Burrows buffer nest temperatures and offer a stable thermal microclimate for threatened seabird chicks during extreme events

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Abstract

Climate change is altering the severity and intensity of extreme weather events. Occupying microhabitats that buffer extreme weather may help species avoid harsh environmental conditions. Monitoring important habitats during extreme weather can highlight species that may benefit from targeted conservation actions. We describe the thermal microclimate and buffering capacity of Atlantic puffin (*Fratercula arctica*) and Leach's storm-petrel (*Hydrobates leucorhous*) burrows during extreme events and test for correlation between weather conditions and burrow characteristics on nest microclimate and buffering capacity. Both species' burrows buffered temperatures during extreme cold weather as nests were 7.4–8.0°C warmer than external temperatures. In extreme warm weather, Leach's storm-petrel and Atlantic puffin burrows were 9.5°C and 5.4°C cooler than outside temperatures, respectively. External temperature and wind speed were strong drivers of burrow temperature. Thus, the buffering capacity varied depending on the specific extreme events. Moreover, smaller burrow volume and greater canopy cover improved burrow buffering capacity during extreme events. Our results suggest that burrows may provide a direct line of defence for seabird chicks against cold and warming events. Given the complex responses of burrow microclimates to extreme events, quantifying how changes in environmental conditions will impact burrow-nesting seabirds in the future is key.

INTRODUCTION

Climate change is altering the severity and intensity of extreme weather events, such as heat-waves, storms, and floods (AghaKouchak et al., 2018). These short-term perturbations have strong direct and indirect impacts on marine and terrestrial species (Shoo et al., 2010; Harris et al., 2020). For example, extreme events can cause local species extinctions (Wernberg et al., 2013), pose energetic challenges (Cooper et al., 2019), and decrease breeding success (Martin et al., 2017). Therefore, it is imperative to detect where resilience lies in natural systems and identify which species will need conserving given that climate extremes are predicted to increase in frequency and intensity in the future (Wingfield et al., 2017; Harris et al., 2018).

Occupying microhabitats that buffer extreme weather may help species avoid variable and harsh external environmental conditions (Shoo et al., 2010; Pike & Mitchell, 2013; Scheffers et al., 2014; de Frenne et al., 2019). Cavity nests, such as burrows, can provide a stable thermal microclimate compared to ambient temperatures (Kesler & Haig, 2005; Mallory & Forbes, 2011; Mersten-Katz et al., 2012; Maziarz & Wesołowski, 2013; Kulaszewicz & Jakubas, 2018). Consequently, burrows structures can act as thermal refugia against unfavourable conditions that exceed lethal thermal maxima and minima (Pike & Mitchell, 2013; Moore, Stow & Kearney, 2018). Many species take refuge in burrows to address thermal challenges, including reptiles facing extreme desert heat (Moore, Stow & Kearney, 2018), mammals in strongly seasonal environments (Milling et al., 2018), and polar seabirds exposed to harsh cold weather (Kulaszewicz & Jakubas, 2018; Michielsen et al., 2019).

Climate change and severe weather are serious threats to seabirds impacting more than 170 million individuals worldwide (Dias et al., 2019). Seabird chicks are particularly vulnerable to extreme weather events because after achieving homeothermy, they typically remain in their nests until fledging. Consequently, chicks are exposed to any adverse weather that occurs during the breeding season. Many seabirds occupy open nests which often have little shelter and can experience high death rates if extreme events hit during the breeding season. For example, thousands of ground-nesting American white pelican (*Pelecanus erythrorhynchos*) chicks perished as a result of several extreme events that produced adverse extended cold, wet, and windy weather in North Dakota over a five-year period (Sovada et al., 2014). Similarly, cliff-nesting razorbills (*Alca torda*) experienced high breeding failure following a summer storm in Scotland (Newell et al., 2015). To avoid environmental extremes and predators, a number of seabirds, including tubenoses, auks, and penguins, nest in burrows which provide additional protection for chicks and adults (Michielsen et al., 2019). However, colonies of burrowing seabirds are also vulnerable to extreme weather, since burrows can flood, cool, and collapse (Glencross, Lavers & Woehler, 2021). For example, extreme cold weather caused a hypothermia-induced mass mortality of Atlantic puffin (*Fratercula arctica*) chicks in Newfoundland (Wilhelm et al., 2013). Therefore, more research is required to identify species which may be vulnerable to extreme events.

Two burrow-nesting species that may face increased risk to extreme events are the Atlantic puffin (*Fratercula arctica*), a ca. 450 g Alcid, and the Leach's storm-petrel (*Hydrobates leucorhous*), a ca. 45 g Procellariid. Both species are classified as "Vulnerable" with decreasing population trends by the International Union for Conservation of Nature (IUCN) Red List (BirdLife International, 2018a,b), and the Leach's storm-petrel has further been assessed as "Threatened" by the Committee on the Status of Endangered Wildlife in Canada (COSEWIC, 2020). Atlantic puffin chicks hatch around June and fledge in late-July to August (Lowther et al., 2002), therefore their breeding season is concentrated during the highest summer temperatures. The Leach's storm-petrel has a longer breeding season where the majority of chicks in Newfoundland hatch in July and fledge in October (Huntington, Butler & Mauck, 1996). Consequently, they experience the seasonal high heat events and are also exposed to hurricanes and cyclones towards the mid-late breeding season. Therefore, heat events and storms have the potential to severely impact both species. Yet, it is currently unknown how much thermal protection burrows provide chicks during adverse weather conditions.

These species are excellent models to test how nest site selection and characteristics impact thermal microclimate and buffering capacity, and provide opportunities to identify whether the species may need specific conservation measures for burrowing habitat. The Atlantic puffin exclusively select nesting sites along steep grass-covered maritime slopes, therefore burrows have no additional shelter and are exposed to high solar radiation, wind, and precipitation (Lowther et al., 2002). By contrast, Leach's storm-petrels nest in a variety of island habitats ranging from open grass meadows to heavily-canopied forests, which may offer additional thermal protection from hot and cold events (Huntington, Butler & Mauck, 1996). Chicks may therefore experience differing microclimate conditions in relation to habitat type.

Here we collected empirical data on internal and external burrow temperatures, burrow characteristics, habitat features, and weather conditions to investigate the thermal microclimate of Atlantic puffin and Leach's storm-petrel burrows during the breeding season. Specifically, we (1) describe the thermal environment of the burrows; (2) test for correlation between external environmental conditions and burrow thermal environment; (3) quantify the thermal buffering capacity of burrows to extreme cold and heat events; and (4) identify the features of burrows with more favourable microclimates (greater buffering effect) during extreme events. We expect to find thermal variability between burrows. We hypothesize that the burrows of both species will buffer the internal nest temperature from the external temperatures because cavity nest typically provide stable thermal environments compared to external temperatures (Kesler & Haig, 2005; Mallory & Forbes, 2011; Mersten-Katz et al., 2012; Maziarz & Wesołowski, 2013; Kulaszewicz & Jakubas, 2018). However, we predict that the burrows of Atlantic puffins will have greater thermal variability and lower buffering capacity than Leach's storm-petrel burrows because of their larger size and lack of canopy cover. Therefore, we further hypothesize that burrows with increased foliage cover and smaller burrow dimensions will have superior thermal buffering capacity.

METHODS

Study Site

We conducted fieldwork on Gull Island (47°15'35.4"N, 52°46'35.0"W), located within Witless Bay Ecological Reserve off the coast of Newfoundland and Labrador, Canada.

To capture the thermal variability in Atlantic puffin and Leach's storm-petrel burrows between mid-incubation to chick fledging, all data were collected between June and September in 2021. This research was provided full approval by the Memorial University Animal Care Committee (protocol number: 20200476). To undertake field work on Gull Island within the Witless Bay Ecological Reserve in 2021, we received a Wilderness and Ecological Reserves Scientific Research Permit. Canadian Wildlife Service banding permits (permit number: 10559 N) were been obtained with appropriate permissions.

Temperature Logger Deployment

To record the temperature within and outside Atlantic puffin and Leach's storm-petrel burrows, we deployed 120 encased ElectricBlue EnvLoggers (model 2.4; ± 0.2°C accuracy). The EnvLoggers recorded temperatures every 30 minutes at 0.1°C resolution. For each species, 30 burrows with an egg and adult present were selected. We placed one temperature logger above the nest, which is typically located at the back of the burrow, and one logger at the burrow's entrance (Fig. 1). The adults were not removed to minimise disturbance.

Seven temperature loggers that were placed within Atlantic puffin burrows, and one logger that was placed outside were lost. Therefore, temperature data from 23 internal loggers and 29 external loggers remained for our analyses. All 60 loggers were successfully retrieved from Leach's storm-petrel burrows.

Weather Conditions

To test for the effect of external weather conditions on the burrow microclimate, we acquired air temperature and wind speed data on Gull Island from mobile weather stations (Kestrel 5500 Weather LiNK) located near the study plots. The weather stations were programmed to record data every 30 minutes.

Burrow and Plot Characteristics

To quantify the influence of burrow characteristics on the microclimate, we measured multiple internal dimensions of each chamber (Fig. 1): *depth* – distance from the burrow entrance to end; *width* – distance between both adjacent burrow walls; and *height* – distance from floor to roof of burrow. To represent the thermal mass required to be heated or cooled, we calculated the burrow *volume* using the elliptical cylinder volume equation (Eq. 1). We further quantified the *entrance area* using ImageJ software which calculates a surface area from a photograph.

$$Volume = \pi \times \frac{Height}{2} \times \frac{Width}{2} \times Depth \quad \textbf{Eq. 1}$$

To detect variation in Leach's storm-petrel burrow microclimates, we selected plots with varying foliage coverage. To estimate canopy cover, a square photograph of the sky above each burrow was taken, and the area covered by trees was later calculated using ImageJ. Atlantic puffins nest exclusively on grassy slopes therefore canopy cover data was not collected for the species.

Burrow Thermal Environment

To compare the thermal environment between burrows, we summarised the mean, maximum, and minimum temperatures in each burrow for the observation period. We further summarised the mean burrow temperature and the temperature range across all burrows. To compare the stability between the internal and external burrow temperatures, we compared the standard deviation of temperatures through the season.

Thermal Buffering Capacity of Burrows Against Extreme Events

To quantify the thermal buffering capacity of burrows to extreme cold and heat events, we calculated the temperature buffer values as the temperatures inside the burrows minus temperatures outside the burrows; therefore, negative values reflect cooler burrow temperatures than air temperatures, while positive values reflect warmer burrow temperatures. Two buffering temperatures were calculated: 1) to compare the internal burrow buffering to ambient temperatures, we calculated the buffer between the internal temperature logger and the weather station air temperature; and 2) to capture the buffering effect from solar heating we calculated the difference between the internal and external temperature logger.

To define extreme events during the breeding season, we extracted the 1st and 99th percentiles of external air temperatures recorded at the weather stations, based on a common definition of an extreme event (McPhillips et al., 2018). We then compare the mean and standard deviation thermal buffering of burrows during hot and cold extremes for both species.

To test if extreme weather impacts the capacity of burrows to buffer external environmental temperatures, we performed a changepoint analysis using package 'changepoint' and function *cpt.mean* with the pruned exact linear time (PELT) method, and determined the penalty parameters with elbow plots (Killick & Eckley, 2014). The *cpt.mean* approach finds changes in mean of data, and denotes a changepoint as the first observation of the new segment. We selected the PELT algorithm because it can search for multiple changepoints that are spread throughout the data rather than confined to one portion (Killick & Eckley, 2014). There were two heat extremes identified from the weather stations during the Atlantic puffin breeding season, while the Leach's storm-petrels experienced one heat extreme, in addition to two storms, Hurricane Larry and Extratropical Cyclone Odette (Fig. 2). Therefore, we ran the analysis through the data of each internal temperature logger to identify the number of burrows that experienced a significant temperature change during the heat extremes and storms.

Correlates of Burrow Thermal Microclimate and Buffering Performance

To test for correlation between external weather conditions and burrow thermal environment, we constructed a generalized additive mixed model (GAMM) for each species using package 'mgcv' and function *gamm* (Wood, 2004, 2017). Internal burrow temperature was included as the response variable. For the predictor variable, the interaction between air temperature and wind speed was scaled and modelled as a smooth term. Predictors were fitted with thin plate regression splines (bs="ts"), which is equivalent to the default *gam* smooth (bs="tp") but with a modification to the smoothing penalty, so that the null space is also penalized slightly and the whole term can therefore be shrunk to zero (Wood, 2004, 2017). Burrow ID was added as a random effect and we modelled a within-burrow corAR1 structure to account for autocorrelation (Models S2.6 and S2.12).

To identify the unique features of burrows that are under- and overperforming during extreme events, we built two GAMM models (Wood, 2004, 2017) for each species: one for the extreme cold (Models S2.16 & S2.20) and one for the extreme warm events (Models S2.14 & S2.18). Buffering temperature per burrow during extreme events (1st and 99th percentiles) was included as the dependent variable. The burrow characteristics of entrance area and volume were scaled and included as predictor variables and modelled as smooth terms. Canopy cover was also scaled and included as a smooth term predictor within the Leach's storm-petrel models. Atlantic puffins nest exclusively on grassy slopes therefore canopy cover was not included in the model for the species. All predictors were fitted with thin plate regression splines (bs="ts"). Burrow ID was added as a random effect and we modelled a within-burrow corAR1 structure to account for autocorrelation.

Model fits were checked with package 'DHARMa' (Hartig, 2022), and concurvity was checked with function *vis.concurvity* from package 'dsm' (Miller et al., 2022). All model structures and selection procedures are available at https://github.com/CerrenRichards/Burrow-Microclimate and Supplementary Material 1.

RESULTS

Burrow Thermal Environment

We find that within the burrows of each species, there was variation in maximum, mean, and minimum internal temperatures (Fig. 3). Moreover, there was consistent variability in the intra-burrow maximum, mean, and minimum temperatures for both species (Fig. 3). While some burrows had consistently high or low internal temperatures with little variability, other burrows experience high variability across the maximum, mean, and minimum temperatures (Fig. 3). The mean internal burrow temperature through the season for Atlantic puffins, 17.92 °C, was warmer than for Leach's storm-petrels, 15.75 °C (Fig. 4). Atlantic puffin burrows ranged between 13.0–25.1 °C, while the Leach's storm-petrel burrows range was 9.7–22.2 °C. Moreover, for both species, the internal burrow temperatures were more stable (Atlantic puffin, SD = 1.71 °C; Leach's storm-petrel, SD = 1.34 °C) than external burrow temperatures (Atlantic puffin, SD = 6.96 °C; Leach's storm-petrel, SD = 3.62 °C), and the weather station temperatures (Forest plot, SD = 3.49 °C; Open plot, SD = 3.59 °C).

Thermal Buffering Capacity of Burrows Against Extreme Events

We find that Atlantic puffin and Leach's storm-petrel burrows buffer environmental temperatures from extreme external hot and cold events (Fig. 5). Atlantic puffin burrows had greater buffering capacity during cold extremes because burrows were, on average [± SD], 8.0 ± 1.5 °C warmer than external temperatures recorded at the weather stations, compared to 5.4 ± 1.8 °C cooler during warm extremes (Fig. 5b&d). By contrast, Leach's storm-petrel burrows were more effective at buffering nest temperatures from warm extremes because their burrows were, on average [± SD], 9.5 ± 1.4 °C cooler than external temperatures recorded at the weather stations. In comparison, during cold extremes their burrows were 7.4 ± 1.2 °C warmer than external temperatures (Fig. 5b&d).

Comparing the temperatures between the internal and external temperature loggers captured the buffering effect from solar heating. Atlantic puffin burrows were exposed to greater solar heating because burrows were, on average, 13.0 ± 5.6 °C cooler than external temperatures during heat extremes, a 7.6 °C difference from the temperatures recorded at the weather station. While, during cold extremes the buffering recorded by the external loggers were similar to those recorded by the weather station because burrows were 7.8 ± 2.1 °C warmer. Similarly, for Leach's storm-petrels, solar heating did not greatly impact burrow buffering because temperature buffering was similar between the external loggers and the

weather stations. During heat extremes, burrows were 8.4 ± 3.5 °C cooler and during cold extremes, burrows were 6.9 ± 1.3 °C warmer than temperatures recorded on the external loggers.

We find that heat events and storms can impact the capacity of burrows to buffer external temperatures. However, the burrow's response varied by extreme event. The changepoint analysis identified a significant increase in the internal temperature of all 23 Atlantic puffin burrows (100%) during the first and second seasonal heat extreme. Similarly, the temperature within 29 of 30 Leach's storm-petrel burrows (97%) significantly increased during the second heat event. Only five Leach's storm-petrel burrows (17%) showed a significant increase in internal temperature during Hurricane Larry (Fig. 5c). Whereas, 27 of 30 Leach's storm-petrel burrows (90%) were significantly colder during Extratropical Cyclone Odette (Fig. 5c).

Correlates of Burrow Thermal Microclimate and Buffering Performance

We find that the thermal microclimate of Atlantic puffin and Leach's storm-petrel burrows is significantly driven by weather conditions. There is a non-linear interaction effect between wind speed and temperature ($p < 0.001$ for Atlantic puffins and Leach's storm-petrels, from GAMM models, see Models S2.6 & S2.12 for coefficient values). For both species, internal burrow temperature is lowest at low values of external air temperature and wind speed. For Atlantic puffin burrow, internal temperature remains the highest when air temperature is the highest, regardless of wind speed. While for Leach's storm-petrel burrows, internal temperature was highest when wind speed is low and air temperature is high.

We find that burrow features and canopy cover influenced the burrow's buffering performance. During heat events, Atlantic puffin nests with more favourable microclimates (cooler than external temperatures) had a smaller burrow volume ($p = 0.025$, from GAMM models, see Model S2.18 for coefficient values) while Leach's storm-petrel nests had greater canopy cover (borderline effect, $p = 0.056$, from GAMM models, see Model S2.14 for coefficient values). During cold events, Atlantic puffin nests with greater buffering capacity (warmer nests than external temperatures) had a smaller burrow volume (borderline effect, $p = 0.056$, from GAMM models, see Model S2.20 for coefficient values). However, unique features of Leach's storm-petrel burrows that might create a more favourable microclimate during extreme cold weather did not emerge (Model S2.16).

DISCUSSION

We find that seabird burrows buffer nest microclimates against seasonal extreme hot and cold temperatures, thus providing a thermally-stable environment for chicks. During seasonal extreme cold weather, Atlantic puffin and Leach's storm-petrel burrows were warmer than the external temperatures, while burrows were cooler during seasonally extreme hot weather. Indeed, our results align with other studies on burrow-dwelling seabirds. For example, Cassin's auklet (*Ptychoramphus aleuticus*) burrow temperatures remained stable on Farallon Island, California, despite large fluctuations in outside ambient temperature (Manuwal, 1974). Likewise, in the high arctic, little auk (*Alle alle*) burrows were warmer than ambient air temperatures (Kulaszewicz & Jakubas, 2018). Burrows also provide ectotherms, such as

insects and lizards, thermal protection from extreme temperatures by buffering lethal hot and cold exposure (Sunday et al., 2014; Moore, Stow & Kearney, 2018). Given that climate extremes are predicted to increase in frequency and intensity in the future (Wingfield et al., 2017; Harris et al., 2018), burrows may therefore provide a direct line of defence for seabird chicks against current and future extreme cold and warming events, as predicted for other species (Moore, Stow & Kearney, 2018).

Although burrows generally buffered environmental extremes, the response of burrows was species specific. Atlantic puffin burrows had greater buffering capacity during cold weather extremes compared to warm weather extremes. This is likely because Atlantic puffin burrows are located on grassy slopes, in close proximity to the ocean, and fully exposed to the summer sun, therefore do not buffer well to heat extremes. Moreover, in both hot and cold extremes, Atlantic puffin burrows with smaller volumes had greater buffering capacity. Similar to the present study, in Wilson's storm-petrel (*Oceanites oceanicus*) nests in Antarctica, smaller nest dimensions (entrance area), greater insulation, and burrow orientation were important for establishing a favourable thermal environment (Michielsen et al., 2019). Thus, our findings suggest that smaller burrows may be relatively insulated by the ground therefore less hot and cold air can enter and circulate through the burrow. By contrast, Leach's storm-petrel burrows buffered temperatures more during warm weather. Compared to Atlantic puffins, their burrows have an additional layer of protection from foliage, such as ground-covering ferns and trees. Forests act as thermal insulators by cooling the understory when ambient temperatures are hot (Ewers & Banks-Leite, 2013; de Frenne et al., 2019; Zellweger et al., 2019). Therefore, it is likely that the forest cover is further insulating the burrows by offering shading from solar heating. This is supported by our data because during warm extremes, greater canopy cover was associated with greater buffering for Leach's storm-petrel burrows. Comparably, in East Africa, naked mole-rat (*Heterocephalus glaber*) burrows located under vegetation had lower temperatures than those under unshaded bare earth (Holtze et al., 2018).

We further find that the thermal response of individual burrows depends on specific extreme events. For example, most Leach's storm-petrel burrows showed a significant change in temperature during Extratropical cyclone Odette, while there was no change in temperature for the majority of burrows during Hurricane Larry. These responses are likely because the ambient temperature did not change dramatically during Hurricane Larry, while Extratropical cyclone Odette brought the coldest temperatures of the season. Future extreme events may present additional challenges and likely complex interactions will need to be considered when evaluating the response of burrows.

Since burrows are less effective at buffering temperatures during extreme weather, the chicks may face problems in the future given warming temperatures driven by climate change. Consequently, habitat management approaches may be needed to reduce nest temperatures during extreme events. Adapting conservation methods from other endangered species, such as sea turtles, could hold the key. For example, conservationists use 'nest shading' to reduce turtle nest temperatures by building small shade structures over egg clutches (Jourdan & Fuentes, 2015; Mutalib & Fadzly, 2015). Alternatively, artificial nest boxes show great promise for improving the breeding success of burrowing seabirds (Libois et al., 2012; Sutherland, Dann & Jessop, 2014), and may offer thermal-protection from heat events. Although,

special consideration of the nest box design will be imperative to prevent overheating or excessive cooling (Lei, Green & Pichegru, 2014; Kelsey et al., 2016; Fischer et al., 2018). This could be a promising avenue for protecting chicks from future extreme events and merits future investigation.

The interplay between air temperature and wind speed emerged as a key driver for the internal thermal microclimate of Atlantic puffin and Leach's storm-petrel burrows. This finding is consistent with other studies. For example, Cassin's auklet burrow temperatures fluctuated in proportion to the changes in ambient temperatures, and temperatures were buffered more within soil burrows, compared to rock crevice nests (Manuwal, 1974). Similarly, external air temperature, wind speed, and wind direction determined the internal temperature of Wilson's storm-petrel nests (Michielsen et al., 2019).

Thus, given the complex responses of burrows microclimates to extreme events, quantifying how changes in a variety of external (wind, temperature, precipitation) and internal (temperature, humidity) environmental conditions will impact burrow-nesting seabirds is a key future direction. This will be particularly critical in Newfoundland since the frequency of extreme windy days have increased over the past decade (Government of Canada, 2022). Moreover, precipitation presents an additional layer of complexity and may pose challenges for seabird chicks. Wet burrows can be lethal to seabird chicks because they are covered in non-waterproof down until they grow adult feathers. Consequently, Atlantic puffin chick body temperature has been observed to significantly decrease during periods of high precipitation (Vongraven, Aarvik & Bech, 1987). Moreover, burrowing seabird colonies are often vulnerable to flooding and collapse during heavy rainfall, particularly in unvegetated areas, which can lead to breeding failure (Tiller et al., 2000; Glencross, Lavers & Woehler, 2021). For example, a mass mortality of Atlantic puffin chicks was recorded following extreme precipitation and cold weather in Witless Bay Ecological Reserve(Wilhelm et al., 2013).

The temperature variations identified in this study may also translate into breeding performance. Burrow thermal variations have previously been documented to influence breeding success and growth rate in seabirds (Kulaszewicz & Jakubas, 2018). Similarly, higher nest temperatures can impede growth, as observed in blue tit (*Cyanistes caeruleus*) and eastern kingbird (*Tyrannus tyrannus*) chicks (Murphy, 1985; Andreasson, Nord & Nilsson, 2018). Therefore, given predicted future warming and increases in extreme events frequency, the next steps may be to investigate how temperature variations influence the growth rates and energy budget of these threatened seabird chicks. Furthermore, the thermal optimum for Atlantic puffin and Leach's storm-petrel chicks is presently unknown. Therefore, research investigating seabird thermal optima is needed to understand whether these burrows are providing a thermal refuge for chicks from extreme events.

CONCLUSION

Here we find that burrows buffer nest temperatures and offer a stable thermal environment for Atlantic puffin and Leach's storm-petrel chicks during extreme events. Our results support commonly observed trends in diverse burrowing ectotherms and endotherms. However, we noted striking differences between

species in buffering capacity during extreme events even though burrowing locations were nearby, which is likely driven by the ground habitat that each species selects. We also noted distinct variations in the intraspecific burrow thermal environments, and found that the internal microclimate of burrows is strongly driven by external weather conditions in both species, implicating the importance of environmental change in driving shifts in nesting success. Consequently, future climate warming and increases in storm frequency and intensity may pose challenges for breeding performance. Next steps may be to investigate how extreme events and temperature variations influence the growth rates and energy budget of chicks. It will also be important for future studies to identify and manage burrows that promote optimal thermal environments for breeding success with conservation tools, such as artificial nest boxes and shading.

Declarations

CRediT author statement

Cerren Richards: Conceptualization, Methodology, Investigation, Writing – Original Draft, Formal Analysis, Visualisation. Sydney M. Collins: Investigation, Writing – Review & Editing. Kayla Fisher: Investigation, Writing – Review & Editing. Robert J. Blackmore: Investigation, Writing – Review & Editing. David A. Fifield: Supervision, Formal Analysis, Funding acquisition, Writing – Review & Editing. Amanda E. Bates: Supervision, Methodology, Formal Analysis, Writing – Review & Editing, Funding acquisition.

Data Sharing and Accessibility

R code covering the major analytical steps is available on GitHub at https://github.com/CerrenRichards/Burrow-Microclimate.

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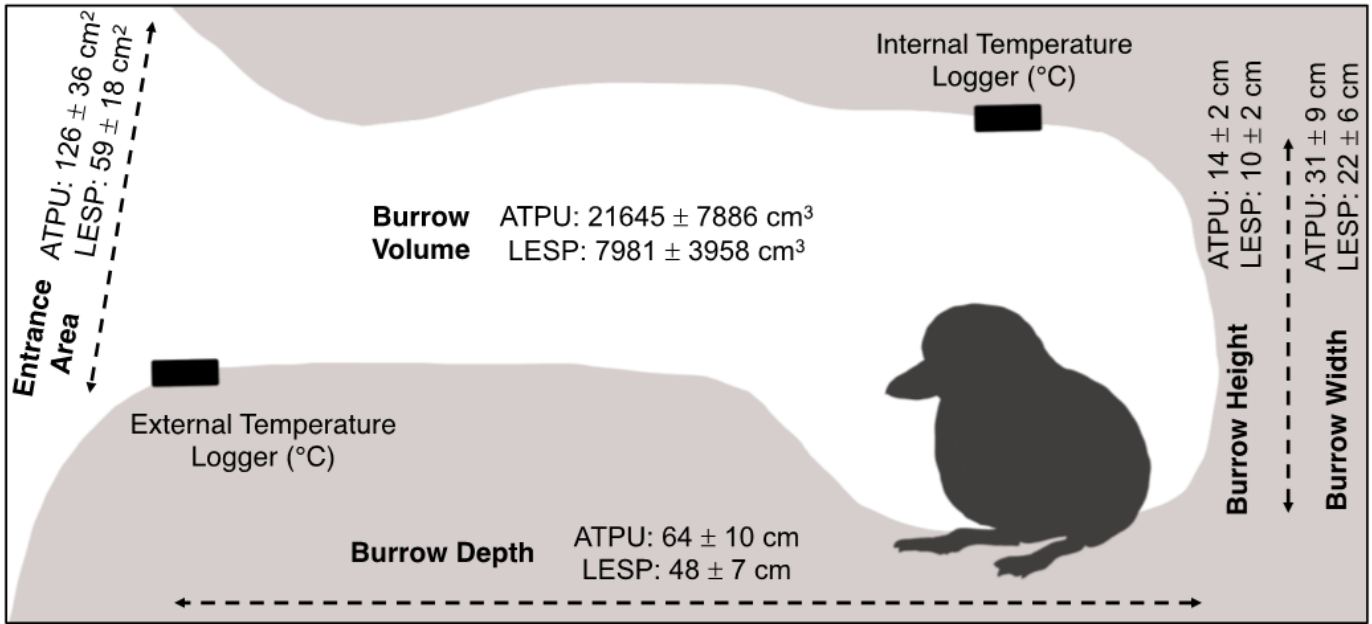
Figures

Figure 1

Schematic diagram representing a chick in a burrow and positioning of temperature loggers. Mean (± SD) measurements of characteristics across 30 Atlantic puffin (ATPU) and 30 Leach's storm petrel (LESP) burrows.
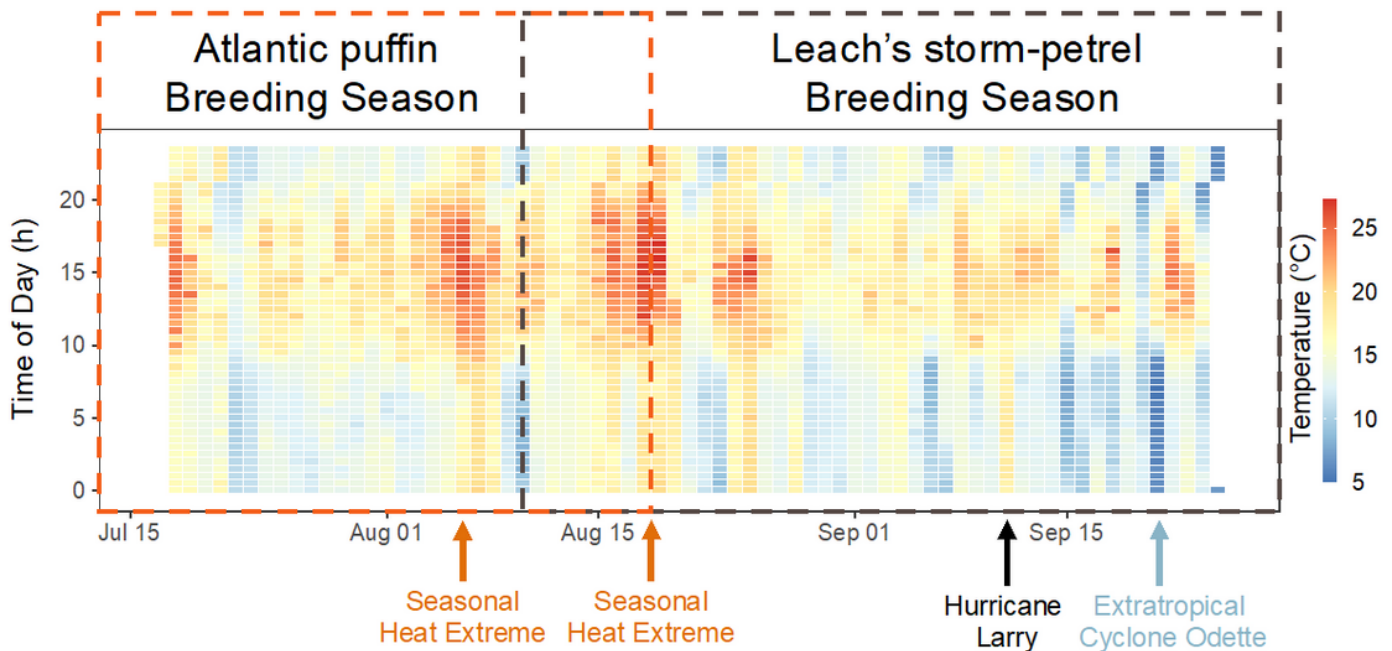
Figure 2

External temperature variation recorded on the weather station during the Atlantic puffin (orange) and Leach's storm-petrel (grey) breeding season in 2021. Arrows indicate the seasonal temperature extremes and storms.
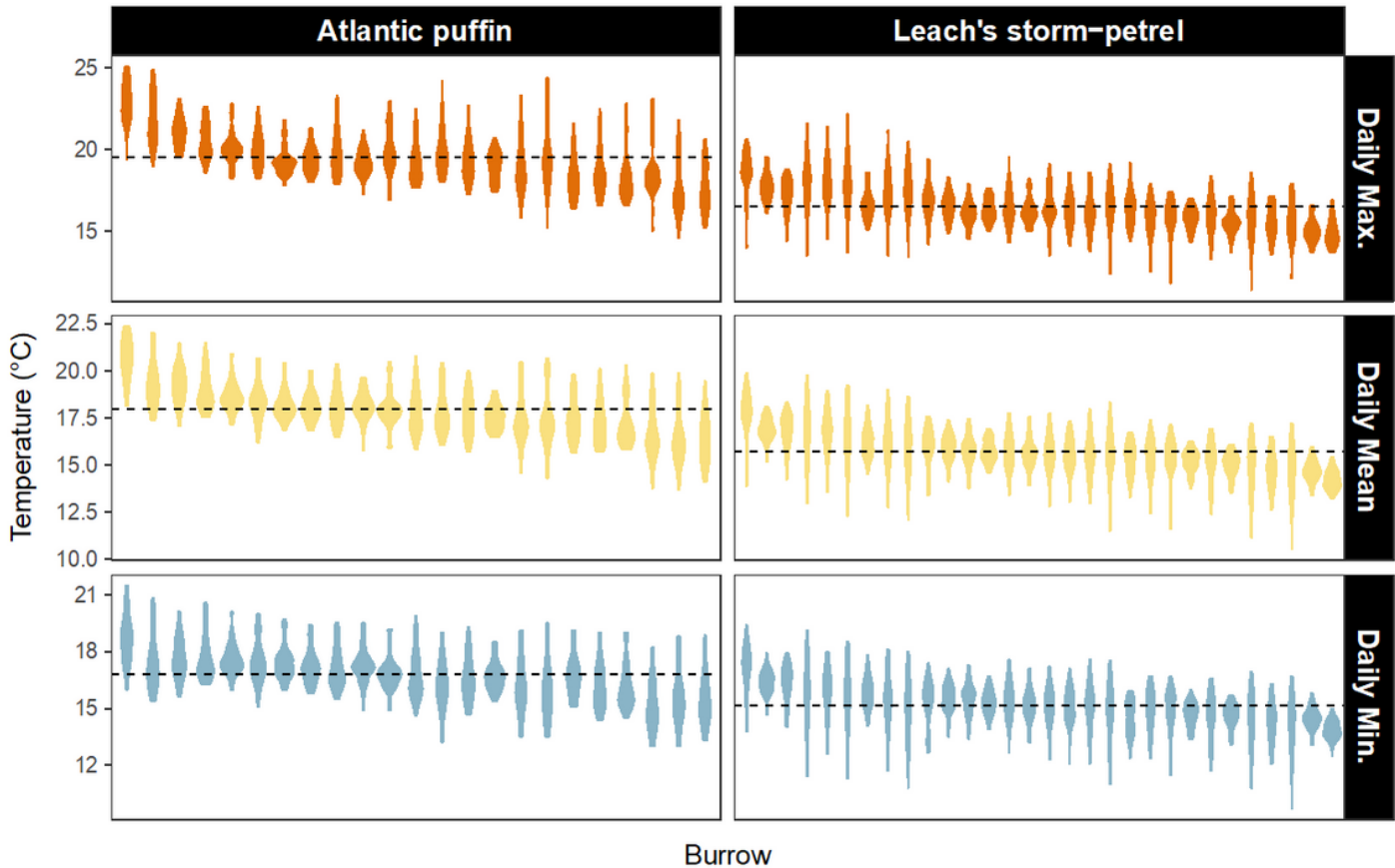

Figure 3

The daily maximum, mean, and minimum temperature variations within 23 Atlantic puffin burrows over 35 days (left) and within 30 Leach's storm-petrel burrows over 49 days (right). The black dotted line represents the mean temperatures across all burrows. Burrows are ordered by average temperature.
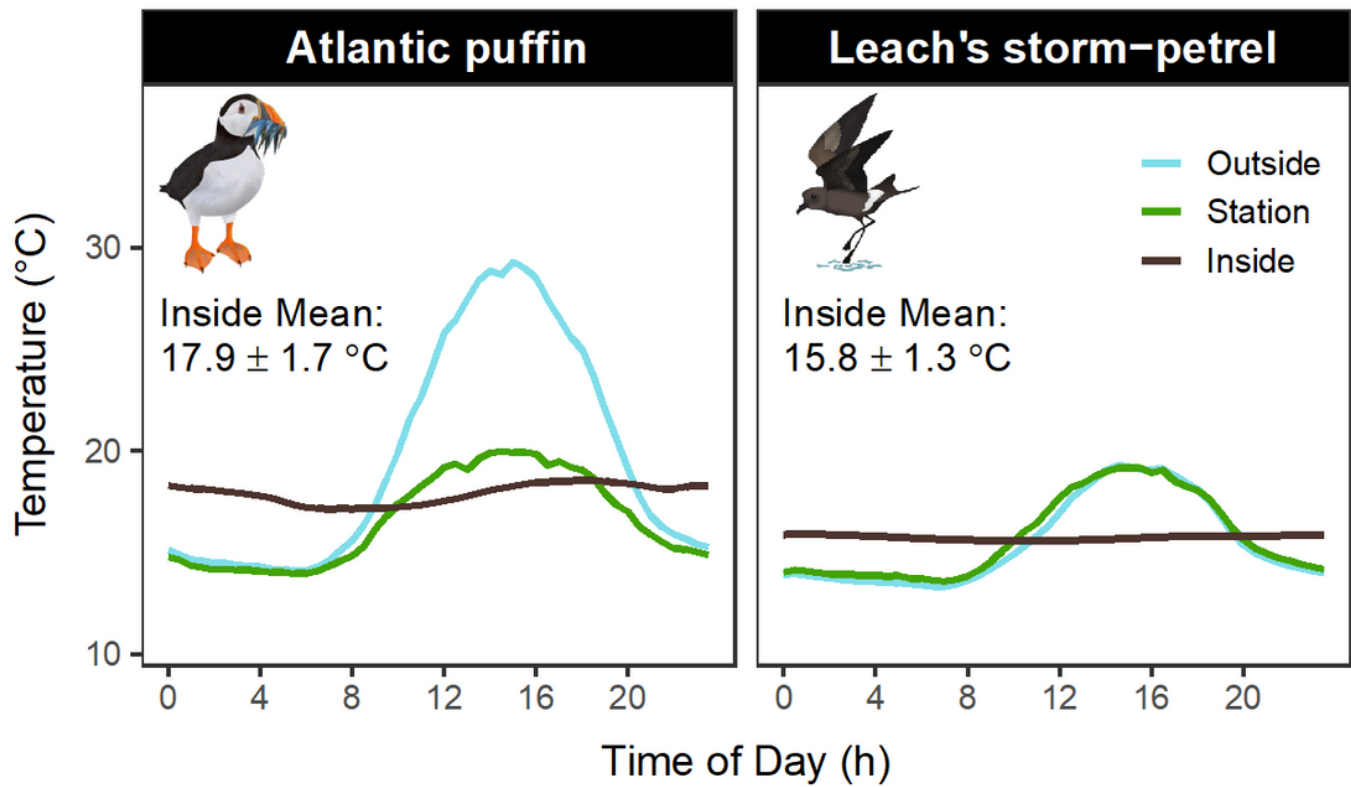
Figure 4

Mean temperature (± SD) through the day within (n = 23) and outside (n = 29) Atlantic puffin burrows over 35 days and within (n = 30) and outside (n = 30) Leach's storm-petrel burrows over 49 days. Temperatures were recorded every 30 minutes. Blue and brown represent the external and internal logger temperatures, respectively, while green represents the temperatures recorded at weather stations.
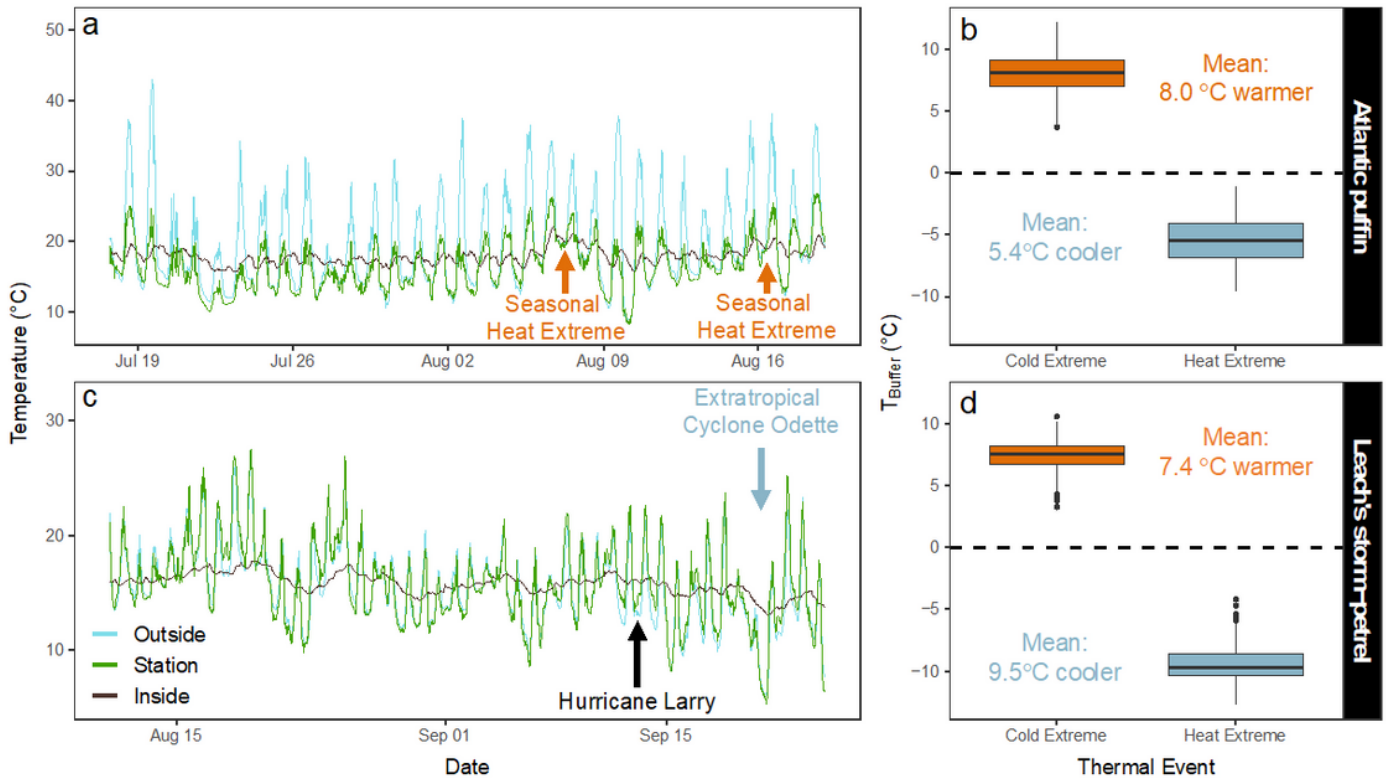
Figure 5

Burrows buffer temperatures from extreme external hot and cold events in (a & b) Atlantic puffin and (c & d) Leach's storm-petrel burrows. (a & c) Mean temperature (± SD) through the season within (n = 23 internal loggers, brown) and outside (n = 29 external loggers: blue, weather station: green) Atlantic puffin burrows over 35 days, and within (n = 30 internal loggers: brown) and outside (n = 30 external loggers: blue, weather station: green) Leach's storm-petrel burrows over 49 days. (b & d) Burrows buffer internal temperatures from extreme external hot and cold events. Black dotted line through zero indicates no buffering effect. Temperature buffer values were calculated as the temperatures inside the burrows minus temperatures outside the burrows at the weather station; therefore, negative values reflect cooler burrow temperatures.

Supplementary Files

This is a list of supplementary files associated with this preprint. Click to download.

- SupplementaryMaterial1.pdf