esa

ECOSPHERE

Snow hardness impacts intranivean locomotion of arctic small mammals

Mathilde Poirier [iD],[1,2,]† Dominique Fauteux [iD],[1,3] Gilles Gauthier [iD],[1,2] Florent Domine [iD],[1,4,5] and Jean-François Lamarre [iD][6]

[1]Centre d'Études Nordiques, Université Laval, Quebec, Québec QC G1V 0A6, Canada
[2]Department of Biology, Université Laval, Quebec, Québec QC G1V 0A6, Canada
[3]Centre for Arctic Knowledge and Exploration, Canadian Museum of Nature, Gatineau, Québec QC J9J 3N7, Canada
[4]Takuvik Joint International Laboratory, Université Laval (Canada) and CNRS-INSU (France), Quebec, Québec QC G1V 0A6, Canada
[5]Department of Chemistry, Université Laval, Quebec, Québec QC G1V 0A6, Canada
[6]Canadian High Arctic Research Station, Polar Knowledge Canada, Cambridge Bay, Nunavut NU X0B 0C0, Canada

Abstract. Fossorial locomotion is often considered as the most energetically costly of all terrestrial locomotion. Small arctic rodents, such as lemmings, dig tunnels not only in the soil but also through the snowpack, which is present for over 8 months of the year. Lemmings typically dig in the softest snow layer called the depth hoar but with climate change, melt-freeze and rain-on-snow (ROS) events are expected to increase in the Arctic, leading to a higher frequency of hardened snowpacks. We assessed the impacts of snow hardness on the locomotion of two lemming species showing different morphological adaptations for digging. We hypothesized that an increase in snow hardness would (1) decrease lemming performance and (2) increase their effort while digging, but those responses would differ between lemming species. We exposed four brown lemmings (*Lemmus trimucronatus*) and three collared lemmings (*Dicrostonyx groenlandicus*) to snow of different hardness (soft, hard, and ROS) during 30-min trials (*n* = 63 trials) in a cold room and filmed their behavior. We found that the digging speed and tunnel length of both species decreased with snow hardness and density, underlining the critical role of snow properties in affecting lemming digging performance. During the ROS trials, time spent digging by lemmings increased considerably and they also started using their incisors to help break the hard snow, validating our second hypothesis. Overall, digging performance was higher in collared lemmings, the species showing more morphological adaptations to digging, than in brown lemmings. We conclude that the digging performance of lemming is highly dependent on snowpack hardness and that the anticipated increase in ROS events may pose a critical energetic challenge for arctic rodent populations.

Key words: Arctic; burrowing behavior; digging; fossorial; hardness; lemming; locomotion; rain-on-snow; rodent; snow; subnivean; tunnel.

† E-mail: mathildepoirier05@gmail.com

Introduction

Life beneath the ground provides many benefits to fossorial animals (Nevo 1979, Reichman and Smith 1990) but also entails some costs. Fossorial locomotion is considered to be the most energetically expensive type of terrestrial locomotion (Seymour et al. 1998). When digging

burrows, rodents first have to shear the soil and then push the loosened soil to empty the tunnel, an energetically expensive sequence of movements (Lovegrove 1989). Species living in soft soil mainly use their forelimbs to shear the soil (i.e., scratch-digging), but others occupying harder types of soil have evolved the chisel-tooth digging behavior, which consists in shearing the soil with their incisors (Stein 2000). Depending on soil type and species, fossorial rodents either push the loosened soil with their front or back legs to compress it into the tunnel walls (e.g., Lin et al. 2017) or they evacuate it at the surface of the ground (e.g., Vleck 1979). The energetic cost of such actions for rodents is influenced by soil conditions as it increases with soil hardness and density (Vleck 1979, Ebensperger and Bozinovic 2000, Luna and Antinuchi 2006).

In northern regions, fossorial animals dig not only in the soil but also in the snowpack that forms every year, a very different medium to dig in. Lemmings are arctic rodents that live in the snowpack for over 8 months of the year and are known to reproduce under the snow if they have enough energy (Millar 2001, Duchesne et al. 2011). Lemmings are divided into two genera, *Dicrostonyx* and *Lemmus*, with the former being considered more adapted to life in the snow due to its white fur color and the growth of large bifid claws in early winter that likely facilitate scratch-digging (Hansen 1957, Zimova et al. 2018). The snowpack protects lemmings against predators hunting on the surface of the snow and against cold temperature (Reid et al. 2012, Bilodeau et al. 2013). However, lemmings need to dig a network of tunnels in the snow to access the ground vegetation upon which they feed, or to escape from some predators. Heterogeneous and changing snow conditions due to local topography or weather patterns could impact the intranivean locomotion of lemmings. However, the impact of snow physical properties on the digging behavior and locomotor efficiency of lemmings remains undocumented.

Typically, the top layer of the arctic snowpack is a hard wind slab composed of snow grains compacted by the wind, a consequence of the absence of erect vegetation (Domine et al. 2002). The wind also redistributes the snow, leading to a shallow snowpack on humps and a deeper and often softer snowpack in hollows (Pomeroy and

Brun 1990, Domine et al. 2002). Soft depth hoar usually forms in the basal layer of the snowpack. This snow type is comprised of loosely bonded, large and hollow faceted crystals that grow due to upward water vapor fluxes induced by a strong vertical temperature gradient within the snowpack (Sturm and Benson 1997). Events such as above-zero temperature or rain-on-snow (ROS) episodes, especially in fall, can also alter the snowpack. When wet snow refreezes, it forms hard melt-freeze layers due to the formation of large melt-freeze clusters (Pomeroy and Brun 1990). In extreme ROS events, large amounts of water infiltrating the snowpack can lead to the formation of thick ice layers (Pomeroy and Brun 1990). ROS events are becoming more frequent in the Arctic due to the exacerbated impact of global warming at high latitudes (Langlois et al. 2017, Peeters et al. 2019) and are thought to be a major threat for small mammals living inside the snowpack (Berteaux et al. 2017, Domine et al. 2018*b*).

Recent studies have shown that lemmings dig their tunnels in the top portion of the soft depth hoar, just beneath harder wind slabs, regardless of its height above the ground (Poirier et al. 2019). Such use of the snowpack is indicative of specialized locomotion related to snow physical conditions, but to our knowledge, no dedicated study has investigated the digging behavior of lemmings within the snowpack, except for some anecdotal observations (Sutton and Hamilton 1932). Increased snow hardness due to more frequent ROS events in the Arctic has been suggested as a potential mechanism behind the collapse of small mammal population cycles in some regions of Scandinavia (Aars and Ims 2002, Ims and Fuglei 2005, Kausrud et al. 2008). If moving through harder snowpack requires more effort and increases energy expenditure, this could compromise survival or winter reproduction of lemmings (Kausrud et al. 2008, Krebs 2011, Fauteux et al. 2015). Considering that lemmings are short-lived, multivoltine species, delayed or missed reproduction events can have a strong impact on their population dynamic.

In this study, we experimentally assessed the effect of snow physical properties on lemming locomotion and behavior within the snowpack. First, we hypothesized that lemming digging performance should decrease with an increase in

snow hardness. We predicted that, in hard snow, their digging speed would decrease, and the total length of their tunnels and vertical movement through the snowpack would be shorter compared with soft snow. Second, we hypothesized that if lemmings need to deploy more efforts to dig in hard snowpacks, they should adjust their behavior and digging technique accordingly. We predicted that exploration time and use of their teeth to break the snow should increase with its hardness. Third, due to morphological differences, we hypothesized that the performance of *Dicrostonyx* such as digging speed should be less impacted by hard snow than *Lemmus*.

METHODS

Study area and study species

We performed the study at the Canadian High Arctic Research Station (CHARS) in Ikaluktutiak (Cambridge Bay), Nunavut (69°07′ N, 105°30′ W), in November 2019. Mean temperature in November is −22.3°C (Government of Canada, https://climate.weather.gc.ca) and the average snow depth is 15 cm in flat terrain (GRIMP, https://grimp.ca/data/cambridge-bay-1). Two lemming species are found in this region, brown (*Lemmus trimucronatus*) and collared lemming (*Dicrostonyx groenlandicus*). Both species are widespread in the Canadian Arctic, but collared lemmings have the northernmost distribution (Jarrel and Fredga 1993).

We live-trapped lemmings in August 2019 on two 100-trap grids located ~4–5 km from CHARS and captured only four brown and three collared lemmings due to their low abundance that year (average population density was estimated at 0.46 ha^{-1}). Trapped lemmings were carried to CHARS and kept in individual cages with cotton bedding, hamster chow (Living World 60362), alfalfa, and water ad libitum in a cold room maintained at 4°C. Starting in mid-October, crushed ice was provided daily in the cages as we noticed that lemmings readily consumed it. From August to November, we simulated seasonal change in photoperiod by gradually decreasing the amount of light every week to follow the natural photoperiod (hours of illumination: from 16 h on August 16 to 3 h on November 19). The simulation was successful in inducing the normal seasonal morphological changes in both lemmings (bifid claws and white fur in collared lemmings; longer and thicker fur in brown lemmings). All were adults with a body mass between 57 and 88 g. Manipulations were approved by the Canadian Museum of Nature animal care committee (protocol 2018.02.001).

Experimental setup

To collect snow samples and perform the experiment, we built two narrow observation boxes (100 × 31 × 8 cm, length × height × width) with windows on each vertical side to see lemmings while digging in the snow (see Appendix S1: Fig. S1 for more details). The floor of each box could be removed to allow us to push it through the snowpack and collect an undisturbed snow sample down to the ground level.

For our experiments, we categorized the snowpack in three main types: soft, hard, and ROS. We obtained samples of soft and hard undisturbed snow at different locations <200 m from CHARS, near slopes conducive to snow depths of 20–30 cm. Considering that the arctic snowpack is vertically heterogeneous (i.e., harder at the top, softer at the bottom), the type of snow was determined according to its top layer. Soft snow was found in areas protected from the wind (e.g., depressions in the ground) and hard snow in areas exposed to the wind. Snow samples were not collected randomly but in similar sites, close to each other, to obtain relatively homogeneous samples for every snow type.

Before collecting a snow sample, we performed a visual stratigraphy at the site based on size and shape of snow grains (Pielmeier and Schneebeli 2003). In every case, visual observation led to the identification of three main snow layers: top (A), middle (B), and bottom (C), with each layer about ~10 cm thick. We considered the vertical arrangement of those three layers throughout the experiment (Fig. 1). We measured the hardness of each snow layer with a thin-blade penetrometer (resolution: 0.1 N; certified accuracy of ±0.6 N (Borstad and Mcclung 2011)). This instrument measures the force required to drive a blade 6 cm deep into the snow. Strictly speaking, hardness should be the force applied divided by the surface area of the contact between the instrument and the snow (1.4 cm^2). For simplicity, we just report here the
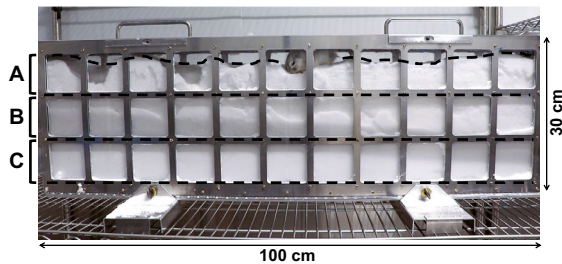
Fig. 1. Observation box used to collect snow samples and conduct digging trials. The sampled snowpack was divided into three different snow layers (A, B, and C) based on visual stratigraphy (see Appendix S1: Fig. S2) and on differences in hardness and density (see Fig. 2). Here, a trial with a collared lemming (located at the surface of the snow) is presented.

force indicated by the instrument (N, Newton) but it can easily be converted to pressure (Pa, Pascal) by dividing the value by 1.4×10^{-4} m^2. We also measured snow density by weighing a fixed volume of snow (100 cm^3) sampled with a box cutter (Conger and McClung 2009).

We simulated the rain-on-snow (ROS) type of snow in the laboratory by creating a 2- to 3-cm melt-freeze layer (i.e., clustered snow crystals) on top of snow samples categorized as hard in our observation box. First, we placed the sample in a room at ambient temperature (~18°C) and we heated the top layer with a heat gun for 5–10 s. Second, we added a thin snow layer of about 1 cm. Third, we heated again for 5–10 s. Fourth, we sprayed a small amount of warm water. We repeated steps 2–4 four times. We then moved the sample back in the −20°C freezer to allow the melted snow to refreeze. We avoided heating the snow too fast or spraying too much water to prevent accumulation of meltwater that would have led to the formation of a thick ice layer. We measured the hardness of this ROS layer, but its density could not be measured because the box cutter could not be introduced properly in the observation box.

Course of the experiment

The digging experiment was conducted in the last 2 weeks of November 2019. Each trial lasted 30 min and started by introducing a captive lemming on top of a snow sample in the observation box (see Video S1). Each lemming ($n = 7$) was tested on each snow type (soft, hard, and ROS) three times (different snow samples each time) for a total of 63 trials. Two trials were conducted simultaneously in two observation boxes, and a camera filmed the whole trials. The boxes were placed one above the other on a shelf to make sure lemmings could not see each other. The experiment took place in a walk-in freezer at −20°C to limit snow metamorphism that would have modified its physical properties. A new snow sample was usually collected prior to each digging trial and kept in a freezer at −20°C. During some trials, lemmings barely scratched through snow samples ($n_{soft} = 2$; $n_{hard} = 3$), which allowed us to reuse them for a second trial. For ROS samples, 17 of them were created from hard snow samples with minimal disturbance and four were reused ROS samples. A total of 37 snow samples were collected in the field.

Video analysis

During the video analysis, we continuously recorded the lemming behavior using the eight categories defined in Table 1 (behaviors lasting <2 s were ignored). When needed, we used the zoom to enlarge the image.

We also compiled other behaviors and performance indicators for each trial:

1. Time elapsed since the beginning of the trial before reaching snow layer B for the first time (i.e., layer A had been crossed).
2. Time elapsed since the beginning of the trial before reaching snow layer C for the first time (i.e., layers A and B had been crossed).
3. Time spent under the snow.
4. Time spent using their teeth while digging or scratching the snow.
5. Tunnel length: total length of the tunnel at the end of the trial, measured in cm.

We also measured the instantaneous digging speed of lemmings while in a specific snow layer (A, B, or C). The speed was calculated either from a unique sequence or as the mean of up to three sequences when possible. We chose sequences of continuous digging (minimum of 6 s to a maximum of 13 s) during which we measured the distance traveled and divided it by the

Table 1. Description of the eight main behaviors of lemmings identified during the trials (see Video S2).

Behavior	Description
Digging	Efficient: Continuous digging with front and hind legs in the snow for >2 s and progression in the snowpack
	Inefficient: Continuous digging with front and hind legs in the snow for >2 s and without progression in the snowpack
Scratching	Scratching at the surface of the snow with only the front legs for <2 s at the same spot but constantly changing spot
Exploring	Walking on top of the snow, looking around or standing on its hind legs
Traveling	Walking through a tunnel that has already been dug
Resting	Sleeping or being inactive
Grooming	Grooming or scratching itself
Unknown	Hiding in the snowpack (i.e., observer cannot see its behavior)

sequence duration to obtain speed (cm/s). We selected sequences where we could easily determine lemming starting and ending points. A scaled picture of the observation box, corrected for distortion with Adobe Lightroom, was used in ImageJ software (Schneider et al. 2012) to accurately measure the distance traveled.

Statistical analyses

We used linear models to assess differences in hardness or density of the top layer (A or AA for ROS) between snow types (soft, hard, and ROS) or differences between layers (A (and AA for ROS), B, C) within every snow type. A square root transformation was used for hardness data to enhance normality and homoscedasticity.

During trials, lemmings often moved across snow layers while digging, which prevented us from associating most behavioral aspects with a specific layer (except digging speed). We therefore examined the link between behavioral variables and the snow type (soft, hard, and ROS) of the top layer, which was the first layer encountered by lemmings during trials. Because the same animals were used repeatedly in several trials, we used animal ID as a random factor. All statistical analyses were performed using the R software (R Core Team 2020).

We used linear mixed-effects models to examine the relationship between digging speed and either density or hardness of the snow layer, lemming species, and their interactions. Generalized linear mixed-effects models (GLMM) with a gamma distribution and a log-link function were used to handle the variance structure when analyzing the influence of snow type, lemming species, and their interaction on the time spent in different behavior, tunnel length, and time spent under snow during each 30-min trial. The exceptions being the time spent on exploration behavior, which was modeled using linear mixed-effect model, and traveling behavior and time spent under snow, which were modeled using the function VarIdent implemented in the nlme package in R (Pinheiro and Bate 2021), with snow type and species as grouping variables. For time spent under the snow, we removed trials where lemmings did not go under the snow.

We used GLMM with a binomial distribution to determine whether snow type and lemming species affected the probability of reaching layer B or C (scored as 1 if they reached it, otherwise 0) during a trial. When a model did not converge well, potentially due to low sample size, we increased the number of nodes in the quadrature formula to two instead of one using the nAGQ argument (Bates et al. 2015). For trials where lemmings reached layer B or C, we also examined if snow type or lemming species affected the time taken to reach those layers using a GLMM with a gamma distribution. For all statistical analyses, we used the second-order Akaike's information criterion (AICc) to select the most parsimonious model. Means are presented with their respective standard error (SE) and slope parameters (β) with their 95% confidence interval throughout. When relevant, R^2_m (variance explained by fixed factors) and R^2_c (variance explained by both fixed and random factors) are given (Nakagawa and Schielzeth 2013).

Results

Snow physical properties

We found strong variations in hardness and density between snow types (soft, hard, and ROS)
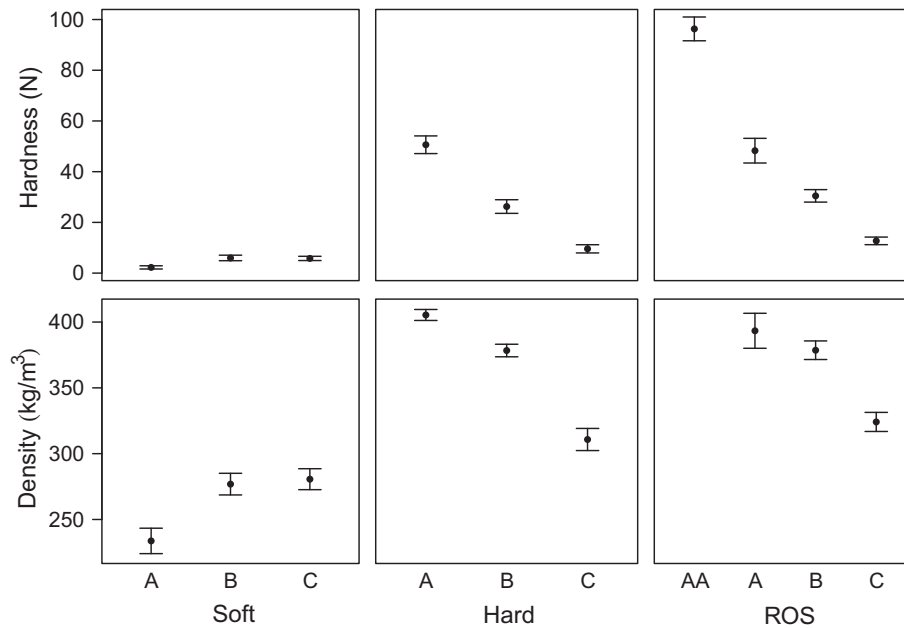
Fig. 2. Mean hardness (top) and density (bottom) of the different layers of the three types of snow (ROS = rain-on-snow) in which lemmings dug, n = 21 measurements per layer and type of snow. Error bars represent SE. AA = surface layer hardened by experimental rain-on-snow (~2–3 cm); A = top layer; B = middle layer; C = bottom layer. It was impossible to measure snow density of the AA layer.

and between layers that we visually determined within snow types (Fig. 2; see Appendix S1: Fig. S2 for examples of snow stratigraphy). As expected, hardness of the top layer was highest for ROS, intermediate for the hard snow and lowest for the soft snow ($\beta_{hard-soft}$ = 5.92, CI = [5.24, 6.60]; $\beta_{ROS-hard}$ = 2.70, CI = [2.02, 3.38]). Density showed a similar trend, being denser in the top layer of hard snow compared with soft snow ($\beta_{hard-soft}$ = 102.40, CI = [79.38, 125.44]). Within snow types, the top layer (i.e., wind slab) was the hardest and densest and the bottom layer (i.e., depth hoar) the softest and least dense, except for the soft snow type (Fig. 2; Appendix S1: Table S1). Snow density and hardness were positively related although hardness increased rapidly only when snow density exceeded ~300 kg/m³ (Appendix S1: Fig. S3).

Digging speed

In all 63 trials, lemmings instinctively dug in the snowpack. However, we observed large differences among individuals of the same species with some being active during most of the trials while others being often immobile.

We found an inverse, non-linear relationship between lemming digging speed and both snow density ($\beta_{density^2}$ = −3.40E−06, CI = [−4.28E−06, −2.52E−06]) and hardness ($\beta_{hardness^{0.5}}$ = −0.06, CI = [−0.08, −0.04]; Fig. 3; Appendix S1: Table S2). Digging speed started to decline more rapidly when snow density was above ~275 kg/m³ (about 60% of maximum value). Regarding snow hardness, lemmings dug at a wide range of speeds below ~10 N (about 12% of maximum hardness) but speed declined sharply above this value. Collared lemmings had a digging speed slightly faster (1.25 times) than brown lemmings regardless of snow density ($\beta_{species}$ = 0.09, CI = [0.00, 0.18]) or hardness ($\beta_{species}$ = 0.09, CI = [0.00, 0.18]; Fig. 3).

Behavior

We found several behavioral differences between lemming species and snow types (soft, hard, or ROS; Fig. 4). There was no difference in the time spent digging (efficient + inefficient) between species, but time spent digging was higher in ROS than other snow types (β = 0.42, CI = [0.10, 0.74]). Inefficient digging almost never occurred in soft or
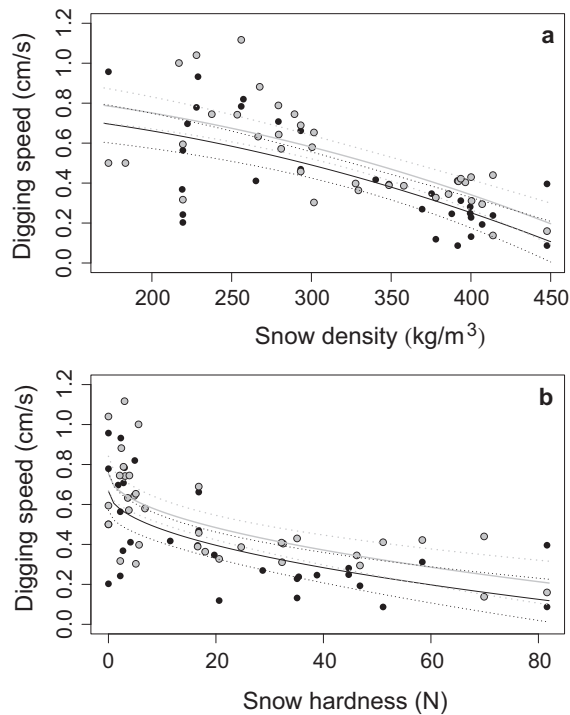
Fig. 3. Relationship between lemming digging speed and (a) snow density and (b) snow hardness. Black circles/lines = brown lemming, gray circles/lines = collared lemming. Dotted lines are 95% CI.

hard snow, but it was common in ROS (50–75% of the time). Collared lemmings spent less time scratching than brown lemmings ($\beta = -0.93$, CI = [−1.13, −0.73]), and both lemmings spent more time scratching in hard and ROS snow types than in soft snow ($\beta_{hard} = 0.43$, CI = [0.19, 0.67]; $\beta_{ROS} = 0.39$, CI = [0.15, 0.63]). Collared lemmings also spent less time exploring than brown lemmings ($\beta = -4.80$, CI = [−9.56, −0.04]). Time spent traveling decreased in hard and ROS snow types compared with soft snow ($\beta_{hard} = -1.31$, CI = [−2.31, −0.31]; $\beta_{ROS} = -1.44$, CI = [−2.48, −0.40]). Finally, time spent resting decreased in ROS compared with soft snow in brown lemmings ($\beta = -0.55$, CI = [−0.88, −0.22]) but resting increased in hard and ROS snow types compared with soft snow in collared lemmings ($\beta_{hard} = 0.87$, CI = [0.34, 1.40]; $\beta_{ROS} = 1.09$, CI = [0.56, 1.62]).

Tunnel length and time spent within the snow

Tunnel length of lemmings decreased in hard and ROS snow types compared with soft snow ($\beta_{hard} = -1.07$, CI = [−1.56, −0.58]; $\beta_{ROS} = -1.40$, CI = [−1.91, −0.89]; Fig. 5) but did not differ between species ($\beta = 0.93$, CI = [−0.15, 2.01]) despite a trend for longer tunnels in collared lemmings. The time spent within the snow was higher for collared lemmings than brown lemmings ($\beta = 12.07$, CI = [7.82, 16.32]), but did not differ between snow type ($\beta_{hard} = 1.93$, CI = [−1.62, 5.48]; $\beta_{ROS} = 1.48$, CI = [−1.50, 4.46]; Fig. 6).

Vertical movement

The probability of reaching layer B was lower in hard and ROS snow types than in soft snow ($\beta_{hard} = -2.23$, CI = [0.54, 3.92]; $\beta_{ROS} = -1.96$, CI = [−3.59, −0.33]), but did not differ between species (Fig. 7a). The probability of reaching layer C was lower in hard and ROS than in soft snow type for brown lemmings only, but this result was not statistically significant (Fig. 7b). Lemmings took more time to reach layer B or C in ROS snow than in soft snow ($\beta = 0.87$, CI = [0.01, 1.73] and $\beta = 0.74$, CI = [0.19, 1.29], respectively; Fig. 8). Collared lemmings took less time than brown lemmings to reach layer C ($\beta = -0.90$, CI = [−1.37, −0.43]) but no difference was found for layer B (Fig. 8).

Digging technique

While digging, lemmings used their front paws to tear the snow at high speed (scratch-digging technique) and their hind legs to kick the loosened snow behind them. However, in some cases, they used their incisors to tear the snow, corresponding to chisel-tooth digging technique (see Video S3, e.g., of the two digging techniques). In soft snow, lemmings never used their incisors to dig and rarely did so in hard snow (4% of the time in brown lemmings). However, in ROS snow, brown and collared lemmings used their incisors 71% and 30% of the time when digging or scratching, respectively.

Discussion

Our experiment provides compelling evidence that lemming locomotion through the snowpack is affected by its physical properties. First, the digging speed of lemmings was reduced by increasing snow hardness and density within the natural range observed in this study. Their progression (i.e., tunnel length and vertical
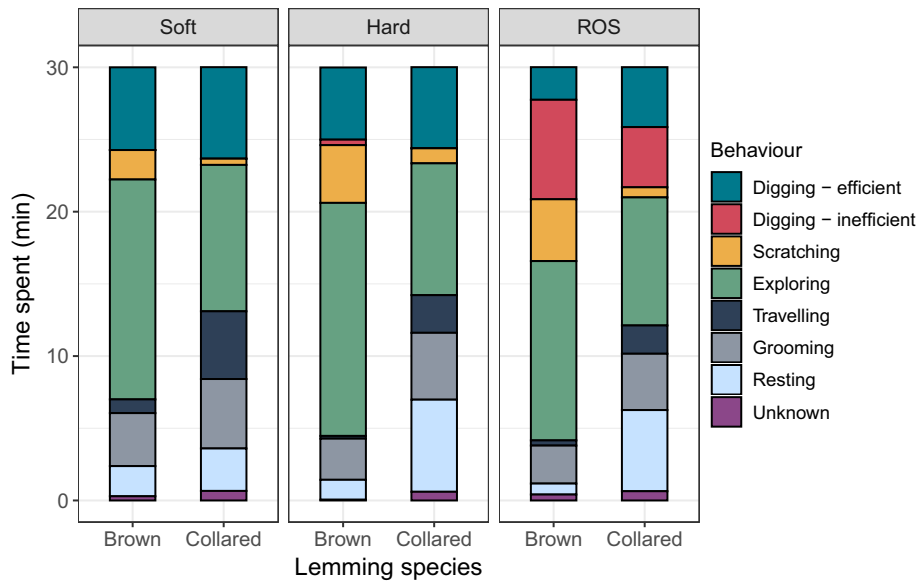
Fig. 4. Proportion of the time lemmings spent doing different behaviors during the 30-min trials in each snow type (soft, hard, and ROS) ($n_{\text{brown}} = 36$, $n_{\text{collared}} = 27$).
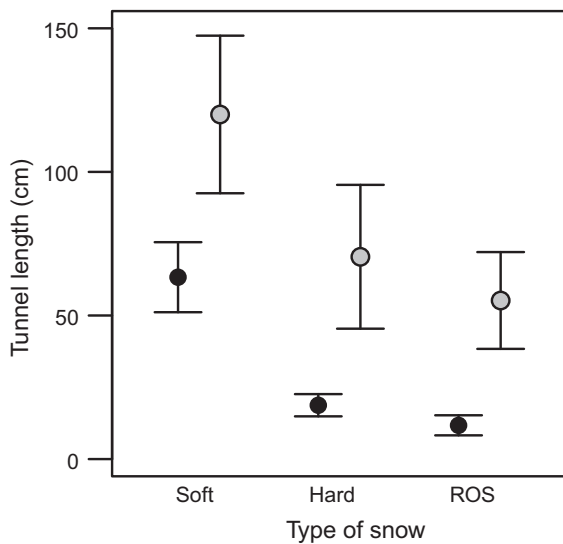

Fig. 5. Mean length of tunnels dug by lemmings in each snow type (soft, hard, and ROS). Black = brown lemmings ($n = 36$), gray = collared lemmings ($n = 27$). Error bars represent SE.
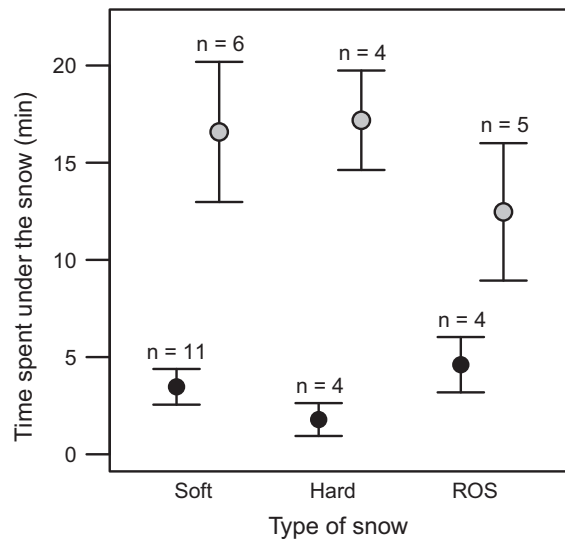
Fig. 6. Mean time spent within the snow by lemmings in each snow type. Black = brown lemmings, gray = collared lemmings. Error bars represent SE. The number above the bars indicates the number of trials where lemmings went in the snow.

movement) in the snowpack was also hampered, which is consistent with the predictions of our first hypothesis. Snow hardened by our experimental simulation of a ROS event had an even stronger impact on lemming locomotion and

behavior, and forced them to use a different digging technique involving their teeth, which supports predictions of our second hypothesis regarding an increased effort in harder snow
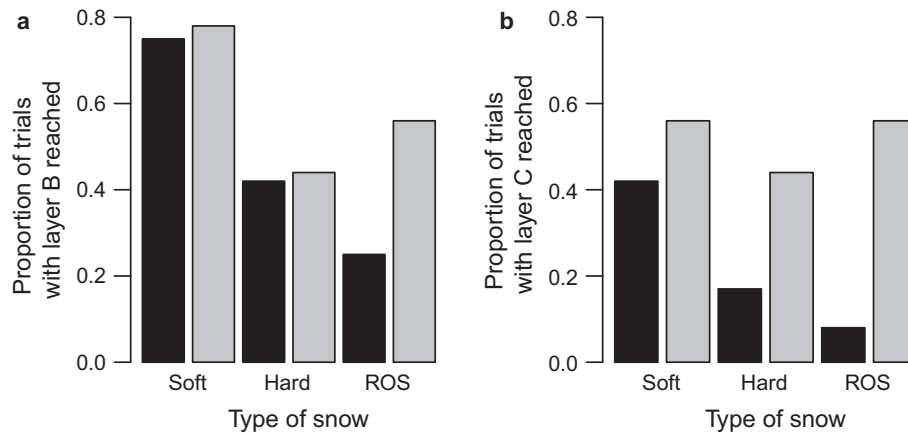
Fig. 7. Proportion of trials where lemmings reached layer B (a) and layer C (b) in each snow type. Black = brown lemmings ($n = 36$), gray = collared lemmings ($n = 27$).
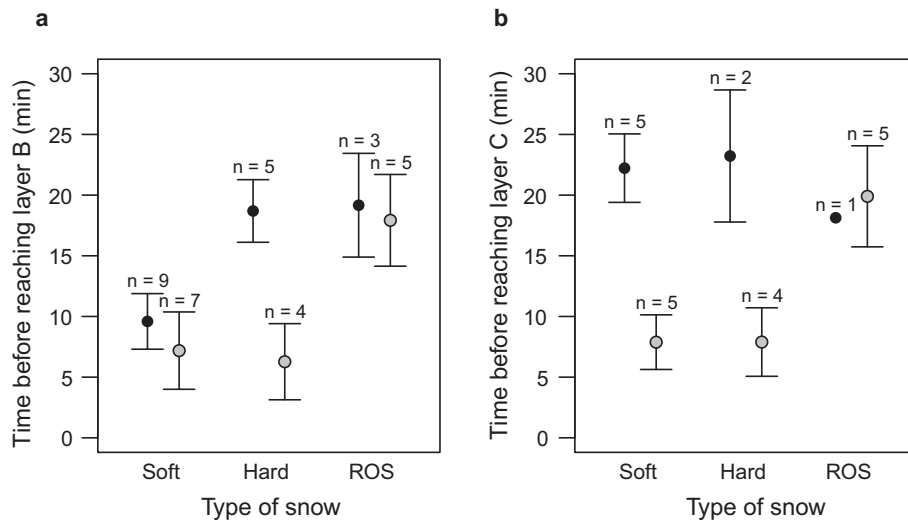

Fig. 8. Mean time taken by lemmings to reach layer B (a) and layer C (b) in each snow type. Black = brown lemming, gray = collared lemming. Error bars represent SE.

types. Finally, the digging performance of collared lemmings was less impacted by hard snow than brown lemmings, which supports our third hypothesis. To our knowledge, this is the first experimental study showing that hard snow, and especially ROS events, considerably reduces the digging performance of lemmings and affects their behavior.

Digging performance and effort in hard snow

Hard snow strongly hampers movements of lemmings using the scratch-dig technique with their front claws. Digging speed decreased as snow hardness increased but more rapidly at low hardness values, suggesting that the shear resistance is the most limiting factor for digging. As snow density increases, lemmings must loosen a greater mass of snow crystals per unit volume when digging, resulting in an increase in the quantity of material they have to push out with their hind feet. A similar reduction in performance was observed in moles digging in dense soil (Lin et al. 2017). When kicking the loosened snow with their hind feet, lemmings may be compacting the snow around them as grains sliding against each other will tend to fill

the empty space between them and lead to a tighter arrangement of snow grains (Anderson and Benson 1963). This snow compaction may allow lemmings to clear their tunnels from loosened snow with less effort compared with other rodents that have to transport the loosened soil to the surface of the ground (Vleck 1979). However, beyond a certain density, snow grains are arranged more tightly against each other, which makes compaction less likely (Arnaud et al. 2000) and could explain why digging speed declined more rapidly at high values of snow density. Unfortunately, we could not measure digging speed in our ROS layer due to insufficient progression of lemmings in this type of snow. However, the drastic increase in inefficient digging in ROS suggests that speed may be very low and close to 0 cm/s at 95 N, the mean hardness of the ROS top layer.

The strong effect of snow hardness on digging speed can explain why tunnel length dug by lemmings during the experiment decreased almost linearly across snow types of increasing hardness. Also, in response to a slower progression in the ROS snow, lemmings apparently compensated by increasing their time spent digging. However, a large proportion of that digging time was inefficient (i.e., no progression in the snowpack). Before initiating digging, lemmings typically explored and scratched the surface of the snow at many places in the experimental box. The increased time spent scratching in the presence of hard snow suggests that lemmings were sampling snow repeatedly and possibly looking for softer snow to initiate digging. Our results also show that lemmings were more reluctant to dig deeper in hard than in soft snowpacks and fewer of them reached the deepest and softest snow layer when they initially encountered a hard layer, especially in ROS snow. All these results are consistent with field observations showing that lemming tunnels are almost always found in the softest layer of the snowpack (Poirier et al. 2019).

Lemmings showed flexibility in their digging technique by using their incisors when scratching or digging in the hard ROS snow. The chisel-tooth digging technique is thought to have evolved primarily in fossorial species living in hard soil types (Stein 2000), but it is not unusual to observe it as a secondary digging mode in other species when facing harder soils (Lessa and Thaeler 1989).

However, considering that this behavior was only observed when lemmings attempted to dig through the hardest snow, chisel-tooth may be less efficient and/or more energetically costly than the more common scratch-digging technique. Despite this switch of technique in the presence of ROS, a large proportion of the time spent digging remained inefficient and their progression in the snow was very slow. Collectively, these results suggest that animals experiencing ROS events under natural conditions will need to spend considerably more effort to fill their basic needs (e.g., accessing food) whenever they have to move through hardened snow. Ultimately, this should increase their energy expenditure as reported in fossorial rodents that need to dig in hard and dense soils (Vleck 1979, Ebensperger and Bozinovic 2000, Luna and Antinuchi 2006).

Interspecific differences in locomotion efficiency in the snowpack

Overall, collared lemmings were more efficient than brown lemmings when moving in the snow as their digging speed, proportion of efficient digging among total digging time, tunnel length, and probability of reaching the deepest layer in the presence of hard snow were greater than for brown lemmings. Some of the differences observed between the two species were not always statistically significant, probably due to our small sample size and sometimes to large individual differences. Nonetheless, all trends detected were always in favor of a higher performance in collared lemmings, never the opposite. This difference is not surprising since collared lemmings develop large claws on their front legs in early winter, unlike brown lemmings (Hansen 1957, Fuller et al. 1975). The specialization of forelimbs for digging could also explain why collared lemmings used their incisors less than brown lemmings in the presence of hard snow. In contrast, brown lemmings spent more time exploring and scratching the surface of the snow, possibly to probe for softer snow. The skull of the two lemming species also presents some morphological differences such as larger angular processes on the mandible of collared lemmings. If this is associated with larger, more powerful jaw muscles in this species, it could increase the efficiency of digging when they use their teeth in ROS snow, but this needs further exploration.

Collared lemmings are known to have the most northerly geographic distribution among small mammals (Jarrel and Fredga 1993), which includes the high arctic polar deserts where brown lemmings are absent. Polar deserts typically have a lower occurrence and, when present, a lower fraction of the snowpack occupied by depth hoar (Domine et al. 2018a), as well as a denser snowpack compared with arctic or subarctic regions (Royer et al. 2021). Therefore, the greater efficiency of collared lemmings to dig in hard snow compared with brown lemmings may partly explain their more northerly distribution where a denser snow type is more prevalent.

Implications

Overall, our study indicates that lemming locomotion in the snowpack is impaired by hard wind slabs and even more by our simulated ROS snow type. Nonetheless, generalization of our findings to the whole Arctic and winter period should be made with caution. First, the design of our experiment forced lemmings to penetrate the snowpack from above, which may not entirely reflect the reality faced by lemmings as they are thought to spend most of their time inside the snowpack. However, we and others have made numerous observations of lemmings on the surface of the snowpack (e.g., Poirier et al. 2019), probably to disperse, find a mate, or escape a predator such as an ermine. Thus, the conditions simulated in our experiment may not be so uncommon. Furthermore, we note that the depth hoar measured in this study during late fall was denser than typical arctic depth hoar, which is usually sampled in late winter or spring (Derksen et al. 2009, Domine et al. 2016, Poirier et al. 2019). This may occur because the upward water vapor fluxes that create depth hoar continues during the winter or because wind compaction was especially strong at our study site. Therefore, changing snow conditions over the winter or spatial variations in physical properties of the snowpack may have a great influence on digging performance of lemmings under natural conditions.

The frequency of melt-freeze and ROS events has already started to increase in some regions of the Arctic due to climate change, and this is likely to continue in the future (Langlois et al. 2017, Peeters et al. 2019). Melt-freeze layers often form in depressions of the ground at the bottom of the snowpack and lemmings tend to avoid digging into them (Poirier et al. 2019). However, if lemmings have to dig horizontally across such hard snow layers to access their food or move vertically to the surface of the snowpack (i.e., when a melt-freeze layer formed in the upper part of the snowpack), this could greatly increase their energy expenditure. Although we showed that lemmings could change their digging technique when faced with snow transformed by ROS, their digging efficiency drastically declined. In the worst case, extreme ROS events can even encapsulate ground vegetation in ice and make it unavailable to lemmings, as was observed for other herbivores such as reindeer (*Rangifer tarandus*), voles, or ptarmigans, thus affecting their populations negatively (Stien et al. 2012, Hansen et al. 2013). More studies assessing the impact of snow properties on lemming behavior, energetic, and population dynamic are required to better understand these processes.

By increasing their effort to move through a snowpack indurated by a ROS, lemmings would have less energy available for reproduction or survival, which could have negative impacts on their populations (Aars and Ims 2002, Korslund and Steen 2006, Kausrud et al. 2008). Given that lemmings are key species of the arctic ecosystem (Ims and Fuglei 2005), a disruption of their cyclic population fluctuations could drastically impact the numerous predators that depend upon them for their own reproduction and survival (Schmidt et al. 2012).

Literature Cited

Aars, J., and R. A. Ims. 2002. Intrinsic and climatic determinants of population demography: the winter dynamics of tundra voles. Ecology 83:3449–3456.

Anderson, D. L., and C. S. Benson. 1963. The densification and diagenesis of snow. Pages 391–411 *in* W. D. Kingery, editor. Ice and snow: properties, processes and applications. MIT Press, Cambridge, Massachusetts, USA.

Arnaud, L., J. M. Barnola, and P. Duval. 2000. Physical modeling of the densification of snow/firn and ice in the upper part of polar ice sheets. Pages 285–305 *in* Proceedings of the International Symposium on Physics of Ice Core Records, Shikotsukohan, Hokkaido, Japan, September 14–17, 1998. Hokkaido University Press, Sapporo, Japan.

Bates, D., M. Mächler, B. M. Bolker, and S. C. Walker. 2015. lme4: linear mixed-effects models using Eigen and S4. R package version 1.1-8. http://CRAN.R-project.org/package=lme4

Berteaux, D., G. Gauthier, F. Domine, R. A. Ims, S. F. Lamoureux, E. Lévesque, and N. Yoccoz. 2017. Effects of changing permafrost and snow conditions on tundra wildlife: critical places and times. Arctic Science 3:65–90.

Bilodeau, F., G. Gauthier, and D. Berteaux. 2013. The effect of snow cover on the vulnerability of lemmings to mammalian predators in the Canadian Arctic. Journal of Mammalogy 94:813–819.

Borstad, C. P., and D. M. Mcclung. 2011. Thin-blade penetration resistance and snow strength. Journal of Glaciology 57:325–336.

Conger, S. M., and D. M. McClung. 2009. Instruments and Methods: comparison of density cutters for snow profile observations. Journal of Glaciology 55:163–169.

Derksen, C., A. Silis, M. Sturm, J. Holmgren, G. E. Liston, H. Huntington, and D. Solie. 2009. Northwest Territories and Nunavut Snow Characteristics from a Subarctic Traverse: implications for Passive Microwave Remote Sensing. Journal of Hydrometeorology 10:448–463.

Domine, F., M. Barrere, and S. Morin. 2016. The growth of shrubs on high Arctic tundra at Bylot Island: impact on snow physical properties and permafrost thermal regime. Biogeosciences Discussions:1–28.

Domine, F., M. Belke-Brea, D. Sarrazin, L. Arnaud, M. Poirier, and T. Joint. 2018*a*. Soil moisture, wind speed and depth hoar formation in the Arctic snowpack. Journal of Glaciology 64:1–29.

Domine, F., A. Cabanes, and L. Legagneux. 2002. Structure, microphysics, and surface area of the Arctic snowpack near Alert during the ALERT 2000 campaign. Atmospheric Environment 36:2753–2765.

Domine, F., G. Gauthier, V. Vionnet, D. Fauteux, M. Dumont, and M. Barrere. 2018*b*. Snow physical properties may be a significant determinant of lemming population dynamics in the high Arctic. Arctic Science 4:813–826.

Duchesne, D., G. Gauthier, and D. Berteaux. 2011. Habitat selection, reproduction and predation of wintering lemmings in the Arctic. Oecologia 167:967–980.

Ebensperger, L. A., and F. Bozinovic. 2000. Energetics and burrowing behaviour in the semifossorial degu *Octodon degus* (Rodentia: Octodontidae). Journal of Zoology 252:179–186.

Fauteux, D., G. Gauthier, and D. Berteaux. 2015. Seasonal demography of a cyclic lemming population in the Canadian Arctic. Journal of Animal Ecology 84:1412–1422.

Fuller, W. A., A. M. Martell, R. F. C. Smith, and S. W. Speller. 1975. High-arctic lemmings, *Dicrostonyx groenlandicus*. II Demography. Canadian Journal of Zoology 53:867–878.

Hansen, B. B., et al. 2013. Climate events synchronize the dynamics of a resident vertebrate community in the High Arctic. Science 339:313–315.

Hansen, R. M. 1957. Remarks on the bifid claws of the varying lemming. American Society of Mammalogist 38:127–128.

Ims, R. A., and E. V. A. Fuglei. 2005. Trophic interaction cycles in tundra ecosystems and the impact of climate change. BioScience 55:311–322.

Jarrel, G. H., and K. Fredga. 1993. How many kinds of lemmings? A taxonomic overview. Pages 45–57 *in* E. N. C. Stenseth, and R. A. Ims, editors. The biology of lemmings. Linnean Society of London, Academic Press, London, UK.

Kausrud, K. L., et al. 2008. Linking climate change to lemming cycles. Nature 456:93–97.

Korslund, L., and H. Steen. 2006. Small rodent winter survival: snow conditions limit access to food resources. Journal of Animal Ecology 75:156–166.

Krebs, C. J. 2011. Of lemmings and snowshoe hares: the ecology of northern Canada. Proceedings of the Royal Society B: Biological Sciences 278:481–489.

Langlois, A., et al. 2017. Detection of rain-on-snow (ROS) events and ice layer formation using passive microwave radiometry: a context for Peary caribou habitat in the Canadian Arctic. Remote Sensing of Environment 189:84–95.

Lessa, E. P., and C. S. Thaeler. 1989. A reassessment of morphological specializations for digging in pocket gophers. Journal of Mammalogy 70:689–700.

Lin, Y., A. Chappuis, S. Rice, and E. R. Dumont. 2017. The effects of soil compactness on the burrowing

performance of sympatric eastern and hairy-tailed moles. Journal of Zoology 301:310–319.

Lovegrove, B. G. 1989. The cost of burrowing by the social mole rats (Bathyergidae) *Cryptomys damarensis* and *Heterocephalus glaber*: the role of soil moisture. Physiological Zoology 62:449–469.

Luna, F., and C. D. Antinuchi. 2006. Cost of foraging in the subterranean rodent *Ctenomys talarum*: effect of soil hardness. Canadian Journal of Zoology 84:661–667.

Millar, J. S. 2001. On reproduction in lemmings. Ecoscience 8:145–150.

Nakagawa, S., and H. Schielzeth. 2013. A general and simple method for obtaining R2 from generalized linear mixed-effects models. Methods in Ecology and Evolution 4:133–142.

Nevo, E. 1979. Adaptive convergence and divergence of subterranean mammals. Annual Review of Ecology and Systematics 10:269–308.

Peeters, B., L. E. Loe, and K. Isaksen. 2019. Spatiotemporal patterns of rain-on-snow and basal ice in high Arctic Svalbard: detection of a climate-cryosphere regime shift. Environmental Research Letters 14:015002.

Pielmeier, C., and M. Schneebeli. 2003. Developments in the stratigraphy of snow. Surveys in Geophysics 24:389–416.

Pinheiro, J., and D. Bate. 2021. nlme: linear and nonlinear mixed effects models. R package version 3.1-152. https://CRAN.R-project.org/package=nlme

Poirier, M., G. Gauthier, and F. Domine. 2019. What guides lemmings movements through the snowpack? Journal of Mammalogy 100:1416–1426.

Pomeroy, J. W. W., and E. Brun. 1990. Physical properties of snow. Snow Ecology: an Interdisciplinary Examination of Snow-Covered Ecosystems 97:45–126.

R Core Team. 2020. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Reichman, O. J., and S. C. Smith. 1990. Burrows and burrowing behaviours by mammals. Pages 197–244 *in* H. H. Genoways, editor. Current mammalogy. Plenum Press, New York, New York, USA and London, UK.

Reid, D. G., F. Bilodeau, C. J. Krebs, G. Gauthier, J. Alice, B. S. Gilbert, M. C. Leung, D. Duchesne,

and E. Hofer. 2012. Lemming winter habitat choice: a snow-fencing experiment. Oecologia 168:935–946.

Royer, A., F. Domine, A. Roy, A. Langlois, N. Marchand, and G. Davesne. 2021. New northern snow-pack classification linked to vegetation cover on a latitudinal mega-transect across Northeastern Canada. Ecoscience, in press. https://doi.org/10.1080/11956860.2021.1898775

Schmidt, N. M., R. A. Ims, T. T. Hoye, O. Gilg, L. H. Hansen, J. Hansen, M. Lund, E. Fuglei, M. C. Forchhammer, and B. Sittler. 2012. Response of an arctic predator guild to collapsing lemming cycles. Proceedings of the Royal Society B: Biological Sciences 279:4417–4422.

Schneider, C. A., W. S. Rasband, and K. W. Eliceiri. 2012. NIH Image to ImageJ: 25 years of image analysis. Nature Methods 9:671–675.

Seymour, R. S., P. C. Withers, and W. W. Weathers. 1998. Energetics of burrowing, running, and free-living in the Namib Desert golden mole (*Eremitalpa namibensis*). Journal of Zoology 244:107–117.

Stein, B. R. 2000. Morphology of subterranean rodents. Pages 19–61 *in* E. A. Lacey, J. L. Patton, and G. N. Cameron, editors. Life underground: the biology of subterranean rodents. The University of Chicago Press, Chicago, Illinois, USA.

Stien, A., et al. 2012. Congruent responses to weather variability in high arctic herbivores. Biology Letters 8:1002–1005.

Sturm, M., and C. S. Benson. 1997. Vapor transport, grain growth and depth-hoar development in the subarctic snow. Journal of Glaciology 43:42–59.

Sutton, G. M., and J. Hamilton. 1932. The mammals of Southampton Island. Pages 1–109 *in* Memoirs of the Carnegie Museum. Volume 12. Carnegie Institute, Pittsburgh, Pennsylvania, USA.

Vleck, D. 1979. The energy cost of burrowing by the pocket gopher *Thomomys bottae*. Physiological Zoology 52:122–136.

Zimova, M., K. Hackländer, J. M. Good, J. Melo-Ferreira, P. C. Alves, and L. S. Mills. 2018. Function and underlying mechanisms of seasonal colour moulting in mammals and birds: what keeps them changing in a warming world? Biological Reviews 93:1478–1498.

DATA AVAILABILITY

Supporting Information

Additional Supporting Information may be found online at: http://onlinelibrary.wiley.com/doi/10.1002/ecs2.3835/full