, 12	420	150	68576.0	< 0.0001
	11-12 Aug	1, 2, 3, 4, 5, 6, 7, 8, 9, 10, 11, 12	483	150	100834.0	< 0.0003
	26-27 Aug	1, 2, 3, 4, 5, 6, 7, 8, 9, 10, 11, 12	485	150	91176.0	< 0.0001
2019	22 Jun	8	19	150	111.5	0.05
	22 Jul	12	50	150	978.5	0.06
	22 Sep	4, 8, 12	88	150	2560.5	< 0.0002

Fig. 2. Boxplots of medians, quartiles, and outliers (black circles) of soil moisture (% volumetric water content) at entrances of active and inactive Leach's Storm-Petrel (*Hydrobates leucorhous*) burrows on Bon Portage Island in 2018 and 2019. Median soil moisture from 1 to 4 measurements was calculated for each burrow in each year.

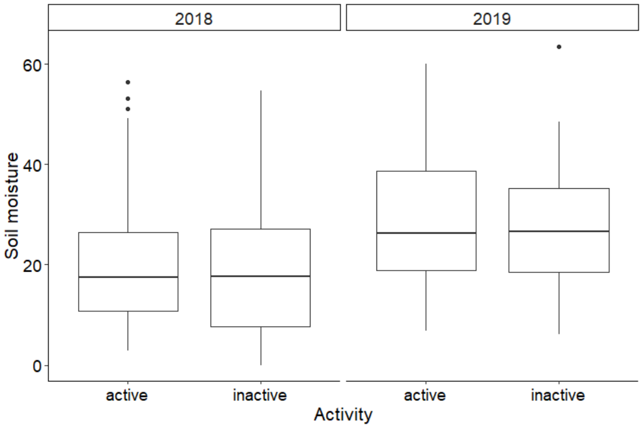
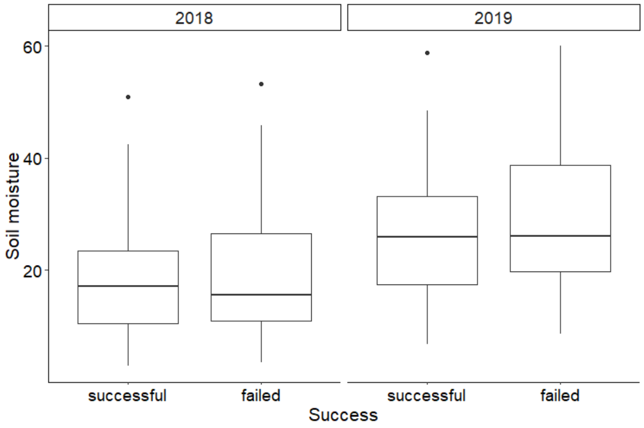


Fig. 3. Boxplots of medians, quartiles, and outliers (black circles) of soil moisture (% volumetric water content) at entrances of successful and failed Leach's Storm-Petrel (*Hydrobates leucorhous*) burrows on Bon Portage Island in 2018 and 2019. Median soil moisture from 1 to 4 measurements was calculated for each burrow in each year.



DISCUSSION

Soil moisture was lower at burrows than at comparison points, but there was no difference in median moisture at active versus at inactive burrows, or at failed versus at successful nests. One reason for the difference between burrows and comparison points may be that lower soil moisture at a given site allows for easier excavation (Kafutshi and Komanda 2011). However, it is more likely that a combination of moisture, compaction, soil type, and density of roots or rocks contribute to ease of excavation (McLaren et al. 2014, Fricke et al. 2015, Charre et al. 2017). Soil moisture is only one microclimate characteristic that may influence reproductive success; other factors, such as intraspecific competition and parental quality may complicate these relationships (Michielsen et al. 2019, Pagenaud et al. 2022). D'Entremont et al. (2020) determined that occupied burrow density was higher in areas where fern or shrub/bramble were the dominant understory on Kent Island. Habitat and understory types should be measured in future studies because they may be related to soil moisture and influence reproductive success, with caveats noted to follow.

Capacity of soil to hold water may change over time as plant communities and soil compaction change (Vanderlinden et al. 2012). In addition to these normal changes over time, burrow use may affect soil characteristics rather than soil characteristics driving burrow use. For example, Bancroft et al. (2005) noted that soil in areas with Wedge-tailed Shearwater (*Puffinus pacificus*) burrows was 28% wetter than in areas without burrows. It is unclear how long it may take for petrels to change surrounding soil characteristics, but individual Leach's Storm-Petrels may live >36 years, and ~95% reuse the same burrow each year (Pollet et al. 2020), so it seems unlikely that soil moisture levels measured during this study reflect conditions when sites were initially chosen for excavation. In addition, prospective first-time nesters may choose a pre-existing burrow, so burrow age may vary widely. In our study, purportedly new burrows could not be distinguished from pre-existing burrows that had had their tags dislodged by, for example, white-tailed deer; thus, within the time frame of this study, we estimate the percent range in new burrows was between 0 and 10%.

Fricke et al. (2015) suggested that factors influencing choice of a site in which to dig a burrow differ from factors used to select a pre-existing burrow; compacted soil may prevent petrels from digging at a new site. For instance, Malachite Kingfishers (*Alcedo cristata*) may balance ease of excavation with soil stability when choosing burrow sites (Kafutshi and Komanda 2011). Soil on Bon Portage Island is classified as "imperfectly drained," with an ever-present water table (Canadian Soil Information Service 2023), which suggests that there may be microclimates that provide better drainage than others. Future studies should include investigation of soil composition to better predict its drainage and suitability for burrow nesting.

In this study, because of logistical constraints, timing and number of visits to each burrow differed, which may not have representatively captured different moisture levels throughout each season. In the future, we suggest sampling burrows on a consistent schedule, or with automated loggers. Additionally, we recognize that soil moisture at burrow entrances likely does not precisely reflect soil moisture and humidity within nest chambers, but the strong differences we observed between entrances and comparison points suggest that our measurements were suitable surrogates. Moreover, taking measurements at entrances was less invasive and less likely to compromise burrow stability. Nonetheless, soil moisture or humidity levels within nest chambers could be monitored in conjunction with entrance soil moisture levels to test if entrance moisture levels can be used to predict nest chamber moisture levels. We attempted to do this with iButtons® (iButtonLink Technology) on Bon Portage (Pollet, personal communication), but petrels buried or removed units so that too few data were obtained.

Because of climate change, inclement weather events are likely to occur more frequently, and this will affect nest success of Leach's Storm-Petrels and other species (Anctil et al. 2014, Öberg et al. 2015, Høyvik Hilde et al. 2016, Dias et al. 2019). In Sep 2019, post-tropical storm Dorian passed through Atlantic Canada, bringing wind gusts of 143 km/h, and rainfall amounts of approximately 130 mm to Southwest Nova Scotia, where Bon Portage Island is located (Snoddon 2020). When checking if nests had fledged post-storm, we observed that 20 out of 119 active burrows in productivity plots contained a dead nestling (Hoeg, unpublished data; Table 2). We presumed that nestlings drowned or succumbed to hypothermia because feathers on carcasses were slicked down or still wet, and some burrows were soggy or still had water inside. However, nearby burrows contained live nestlings. It may be that older nestlings with more developed plumage may have been able to survive by moving to a drier area or were better able to repel water, whereas downy nestlings could not. Another factor to consider is that soil surrounding flooded burrows may have been more saturated to begin with, so that soil drainage was slower than incoming rainfall, resulting in flooding. Nestling drownings were not reported at another monitored petrel colony (Country Island; 45°06′N, 061°32′W) in north-eastern Nova Scotia (Jen Rock, personal communication), and we did not observe a similar event in 2020 or 2021 on Bon Portage Island. Although fledging success was lower in 2019 than in 2018 (Table 2), it is unclear whether drowned nestlings would have fledged or not if a storm had not occurred. However, Boersma and Rebstock (2014) determined that nestling Magellanic Penguin deaths from flooding caused by rainfall were additive to other causes. If petrel nestling drownings were similarly independent of other factors, such as predation, this may explain lower reproductive success in 2019.

Table 2. Classifications of Leach's Storm-Petrel (*Hydrobates leucorhous*) burrows where soil moisture measurements were taken on Bon Portage Island in 2018 and 2019.

		% of burrows			
Year	N burrows	active	inactive	collapsed	unknown status
2018	481	42	15	22	21
2019	91	40	32	20	8

Leach's Storm-Petrels are listed as "Threatened" in Atlantic Canada (COSEWIC 2020), and a collaborative effort (Birds Canada leading with support from Global Conservation Solutions) is underway to develop a conservation action plan. Climate change is considered a threat due to potential changing oceanic conditions that can disrupt food availability and increase inclement weather that can strand adults and fledglings on land and drown nestlings (COSEWIC 2020, Pollet et al. 2020, 2023). Although heavy rainfall and flooding have not yet been noted as a concern at other petrel colonies, it is more likely to become one in the future, particularly for burrow locations where soil is imperfectly drained and soil moisture remains high. Future studies should also use weather stations to monitor rainfall amounts during petrel breeding seasons to provide more insight into factors contributing to reproductive failure. Soil moisture data, in conjunction with knowledge of soil composition and compaction, may be useful in predicting which petrel burrows are more likely to be affected by inclement weather.

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Data Availability:

The data and code that support the findings of this study are openly available in Open Science Framework at https://doi.org/10.17605/OSF.IO/2ZRWH. Ethical approval for this research study was granted by Acadia University's Animal Care Committee under protocol number 03-17R#2.

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