



## Research Article

# Influence of habitat on fine-scale space use by brown lemmings (*Lemmus trimucronatus*) in the High Arctic

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### Abstract

Space use by small mammals should mirror their immediate needs for food and predator shelters but can also be influenced by seasonal changes in biotic and abiotic factors. Lemmings are keystone species of the tundra food web, but information on their spatial distribution in relation to habitat heterogeneity is still scant, especially at a fine scale. In this study, we used spatially explicit capture–recapture methods to determine how topography, hydrology, vegetation, and soil characteristics influence the fine-scale spatial variations in summer density of brown lemmings (*Lemmus trimucronatus*). Lemmings were monitored throughout the summer in wet and mesic tundra habitats and in a predator exclusion grid, which was also located in mesic tundra. We found that in wet tundra, lemming densities were higher at sites with a rugged topography dominated by hummocks, but only during snow melt. In both mesic tundra sites, lemming densities were higher in sites with poor drainage and low aspect throughout the summer. We found no clear association between lemming densities and any tested vegetation or soil variables. Overall, hydrology and topography appear to play a dominant role in small-scale space use of brown lemmings with a secondary role for predator avoidance and food plant abundance.

**Key words:** Arctic, behavioral ecology, habitat use, hydrology, lemmings, microtopography, vegetation.

### Influence de l'habitat sur l'utilisation de l'espace à fine échelle par les lemmings bruns (*Lemmus trimucronatus*) dans le haut Arctique

### Résumé

L'utilisation de l'espace par les petits mammifères devrait refléter leurs besoins immédiats de nourriture et de protection des prédateurs, mais elle peut aussi être influencée par des changements saisonniers dans les facteurs biotiques et abiotiques. Les lemmings sont des espèces clés dans le réseau alimentaire de la toundra, pourtant les connaissances sur leur répartition spatiale en relation avec l'hétérogénéité des habitats sont limitées, surtout à fine échelle spatiale. Dans cette étude, nous avons utilisé des méthodes de captures-recaptures spatialement explicites pour déterminer comment la topographie, l'hydrologie, la végétation et les caractéristiques des sols influencent les variations à fine échelle spatiale des densités estivales de lemmings bruns (*Lemmus trimucronatus*). Les lemmings ont été suivis tout au long de l'été dans des habitats de toundra humide et mésique et dans une grille d'exclusion des prédateurs qui se situait aussi en toundra mésique. Nous avons constaté que dans la toundra humide, les densités de lemmings étaient plus élevées dans les sites avec une topographie accidentée dominée par des hummocks, mais seulement pendant la fonte de la neige en juin. Dans les deux sites en toundra mésique, les densités de lemmings étaient plus élevées là où la pente était faible et le drainage mauvais pendant tout l'été. Nous n'avons trouvé aucun effet des variables végétales ou des sols que nous avons testées. Dans l'ensemble, l'hydrologie et la topographie semblent jouer un rôle prépondérant dans l'utilisation de l'espace par le lemming brun à fine échelle, alors que l'évitement des prédateurs et l'abondance des plantes fourragères auraient un rôle secondaire.

**Mots clés:** Arctique, écologie comportementale, hydrologie, lemmings, microtopographie, utilisation de l'habitat, végétation.

Habitat use reflects where animals are found and how they interact with their environment (Elton 1966; Fretwell 1969). It is generally measured by how often and how many individuals use a specific set of biotic and abiotic characteristics, information that has a high value for conservation efforts. In addition to abiotic factors such as topography and extreme events like wildfires, habitat

use can also be driven by species interactions such as the need to find food and mates and avoid predators (Lashley et al. 2015; Nifong and Silliman 2017; Chance et al. 2020; Pirotta et al. 2020). Such behaviors may ultimately affect whole food webs with cascading trophic effects at different spatial scales (Breed et al. 2017; Roder et al. 2020).

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Habitat use operates at different temporal and spatial scales with implications for species distribution and interactions (Johnson 1980). Fine-scale habitat use is particularly useful to reveal how individuals are affected by microtopography and hydrology, exploit patches of concentrated food, interact with conspecifics and competitors, or respond to predation through the use of refuges (Červinka et al. 2013; Garnick et al. 2014; Brzeziński et al. 2018). For example, yellow-bellied marmots (*Marmota flaviventris*) mostly dig burrows in gentle slopes (Svendsen 1976), whereas mice and voles move out of floodplains during inundations in Colorado (Andersen et al. 2000). Saetnan et al. (2009) showed that field voles (*Microtus agrestis*) mainly use habitats rich in herbaceous plants and willows, which are important food items. Sometimes, interspecific competition influences habitat use as in brown and collared lemmings (*Lemmus trimucronatus* and *Dicrostonyx groenlandicus*) where the presence of the former species negatively affects the density of the latter in its preferred habitat (Morris et al. 2000).

The way that predators and prey use habitats is often influenced by one another with the latter searching for refuges in response to being hunted (Benoit-Bird et al. 2013; Everatt et al. 2015; Winnie and Creel 2017; Dellinger et al. 2019). As a result, prey can change their foraging behavior, for instance, by choosing less profitable feeding sites to reduce predation risk and increase their fitness (Lima and Valone 1986). For example, East European voles (*M. levis*) use covered feeding patches more than those that are uncovered (i.e., the most productive) when avian predators are present (Koivisto et al. 2018). However, in contrast with structurally complex habitats such as forests, drivers of habitat use in simpler landscapes such as the tundra may be more subtle and difficult to determine.

In the High Arctic tundra, brown lemmings are a key prey for many predators (Bêty et al. 2002; Gilg et al. 2003; Krebs 2011; Therrien et al. 2014) and use different habitats depending on the season (Batzli et al. 1983; Rodgers and Lewis 1986). During summer in Alaska, lemmings predominantly use lowlands with high food availability and a heterogeneous topography (Batzli et al. 1983), presumably to minimize detection by predators. Predation may be an especially important factor as lemmings suffer high mortality rates caused by both mammalian and avian predators during the summer (Gilg et al. 2003; Therrien et al. 2014; Fauteux et al. 2015). In winter, lemmings move to depressions or near steep slopes with deep snow accumulation where they dig tunnels in the snow to move around (Duchesne et al. 2011; Poirier et al. 2019). Brown lemmings eat mosses and grasses all year long and willows are also an important food item in some areas, especially during winter (Rodgers and Lewis 1985; Soininen et al. 2015; Fauteux et al. 2017). Although some studies have documented the general habitats in which lemmings are found, we still know very little about how brown lemmings use space in relation to habitat features at a fine spatial scale. Habitat use by lemmings is likely to change seasonally in response to factors including heterogeneity in microtopography, presence of water bodies, snow melt, food availability, and predator activity.

The goal of this study was to identify biotic and abiotic variables that are the most important in determining summer space use of brown lemmings at a fine spatial scale. This was achieved using lemming densities estimated from a long-term live-trapping data set (12 years) conducted in areas with contrasting microtopography, plant, and predator conditions. Our scale of analysis corresponds roughly to the third order identified by Johnson (1980), which is the home range scale. Based on past studies emphasizing the role of predators in controlling lemming populations in the High Arctic during the summer (Gilg et al. 2003; Therrien et al. 2014; Fauteux et al. 2016), we hypothesized that lemmings should use space to reduce their vulnerability to predation. We first predicted that brown lemmings

should predominantly use sites with a rugged microtopography (i.e., with hummocks and/or frost cracks) that could hamper detection by predators. Because burrows are good shelters in a landscape dominated by permafrost, we also predicted that they should use more sites with soil suitable for digging, i.e., those with soft soil, organic matter, and a deep active layer. We also hypothesized that lemmings should use space to maximize food acquisition. Thus, we predicted that brown lemmings would predominantly use sites with a high abundance of willows, grasses, forbs, and palatable mosses (e.g., *Aulacomnium* spp. and *Polytrichum* spp.), all important food plants (Soininen et al. 2015). Finally, at snowmelt, we hypothesized that lemmings should use habitat to avoid flooding and predicted that they would use well-drained areas and stay away from standing water.

## Materials and methods.

### Study area.

Fieldwork was conducted in the Qarlikturvik Valley of Bylot Island, Sirmilik National Park, Nunavut (73°N, 80°W). The valley is located at the southwest end of the island and is bordered by mountains and glaciers to the north and east, the sea to the west, and rolling hills to the south. The lowlands of the valley are composed of 2 main habitats, wetlands in low-lying areas and mesic tundra in higher ground and along slopes. Wetlands are characterized by either low-center polygons—which are depressions covered by vegetation, often filled with water at snow melt and surrounded by drier vegetation along their rims—or high-center polygons where water is present in troughs surrounding the drier, elevated center of polygons (Billings and Peterson 1980). The mesic tundra is largely covered by vegetation and is often characterized by hummocks with a rugged microtopography. Drainage is variable but generally good along slopes, and standing water is rare. The wetland vegetation is composed of mosses (e.g., *Aulacomnium* spp., *Polytrichum* spp.) and graminoids (e.g., *Eriophorum* spp., *Dupontia fisherii*), whereas the mesic tundra vegetation is dominated by herbaceous plants (e.g., *Saxifraga* spp.), shrubs (e.g., *Salix* spp.), and graminoids (e.g., *Arctagrostis latifolia*; Gauthier et al. 1996; Bilodeau et al. 2014). The average temperature is 4.5°C during the summer and −32.8°C during winter and snow covers the ground from October to early June (CEN 2022).

The Brown Lemming and Collared Lemming are the only 2 species of rodents present on the island. We focused on brown lemmings, which exhibit large-amplitude population cycles with peaks every 3 to 4 years (Fauteux et al. 2015), and ignored collared lemmings due to their low abundance at our study site. Lemmings have many predators, especially during the summer, when resident mammals including the Arctic fox (*Vulpes lagopus*) and Ermine (*Mustela richardsonii*) and migratory birds including the Snowy Owl (*Bubo scandiacus*), Rough-legged Hawk (*Buteo lagopus*), and Long-tailed Jaeger (*Stercorarius longicaudus*) are all present.

### Trapping protocol.

Lemming populations were monitored annually from 2008 to 2019 on 2 live-trapping grids, one located in the wetland habitat and one in mesic tundra. Each grid covered an area of approximately 11 ha and was laid out in a 12 × 12 Cartesian plane for a total of 144 trapping stations spaced out every 30 m. A third trapping grid surrounded by a fence and covered by a net to exclude predators was added in 2013 as part of an experiment to reduce the predation rate on lemmings (hereafter predator enclosure; see details in Fauteux et al. 2016). This grid covered approximately 9 ha and was composed of 8 × 12 trapping stations arranged in a similar fashion as the other grids.

Each trapping station had 1 Longworth trap baited with a mixture of peanut butter, flour, and oat along with a piece of apple, as well as synthetic fabric batting to keep trapped lemmings warm and dry. Traps were set in sites with signs of lemming activity such as feces or burrows <15 m from each trapping station whenever possible. The exact position of traps, and not stations, were used in the analyses. There were 3 primary trapping periods per grid each summer (mid-June at the end of snowmelt, mid-July, and mid-August) and traps were active for 72 h with visits every 12 h (for a total of 6 secondary trapping periods per primary period). Each time a lemming was caught, the station and the lemming identification number (if it was a recapture) were noted. Captured animals were marked with a Passive Integrated Transponder (PIT, AVID; Avid Identification Systems, Inc., Norco, California) or an ear tag (Monel 1005-1, National Band & Tag Co., Newport, Kentucky). All manipulations were authorized by the Université Laval animal care committee and Parks Canada and followed American Society of Mammalogists guidelines (Sikes et al. 2016). All data collected during trapping have been published in the open-access data repository NordicanaD (Gauthier 2020).

### Habitat sampling.

Habitat variables were sampled at all 384 trapping stations of the 3 grids between 23 and 31 July 2019 and we assumed that habitat characteristics were constant over the years.

We assessed the abundance of hummocks (Hum) in a circular plot with a radius of 5 m centered on each station on a scale between 0 (absent) and 3. A station with a class 1 had only a few scattered hummocks, a class 2 had several patches of uniformly distributed hummocks with flat areas in between them, and a class 3 had a uniform distribution of hummocks with little or no flat areas between them. The height of the tallest hummock in a plot was measured (nearest cm) using a measuring tape (Hum\_height). The slope (Aspect) of the plot was measured using a clinometer by a single observer for consistency. The total length of frost cracks in the soil (Linear\_crack\_length) large enough for lemmings to travel in ( $\geq 4$  cm wide) was also measured (nearest cm) within the same area.

Soil hardness (Soil\_hard) was measured with an electronic penetrometer (Chatillon DFX II, 250 N). We measured the force (in N, accuracy:  $\pm 0.75$  N) it took to push an extension rod with a pointed end 10 cm into the soil. Four measurements were taken in the 4 corners of a 1 m  $\times$  1 m quadrat facing north and centered on the station. We averaged those 4 measures to a single value per station. We measured the depth (nearest cm) of the active layer (Depth\_Act) at the same 4 locations by pushing a metal rod into the soil until the permafrost was reached and then used the average value.

Within the same 1 m  $\times$  1 m quadrat, we visually estimated the cover (proportion to the nearest 0.01; total exceeded 1.00 but sometimes was lower due to bare ground or unidentifiable organic matter) of the following plant categories: *Aulacomnium* spp. (Aulacom), *Polytrichum* spp. (Polytrich), *Sphagnum* spp. and lichen (Sphagnum\_Lichen), other mosses (Other\_mosses), willows (Willows) that consist of prostrate species with horizontal stems (*Salix arctic*, *S. herbacea*, and *S. reticulata*), *Cassiope tetragona* (Cassiope), and herbaceous plants (Herb). Plant categories were selected based on preference or avoidance to them by lemmings (Soininen et al. 2015). Within the 5-m circular plot around the station, we visually estimated the cover (proportion to the nearest 0.01) of organic matter (i.e., green and dead vegetation, including mosses, lichens, and vascular plants; Org\_Mat).

Drainage was visually estimated within a radius of 5 m around each station on a scale from 1 (poorly drained with little runoff, presence of standing water, very wet) to 5 (well drained, extensive

runoff, absence of standing water). Because drainage categories 1, 2, and 3 were rare in the mesic grid (drainage was mostly in categories 4 and 5), scales 1 and 2 were merged and 3 and 4 were also merged for data analysis in this habitat. Finally, we estimated the proportion (to the nearest 0.01) of the area within 10 m of each station covered by permanent water bodies (Water).

### Autocorrelation analyses.

We initially checked for presence of spatial autocorrelation in the distribution of Brown Lemming captures within each trapping grid with a Mantel test. We built a dissemblance matrix (number of captures at each trapping station) and compared it with a distance matrix (distance between traps separated in classes of 30 m; Borcard et al. 2011). We first ran an analysis with those matrices for each primary trapping period, trapping grid, and years separately—except in 2013 and 2018 when we captured  $\leq 3$  lemmings during any primary trapping period. We then repeated these analyses by combining data in various ways. We first combined data of the 3 trapping periods within the dissemblance matrices—keeping years and grids separated, and then combined data across all years—keeping trapping periods and grids separated. These analyses should determine whether “hotspots” of lemmings were present in the trapping grids and if those varied between years or summer periods. When the global Mantel test was significant ( $P < 0.05$ ) for an analysis, we proceeded with an inspection of the correlogram to determine at which distance classes (30 to 330 m) correlations ( $r_m$ ) were significant ( $P < 0.05$ ). A positive  $r_m$  for a particular distance class indicated that traps spaced by this distance were similar in terms of lemming captures, whereas the opposite was true for a negative  $r_m$  (Sokal 1986). Mantel tests and correlograms were also conducted to check for the presence of spatial autocorrelation in habitat variables. The dissemblance matrix was built with habitat characteristics (e.g., cover proportion or abundance index), and compared with a distance matrix (distance between traps separated in classes of 30 m).

### Habitat use analyses.

We used spatially explicit capture–recapture (SECR) models to estimate lemming densities and examine the relationships between density and habitat variables at each trapping station with the “secr” R package (Efford et al. 2009; Efford 2020). An important advantage of SECR models is that they account for the spatial component of captures by considering a variable detection probability based on both trap location and the estimated center of activity of each animal. However, such models require relatively large sample size, so we limited our analyses to years of moderate to high lemming density only (15 captures per primary period minimum or a minimum density of approximately  $>1$  lemmings/ha). We used the full likelihood parameterization to model density as a function of heterogeneous habitat variables over the state space and a half-normal detection function to model detection probabilities (Krebs et al. 2011).

We developed a set of candidate models based on specific hypotheses. Because the SECR models were highly computer-intensive, we did not test every combination of all variables, but instead built models so that alternative hypotheses related to hydrology, topography, and vegetation were tested (Anderson 2008). Before doing so, we examined for the presence of collinearity between habitat variables and avoided including variables that were highly correlated ( $r > 0.7$ ) in the same models. The candidate set of models used to examine relationships between animal density (D) and habitat variables (Supplementary Data SD1). Some models were specific to certain trapping grids or periods due to variables being too spatially uniform, such as the rarity of standing

water (variable “Water”) in the mesic trapping grids or frost cracks being only at 1 or 2 stations out of 144. Those did not provide any contrasts for tests. Because of these specificities, a different subset of models (Supplementary Data SD1) was used for analysis of the data of each trapping grid and primary period combination. We considered each year as a “session” in the models allowing us to control for annual variations in  $D$ . For all models, session-specific detection probabilities ( $g_0$ ) and animal movement ( $\sigma$ ) were estimated. Through preliminary analyses, we confirmed that null models ( $D \sim 1$ ,  $g_0 \sim 1$ ,  $\sigma \sim 1$ ) generally performed badly with high  $\Delta\text{AICc}$  compared to the models with “session” as a covariate and were thus not included in the model selection procedure. We used a theoretical buffer of 100 m around each trap to build the state space, where detection probabilities are estimated, because it represents 3 to 4 times the movement parameters ( $\sigma$ ; Krebs et al. 2011). The length of the buffer was recommended by Krebs et al. (2011) to limit the total state-space mask to a reasonable level and specify the area where spatial detection probability is estimated around all traps. Maximum likelihood was estimated with the Nelder–Mead optimization algorithm. We selected the most parsimonious models with the second-order Akaike Information Criterion (AICc) and reported the coefficients of variables found in the most parsimonious models ( $\Delta\text{AICc} < 4$ ). When more than 1 nested models were found among the top models, we averaged coefficients of variables across all nested models and presented their respective 95% confidence intervals.

## Results

### Lemming densities.

Brown Lemming densities showed large fluctuations over time, ranging from 0 to 8/ha at each primary trapping session (Supplementary Data SD2). In years of high lemming abundance, captures (including recaptures) can be as high as 250 in a single primary trapping period (e.g., wet trapping grid in July 2014) or can be totally absent in low abundance years (e.g., wet trapping grid in June and August 2012). Lemming densities were on average higher in the predator exclusion grid (2.41/ha) than in the other grids (1.36 to 1.42/ha). Years of low lemming abundance (density  $< 1$  lemming/ha) were 2009, 2012, 2013, 2017, and 2018, and were excluded from the SECR analyses of lemming habitat use.

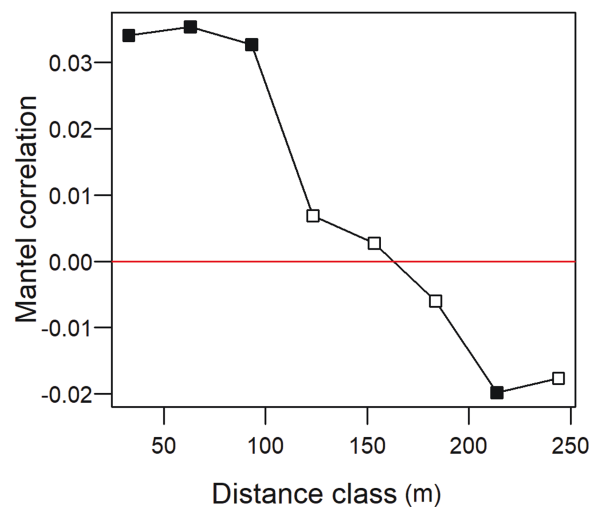
### Autocorrelation analyses.

Although significant autocorrelations in lemming captures between trapping stations were occasionally detected, such situations were uncommon. Out of 53 autocorrelation analyses made on each combination of primary trapping period, trapping grid, and year, only 7 were significant (13%). When pooling capture data of all primary periods within years, autocorrelation was significant on 4 occasions out of 19 (21%) and when pooling data across years for each primary period, only 1 out of 9 (11%) was significant (Table 1). When present, autocorrelations were weak and typically showed a positive association in lemming densities between stations located at  $< 100$  m (Fig. 1). Most autocorrelations were observed in the mesic trapping grid (7 out of 12 significant analyses) and most often in years 2014 and 2015 characterized with high lemming abundance (Fauteux and Gauthier 2022). Since spatial autocorrelation in lemming captures was observed for only a small fraction of the situations, we proceeded to habitat use analysis with the assumption that autocorrelation caused a negligible bias. Also, we visually found no evidence of spatial autocorrelation induced by an edge effect in the predator exclusion grid (Supplementary Data SD3).

Autocorrelation was found in 2 of the 7 habitat variables tested. Aspect was positively correlated between stations located  $\leq 150$  m in

**Table 1.** Proportion of autocorrelation analyses with significant results ( $P < 0.05$ ) for Brown Lemming densities in the wet, mesic, and predator exclusion trapping grids. Several analyses were run: (i) separate analysis for each trapping grid, year, and primary period (Individual session); (ii) analysis with primary periods pooled (Year); and (iii) analysis with years pooled (Primary period). Sample size is provided in parentheses.

| Type of analysis    | Period | Trapping grid |          |                    |
|---------------------|--------|---------------|----------|--------------------|
|                     |        | Wet           | Mesic    | Predator exclusion |
| Individual sessions | June   | 0 (7)         | 0.17 (6) | 0 (5)              |
|                     | July   | 0.14 (7)      | 0.29 (7) | 0 (4)              |
|                     | August | 0.29 (7)      | 0.17 (6) | 0 (4)              |
| Year                | —      | 0.14 (7)      | 0.29 (7) | 0.20 (5)           |
| Primary period      | —      | 0 (3)         | 0 (3)    | 0.33 (3)           |



**Fig. 1.** Correlogram showing Mantel correlation coefficients ( $r_m$ ) of the number of brown lemmings captured for each distance class (30-m increment) in the mesic trapping grid during summer 2014 ( $z = 6,453,662$ ;  $P = 0.049$ ) at Bylot Island. Full squares indicate significant ( $P < 0.05$ ) spatial autocorrelation for the specific distance class.

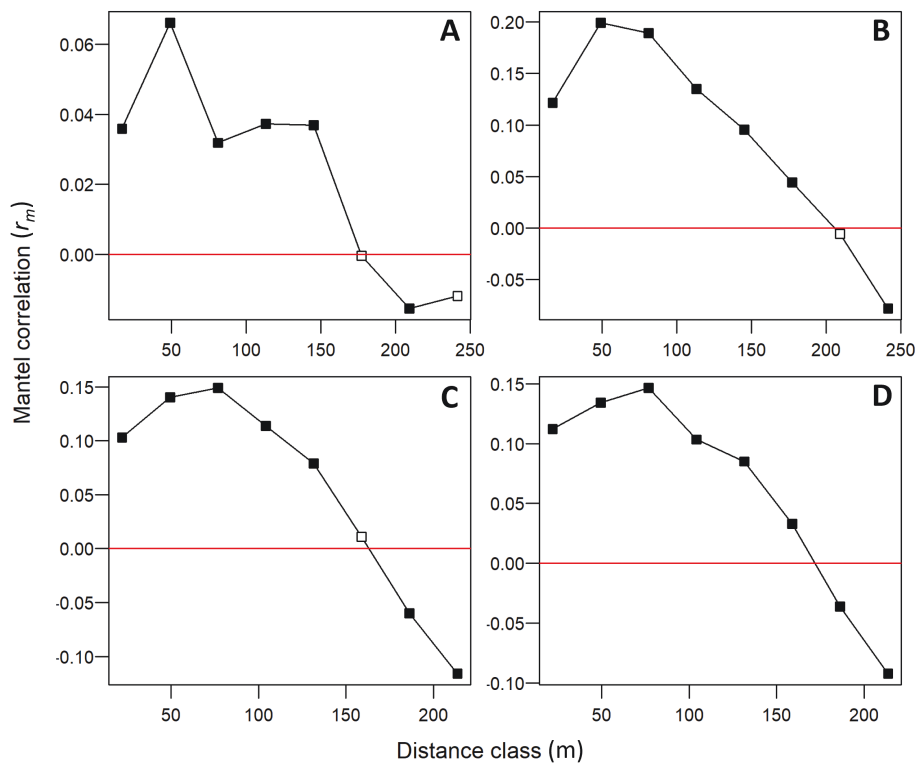
the mesic and predator exclusion grids, and similarly for Drainage between stations located at  $\leq 180$  m in the mesic grid and  $\leq 140$  m in the predator exclusion grid (Fig. 2). The correlation was negative for both habitat variables between stations located  $> 210$  m in the mesic grid and  $\geq 180$  m in the predator exclusion grid (Fig. 2).

### Habitat use.

In the wet trapping grid, spatial variations in Brown Lemming abundance in June was influenced by topography. More precisely, their densities were positively associated with a high abundance of hummocks (Table 2; Fig. 3; Supplementary Data SD4). In July, densities were positively associated with a single variable, the cover occupied by *Aulacomnium* spp. mosses (Table 2; Fig. 3). However, the model “session” with no habitat variable also had high statistical support ( $\Delta\text{AICc} = 0.83$ ), which was a warning for poor support, or spurious effect, despite the 95% confidence interval of *Aulacomnium* spp. that did not include 0 (Table 2). In contrast, densities in August were not related to any habitat feature.

In both the mesic and predator exclusion grids, variables related to topography best explained variations in Brown Lemming abundance over the summer (Supplementary Data SD5 and SD6). Lemming densities were negatively related to the variables Drainage





**Fig. 2.** Correlogram showing Mantel correlation coefficients ( $r_m$ ; 30-m increment) for Aspect in the mesic trapping grid (A) and the predator enclosure grid (B) and for Drainage in the mesic trapping grid (C) and in the predator enclosure grid (D) by Atlot Island. Solid squares indicate significant ( $P < 0.05$ ) spatial autocorrelation for the specific distance class.

and Aspect at several primary periods (Table 2; Fig. 3), indicating that lemmings occurred in high numbers in relatively flat sites with poor drainage in this type of habitat. We found no links between lemming densities and soil hardness, depth of the active layer, or organic matter cover in the 3 trapping grids.

## Discussion

The High Arctic tundra is a structurally simple habitat due to the absence of tall shrubs and erect trees, but for small burrowing animals like lemmings, this landscape is far from being homogeneous even within their restricted home range. We found that variables related to hydrology and topography were the main drivers of fine-scale space use by brown lemmings during the summer and that ruggedness (i.e., presence of hummocks) was also important, but to a lesser degree. Hummocks in wet tundra at the time of snowmelt were heavily used, potentially as refuges against predation and/or to avoid risks of flooding. Interestingly, we generally found no support for local habitat use based on any vegetation despite some food preferences observed in previous studies (Soininen et al. 2015). The autocorrelation analysis did not reveal any strong and consistent spatial structure, suggesting weak spatial aggregations within the trapping grids.

The wet habitat that we sampled is associated with low-center polygons (mostly <30 m in diameter) characterized by shallow depressions permanently filled with water and surrounded by raised mesic edges and narrow wet troughs. In between these depressions are found small, slightly more elevated, temporary pools that drain soon after snow melt and are relatively flat. The rest of that habitat is composed of a rugged microtopography along polygon rims (hummocks, frost cracks, and troughs; Batzli et al. 1983), providing ideal runways for lemmings to move around without being seen, and thus can reduce their vulnerability to predators. This structure

could explain why hummocks are positively related to lemming densities in the wet habitat. Duchesne et al. (2011) reported that lemmings also prefer areas dominated by hummocks during winter, which may explain why the strongest association between lemming density and hummocks was found in June, at snow melt. The rugged microtopography provided by hummocks may help lemmings avoid running water caused by fast snow melt and thus be beneficial to their survival. Given the potential benefits of microtopography to minimize detection by predators during their movements, it is surprising that lemming density was not related to hummock abundance in the mesic habitat. A possible explanation is that hummocks were such a dominant feature in this habitat that they did not represent a limiting microhabitat in this landscape (Mysterud and Ims 1998).

The high abundance of brown lemmings in poorly drained areas of the mesic habitat is in accordance with their known preference for wet habitats, where they can find many of their preferred food plants (Batzli et al. 1983). The mesic tundra offers a diversity of landscapes where flat areas tend to be wetter than those along slopes, which are typically drier and dominated by different plants due to high runoff (Bliss and Gold 1994; Virtanen et al. 1997; Young et al. 1997). It is therefore not surprising that brown lemmings were not present in areas with a high aspect. Steep slopes are also prone to the formation of snowbeds under certain wind conditions in winter (Jones et al. 2001), which explains why they are heavily used by lemmings in winter (Duchesne et al. 2011; Schmidt et al. 2021). However, snowbeds persist for a long time after snowmelt, which can lead to the formation of a refrozen basal layer (Colbeck 1982)—which may prevent lemmings from using the subnivean space, delay plant growth, and cause the release of excessive amounts of water during a prolonged period—posing a risk for tunnel flooding (Isard 1986; Björk and Molau 2007). Not surprisingly, Drainage and Aspect showed positive spatial autocorrelation, which could explain why

**Table 2.** Model-averaged parameter values of habitat variables retained in best-ranked models ( $\Delta AIC_c < 4$ ; [Supplementary Data SD4](#)) explaining variations in Brown Lemming densities for each trapping grid and trapping period. The table shows the coefficient ( $\beta$ ) and lower and upper 95% confidence interval (CI) for each variable estimated by model averaging. Variables in bold are those with a 95% confidence interval that excludes 0.

| Trapping grid   | Period                   | Variable                     | B               | Low 95% CI   | High 95% CI  |
|-----------------|--------------------------|------------------------------|-----------------|--------------|--------------|
| Wet             | June                     | <b>Humm<sup>a</sup></b>      | <b>0.24</b>     | <b>0.00</b>  | <b>0.49</b>  |
|                 |                          | Aulacomnium <sup>b</sup>     | 0.38            | -0.81        | 1.56         |
|                 | July                     | <b>Aulacomnium</b>           | <b>1.07</b>     | <b>0.02</b>  | <b>2.13</b>  |
|                 |                          | Water <sup>c</sup>           | 0.51            | -0.49        | 1.51         |
|                 |                          | Willows <sup>d</sup>         | 0.62            | -2.02        | 3.26         |
|                 |                          | Herbaceous <sup>e</sup>      | 1.57            | -2.78        | 5.92         |
|                 |                          | Polytrichum <sup>f</sup>     | 0.18            | -1.39        | 1.75         |
|                 |                          | Sphagnum_Lichen <sup>g</sup> | -1.64           | -4.26        | 0.97         |
|                 |                          | Other_Mosses <sup>h</sup>    | 0.23            | -0.48        | 0.94         |
| August          | Depth_Act <sup>i</sup>   | -0.57                        | -3.34           | 2.20         |              |
| Mesic           | June                     | <b>Aspect</b>                | <b>-0.13</b>    | <b>-0.18</b> | <b>-0.08</b> |
|                 |                          | July                         | <b>Drainage</b> | <b>-0.32</b> | <b>-0.50</b> |
|                 | Water                    |                              | -0.15           | -1.49        | 1.20         |
|                 | Soil_hard <sup>j</sup>   |                              | -1.29           | -2.87        | 0.28         |
|                 | Humm_height <sup>k</sup> |                              | -0.21           | -2.40        | 1.99         |
|                 | Polytrichum              |                              | -0.24           | -1.97        | 1.48         |
|                 | Herbaceous               |                              | -0.19           | -2.50        | 2.13         |
|                 | August                   |                              | <b>Aspect</b>   | <b>-0.10</b> | <b>-0.14</b> |
|                 | Predator enclosure       | June                         | <b>Aspect</b>   | <b>-0.14</b> | <b>-0.27</b> |
| <b>Drainage</b> |                          |                              | <b>-0.41</b>    | <b>-0.82</b> | <b>-0.01</b> |
| Depth_Act       |                          |                              | -1.06           | -4.64        | 2.52         |
| Polytrichum     |                          |                              | 1.89            | -2.10        | 5.88         |
| Other_Mosses    |                          |                              | -1.72           | -4.39        | 0.96         |
| Humm_height     |                          |                              | 3.43            | -1.23        | 8.09         |
| July            |                          | <b>Aspect</b>                | <b>-0.12</b>    | <b>-0.20</b> | <b>-0.04</b> |
|                 |                          | Herbaceous                   | 1.19            | -9.00        | 11.39        |
|                 |                          | Depth_Act                    | -0.69           | -4.43        | 3.05         |
|                 |                          | Drainage                     | -0.14           | -0.39        | 0.12         |
|                 |                          | August                       | <b>Aspect</b>   | <b>-0.07</b> | <b>-0.14</b> |
|                 |                          | Humm_height                  | 1.55            | -1.08        | 4.17         |

<sup>a</sup>Hummock abundance.

<sup>b</sup>Aulacomnium spp. cover.

<sup>c</sup>Water cover.

<sup>d</sup>Willow cover.

<sup>e</sup>Herbaceous cover.

<sup>f</sup>Polytrichum spp. cover.

<sup>g</sup>Sphagnum and Lichen cover.

<sup>h</sup>Cover of mosses other than Polytrichum spp. and Aulacomnium spp.

<sup>i</sup>Average depth of the active layer.

<sup>j</sup>Average soil hardness.

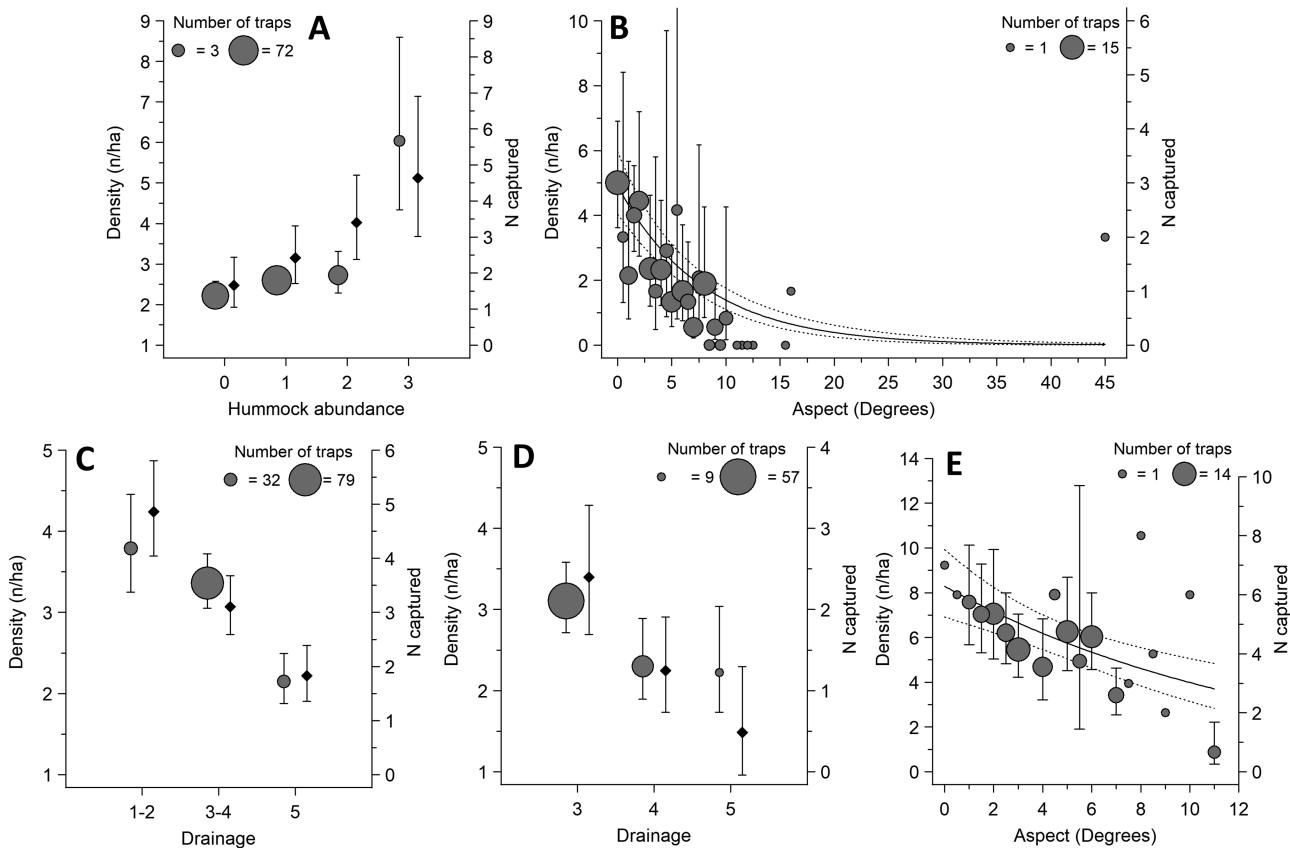
<sup>k</sup>Height of the tallest hummock.

most spatial autocorrelations in lemming captures were located in the mesic tundra—a habitat characterized by rolling hills unlike wet lowlands.

Contrary to what was reported in Alaska (Batzli et al. 1983), food plant availability was not a dominant factor affecting habitat use of lemmings on Bylot Island. There are 3 possible reasons for this difference. First, the study in Alaska was conducted at a larger spatial scale (i.e., between trapping grids, from ~36 m to ~1 km) compared to our study (i.e., within trapping grids, ~30 m) and differences in plant availability may be greater at larger scales. Second, lemmings reach much higher densities in Alaska than on Bylot Island, and

thus food competition or congener avoidance may have a greater influence on habitat use at the former site. Third, considering that lemming densities on Bylot Island never exceeded 10/ha, as compared to those observed in Alaska that can reach >200/ha (Pitelka and Batzli 2007), a threshold—present due to nonlinear responses to plant availability that induce changes in lemming density—may have not been reached.

Contrary to our expectations, soil hardness, cover by organic matter, and active layer depth had no effect on lemming densities. This pattern could be partly explained by the limited variability that we observed in these values among our sampling stations. It is



**Fig. 3.** Relationships between Brown Lemming densities and various habitat variables: (A) Hummock abundance in the wet grid in June; (B) Aspect in the mesic grid in June; (C) Drainage in the mesic grid in July; (D) Drainage in the predator enclosure in June; and (E) Aspect in the predator enclosure grid in August. Predicted densities are represented by black diamonds in A, C, and D or by black lines in the other graphs along with their 95% confidence intervals (vertical solid lines in A, C, and D or dashed lines in other graphs). Gray circles represent the mean number of individuals captured per trapping station, all years combined (right y axis), for each observed value of the independent variables with their 95% confidence intervals (vertical black lines). The size of the gray circles is proportional to the number of traps with the same habitat value. These values are presented for illustrative purpose only, because predictions are derived from the SECR models, which include 3 parameters (i.e., density, detection probability, and movement parameter), each with its respective error (see Materials and methods).

possible that when measurements were taken in July, the soil was soft enough and the active layer deep enough to allow lemmings to dig burrows almost everywhere. Moreover, the rugged microtopography created by frost actions such as hummocks, frost cracks, or soil collapse due to thermal erosion of ground ice through water infiltration (Fortier et al. 2007) may offer numerous opportunities for lemmings to move or hide underground without actively digging burrows in the soil.

For this study, we assumed that habitat characteristics that we measured did not change over the summer and among years. Thus, our results mainly reveal how the relative differences in those measures may affect local lemming habitat use and if those physical and botanical differences—that indeed change very slowly over the years—have an effect over multiple months and years. It is however possible that snow cover—which varies extensively among years—may have had an impact on local habitat use and certain habitat characteristics (e.g., active layer depth), but having annual data retroactively at such fine scale was not possible for the current study.

Overall, our results suggest a primary role of hydrology in affecting the fine-scale habitat use of brown lemmings. Hydrology is a pervasive force leading to the formation of heterogeneous landscapes in the tundra underlined by permafrost and can contribute to the creation of myriad microhabitats for lemmings including hummocks, frost cracks, or gullies. In addition, running water at

snowmelt may pose short-term risks to lemmings due to flooding of low-lying areas or burrows. Permafrost thawing—which can change the underground hydrology (Walvoord and Kurylyk 2016) and surface topography (Godin and Fortier 2012), changing snow accumulation (Derksen and Brown 2012; Bintanja and Selten 2014), and more intense and sudden spring runoff (Adam et al. 2009) are all potential challenges that lemmings may face with climate warming. Those will add to other threats currently faced by some lemming populations including increasing rain-on-snow in fall and winter, and changing snow conditions (Ims et al. 2008; Kausrud et al. 2008; Berteaux et al. 2017; Domine et al. 2018). Thus, the rapid warming Arctic climate may have both positive effects on lemmings by creating more heterogeneous microhabitats to hide in, but also negative with an increased risk of flooding or of exposure to predators due to increased movements outside burrows at snow melt.

### Supplementary data

Supplementary data are available at *Journal of Mammalogy* online.

**Supplementary Data SD1.**—Candidate models for testing habitat effects on lemming density.

**Supplementary Data SD2.**—Sample size per trapping grid, month, and year.

**Supplementary Data SD3.**—Heatmap of total lemming captures in the predator enclosure grid.

**Supplementary Data SD4.**—Ranking of the top models testing habitat variables in the wet grid.

**Supplementary Data SD5.**—Ranking of the top models testing habitat variables in the mesic grid.

**Supplementary Data SD6.**—Ranking of the top models testing habitat variables in the predator enclosure grid.

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## Author contributions

MV, DF, and GG—equally contributed to the conceptualization and developed the methods; MV and DF conducted analyses and created visuals (graphs); MV wrote the original draft; DF and GG—supervision and revision and edition of the manuscript; GG—funding acquisition.

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## Conflict of interest

None declared.

## Data availability

All data on lemming captures may be found on the public repository NordicanaD: [Gauthier \(2020\)](#).

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