Impact des propriétés physiques de la neige sur les populations de lemmings en Arctique

Thèse

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Résumé

Le manteau neigeux constitue un élément clé des paysages nordiques en hiver et peut affecter les espèces qui y vivent de multiples façons. Les processus hivernaux qui influencent l'écologie des espèces nordiques demeurent mal compris, même si de plus en plus d'études suggèrent qu'ils pourraient jouer un rôle essentiel dans leur cycle annuel. C'est le cas des lemmings, de petits rongeurs arctiques aux fluctuations cycliques de populations, qui demeurent actifs tout l'hiver sous le manteau neigeux. Ces petits mammifères jouent un rôle essentiel dans l'écosystème arctique, comme ils sont la proie principale de nombreux prédateurs retrouvés dans ces régions. Cette thèse examine l'impact de la neige sur les populations de lemmings bruns (*Lemmus trimucronatus*) et de lemmings variables (*Dicrostonyx groenlandicus*), les principales espèces retrouvées dans le Haut-Arctique canadien. Plus spécifiquement, cette thèse vise à comprendre l'impact des propriétés physiques de la neige sur (1) l'utilisation des différentes couches du manteau neigeux par les lemmings, (2) leur performance et leur effort déployé pour creuser dans la neige, (3) leur utilisation de l'habitat hivernal, et (4) leurs paramètres démographiques. Nous avions également pour but de contraster les impacts des propriétés physiques de la neige entre les deux espèces de lemmings. Cette étude a pris place à l'île Bylot, au Nunavut, où un suivi à long terme a permis l'utilisation de données provenant d'une série temporelle s'étalant de 2004 à 2022. En caractérisant les tunnels de lemmings dans le manteau neigeux, nous avons trouvé que ceux-ci sont toujours creusés dans la couche basale de givre de profondeur, généralement la couche la plus friable du manteau neigeux arctique. Contrairement à la croyance générale, les tunnels de lemmings sont creusés plus haut que le niveau du sol, tout juste sous une couche de neige plus dure, probablement pour éviter l'effondrement de leurs tunnels et ainsi les réutiliser. Ensuite, en exposant des individus captifs à de la neige de différentes duretés, nous avons montré que les lemmings creusent plus lentement et déploient plus d'effort à creuser dans une neige dure par rapport à une neige plus molle. L'étude de leurs nids d'hiver à travers le paysage nous a permis de mettre en lumière que les lemmings utilisent davantage les habitats où les manteaux neigeux sont plus épais, probablement pour réduire leur coût de thermorégulation. Cependant, l'utilisation préférentielle de ces sites vient souvent avec le compromis de la présence d'une couche basale de plus forte densité, ce qui semble nuire à la reproduction hivernale des lemmings. Nous avons également mis en

évidence que les épisodes de pluie-sur-neige et de fonte-regel menant au durcissement de la couche basale de neige influencent négativement la reproduction ainsi que la croissance hivernale des populations de lemmings. Concernant les différences interspécifiques, nous avons trouvé que les lemmings variables sont plus performants à creuser dans la neige comparativement aux lemmings bruns et qu'ils ont un taux de reproduction hivernal plus élevé, appuyant l'hypothèse d'une meilleure adaptation à la vie hivernale. En somme, mes travaux soutiennent l'idée qu'un durcissement du manteau neigeux est néfaste pour les populations de lemmings, principalement en diminuant leur capacité à se reproduire en hiver, ce qui pourrait entraîner des répercussions sur leurs principaux prédateurs. Dans un contexte où les changements climatiques menacent de perturber le manteau neigeux, il est nécessaire d'approfondir notre compréhension de ses interactions avec les espèces nordiques. En fournissant des évidences quant à l'influence des propriétés physiques du manteau neigeux sur la thermorégulation et sur la locomotion des espèces nordiques, ma thèse contribue significativement à l'avancement des connaissances en écologie hivernale.

Abstract

The snowpack constitutes a key element of Nordic landscapes in winter and can affect the species inhabiting them in various ways. Winter processes influencing the ecology of Nordic species remain poorly understood, even though an increasing number of studies suggest that they might play a crucial role in their annual cycle. This is the case for lemmings, small Arctic rodents with cyclic population fluctuations, which remain active throughout the winter under the snowpack. These small mammals play a vital role in the Arctic ecosystem as primary prey of numerous predators in the region. This thesis aims to elucidate the impact of snow on populations of brown lemmings (*Lemmus trimucronatus*) and collared lemmings (*Dicrostonyx groenlandicus*), the main species found in the Canadian High Arctic. More specifically, this thesis examines the impact of snow physical properties on (1) lemming use of the different snow layers; (2) their efficiency and effort to dig in the snow; (3) their winter habitat use; and (4) their demographic parameters. We also aimed to contrast the impact of snow properties between the two lemming species. This study took place on Bylot Island, Nunavut, where a long-term monitoring provided a time series data spanning from 2004 to 2022. By characterizing lemming tunnels within the snowpack, we discovered that they are consistently dug in the basal depth hoar, typically the softest layer of the arctic snowpack. Contrary to common belief, tunnels are excavated slightly above ground level, just beneath a harder snow layer, likely to prevent tunnel collapse and facilitate reuse. Then, in an experiment in which we exposed captive individuals to snow of varying hardness, we found that lemmings decrease their digging speed and increase their digging effort in hard snow compared to softest snow. The study of their winter nests across the landscape allowed us to highlight that lemmings use habitats where snowpacks is deeper, likely to reduce their thermoregulation costs. However, preferential use of these sites often comes at the cost of a denser basal snow layer, which appears to hinder the winter reproduction of lemmings. We also demonstrated that rain-on-snow and melt-freeze events leading to a hardening of the basal snow layer negatively impact winter reproduction and population growth of lemmings. Regarding interspecific differences, we found that collared lemmings are better at digging in the snowpack compared to brown lemmings and that they have a higher winter reproductive rate, which supports the hypothesis of a better adaptation to winter conditions. In summary, my work supports the idea that a hardening of the snowpack is detrimental to lemming

populations, primarily by reducing their ability to reproduce in winter, which could have implications for their main predators. In a context where climate change threaten to disrupt the snowpack, it is essential to deepen our understanding of its interactions with Nordic species. By providing evidence of an influence of physical properties of the snowpack on thermoregulation and locomotion of Nordic species, my thesis significantly contributes to advancing our knowledge on winter ecology.

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« Ce qui compte, ce n'est pas de gravir cette montagne, ou bien celle-ci, ou bien encore celle-là, mais de parcourir le chemin. Et de le faire avec attention, persévérance, avec le cœur ouvert et l'esprit vigilant. Ce n'est pas le nom du sommet que nous avons gravi qui nous transforme, mais la présence et l'amour que nous avons mis dans la marche. Le monde est beau par la variété de ses paysages. » – Frédéric Lenoir, L'Âme du monde

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Avant-propos

Cette thèse est composée de 6 sections, dont une introduction et une conclusion générale rédigées dans la langue française. Le cœur de la thèse est constitué de 4 chapitres présentés sous forme d'articles scientifiques révisés par les pairs et rédigés en anglais. L'introduction présente une revue de littérature sur l'état des connaissances en lien avec le sujet de ma thèse ainsi que mes principaux objectifs de recherche. Dans la conclusion, je discute des principaux résultats de mes chapitres, tout en présentant leurs limites, et je présente également quelques perspectives de recherche. Je suis la principale auteure des 4 chapitres de ma thèse. Gilles Gauthier et Florent Dominé, mes directeurs de thèse, sont coauteurs de tous mes Chapitres. Dominique Fauteux (Musée Canadien de la Nature) est également un collaborateur important qui figure comme coauteur sur 3 de mes 4 chapitres. Puis, Jean-François Lamarre (Savoir Polaire Canada) a collaboré à mon Chapitre 2. Les Chapitres 1, 2 et 3 sont publiés et sont présentés tels quels dans cette présente thèse. Le Chapitre 4 est en préparation et sera soumis quelque peu après le dépôt initial de cette thèse.

Le Chapitre 1 intitulé « What guides lemming movements through the snowpack? » a été publié dans la revue *Journal of Mammalogy* en septembre 2019. Gilles Gauthier et Florent Dominé sont coauteurs de cet article (https://doi.org/10.1093/jmammal/gyz129).

Le Chapitre 2 intitulé « Snow hardness impacts intranivean locomotion of arctic small mammals » a été publié dans la revue *Ecosphere* en juillet 2021. Dominique Fauteux (Musée Canadien de la Nature), Gilles Gauthier, Florent Dominé et Jean-François Lamarre (Savoir Polaire Canada) sont coauteurs de cet article (https://doi.org/10.1002/ecs2.3835).

Le Chapitre 3 intitulé « Lemming winter habitat: the quest for warm and soft snow » a été publié dans la revue *Oecologia* en Juin 2023. Gilles Gauthier, Florent Dominé et Dominique Fauteux (Musée Canadien de la Nature) sont coauteurs de cet article (https://doi.org/10.1007/s00442-023-05385-y).

Le Chapitre 4 intitulé « Demography of high Arctic lemmings in response to snow physical properties » sera soumis pour publication à l'automne 2023. Gilles Gauthier, Florent Dominé et Dominique Fauteux (Musée Canadien de la Nature) sont coauteurs de cet article.

En tant qu'auteure principale de ces quatre chapitres, j'ai conçu les objectifs, collecté une grande partie des données sur le terrain, réalisé les analyses statistiques et rédigé les manuscrits. Mon directeur Gilles Gauthier a largement contribué à toutes ces étapes en plus de me fournir de nombreux commentaires et conseils visant à améliorer mon projet ainsi que ma rédaction scientifique. Mon codirecteur Florent Dominé a également étroitement collaboré à la conception des objectifs ainsi qu'à la rédaction des manuscrits, en plus de m'aider dans mes réflexions via les nombreuses discussions sur la physique de la neige. Mon collaborateur Dominique Fauteux s'est fortement impliqué dans les Chapitres 2-3-4, notamment en ce qui concerne les données amassées sur le terrain, les analyses statistiques et la rédaction, en plus d'aider à la conception des objectifs de mon Chapitre 2. Mon collaborateur Jean-François Lamarre a apporté un fort support logistique dans le cadre de mon Chapitre 2 en plus de fournir des conseils pour la rédaction de ce chapitre.

Introduction

Contexte général

La neige, c'est bien plus qu'un mélange d'air et de cristaux de glace. C'est bien plus qu'une matière à pelleter jour après jour durant les longs mois d'hiver au Québec. La neige c'est aussi un refuge, une maison. Une maison pour les peuples inuit de l'Arctique canadien qui, il y a moins de 100 ans de cela, en faisaient leur demeure principale en hiver (Stern and Stevenson 2006). Maintenant, en plus d'être un abri temporaire pour les résidents du Haut-Arctique canadien et autres aventuriers des climats polaires, la neige constitue un important refuge pour de nombreuses espèces nordiques.

Pour les espèces nordiques, être intrinsèquement liées à un substrat aussi éphémère et imprévisible qu'est le manteau neigeux représente un défi de taille. La formation du manteau neigeux et ses propriétés sont directement dépendantes des conditions météorologiques qui varient d'une année à l'autre. De plus, les changements climatiques menacent de perturber le développement normal du manteau neigeux arctique et de durcir ce dernier via l'augmentation des épisodes de pluie-sur-neige.

Étudier les interactions entre les animaux et le manteau neigeux arctique présente de nombreux défis logistiques. Il est néanmoins essentiel de mieux documenter ces relations complexes qui pourraient avoir un impact bien plus important sur la dynamique des populations que ce qui en était évalué il y a quelques décennies. Parmi ces espèces, le lemming est un petit mammifère arctique qui entretient un lien très étroit avec la neige en hiver, devant creuser des réseaux de tunnels complexes dans celui-ci afin de se déplacer. Ce petit rongeur nous a donc semblé être un modèle d'étude idéal pour mieux comprendre l'impact des propriétés physiques de la neige sur la faune arctique.

Relations entre les animaux et le manteau neigeux

La nature des relations entre les animaux et le manteau neigeux dépend de nombreux facteurs, tels les traits écologiques des espèces et les caractéristiques du manteau neigeux. Selon ses caractéristiques, le manteau neigeux peut soit avantager ou défavoriser la locomotion, la prise alimentaire et la thermorégulation des espèces.

Impact du manteau neigeux sur la locomotion

Pour plusieurs espèces, la présence d'un manteau neigeux représente un obstacle à leurs déplacements quotidiens. Certaines espèces possèdent des adaptations morphologiques favorisant leurs déplacements à la surface de la neige, comme c'est le cas des pattes élargies du lynx (*Lynx canadensis*), du lièvre (*Lepus americanus*) et du caribou (*Rangifer tarandus*) qui limitent l'enfoncement dans la neige (Formozov 1946, Murray et al. 1994). D'autres espèces vont plutôt adapter leur comportement de façon à utiliser davantage les habitats où la neige leur sera plus favorable pour se déplacer. Par exemple, le coyote (*Canis latrans*) utilise davantage les habitats où le couvert nival est plus dur et mince ainsi que les pistes d'autres individus pour se déplacer (Murray et al. 1994). Certaines espèces doivent faire des compromis, comme la martre (*Martes caurina*) qui utilise davantage les habitats avec un épais manteau neigeux pour se réfugier des froides températures, malgré une augmentation des dépenses énergétiques à se déplacer dans ce type de milieu (Martin et al. 2020).

Impact du manteau neigeux sur la prise alimentaire

Pour les herbivores se nourrissant de végétation au niveau du sol, la présence d'un couvert nival représente une barrière à la prise alimentaire (Formozov 1946, Johnsen et al. 2017), d'autant plus lorsque ce dernier est de forte dureté. Les épisodes de pluie-sur-neige formant une couche de glace au niveau du sol sont reconnus pour entraîner des mortalités chez les populations de caribous, de bœufs musqués (*Ovibos moschatus*) et de campagnols (*Microtus kuis*) en les empêchant de s'alimenter (Rennert et al. 2009, Stien et al. 2012, Langlois et al. 2017). À l'inverse, pour les carnivores devant pourchasser leurs proies à la surface de la neige, une neige plus dure leur serait favorable. Le lynx, par exemple, voit son succès de chasse sur sa proie principale, le lièvre, augmenter avec la dureté de la neige (Stenseth et al. 2004). Pour d'autres espèces, la présence d'un manteau neigeux donnerait accès à de nouvelles opportunités alimentaires. Le lagopède (*Lagopus spp.*), par exemple, pourrait bénéficier d'un épais couvert de neige lui donnant accès à des bourgeons sur de la végétation en hauteur, autrement inatteignables (St-georges et al. 1995).

Le manteau neigeux comme refuge thermique

La neige est un excellent isolant thermique et est ainsi utilisée par plusieurs espèces comme un refuge contre les froides températures à l'hiver (Formozov 1946, Marchand 2013).

Certaines espèces telles l'ours polaire (*Ursus maritimus*) et le carcajou (*Gulo gulo*) creusent dans la neige pour y établir leur tanière de reproduction, et la survie de leurs jeunes semble être étroitement liée aux propriétés isolantes de la neige où ils se trouvent (Magoun and Copeland 1998, Durner et al. 2003). Parmi les espèces aviaires qui utilisent la neige comme refuge thermique, le tétras lyre (*Lyrurus tetrix*) est l'une de celles qui passent le plus de temps sous la neige en hiver (Marjakangas et al. 1984, Marchand 2013). Il est estimé que l'oiseau quitte son refuge seulement 5 % du temps afin de se nourrir (Marjakangas et al. 1984). Les micromammifères nordiques sont quant à eux reconnus pour passer la quasi-totalité de leur temps à l'intérieur du manteau neigeux, dans les couches basales, où ils s'alimentent de végétation au niveau du sol (Marchand 2013).

Importance du manteau neigeux pour les lemmings et autres micromammifères arctiques

Dans certaines régions de l'Arctique où l'hiver se fait long, les lemmings et autres petits mammifères passent jusqu'à 9 mois par année à l'intérieur du manteau neigeux. Lorsqu'ils ont l'énergie pour le faire, les lemmings ont également la capacité de se reproduire sous la neige (Millar 2001) même si le phénomène demeure mal compris. Il va ainsi sans dire que les propriétés physiques de la neige ont le potentiel d'influencer les populations de ces petits animaux qui dépendent de la protection offerte par ce couvert nival pour se protéger des froids extrêmes (Chappell 1980a).

La vie dans l'espace sous-nival

L'espace sous-nival fait référence à la couche basale de neige dans laquelle il est admis que les petits mammifères passent la majeure partie de leur temps à l'hiver (Marchand 2013, Pauli et al. 2013, Thompson et al. 2021). Cet espace est caractérisé par un microclimat beaucoup plus favorable que celui retrouvé à la surface de la neige (Duchesne et al. 2011a, Marchand 2013). Chappell (1980a) a en effet montré que, pour les petits mammifères, vivre dans l'espace sous-nival plutôt qu'à la surface de la neige permettrait d'économiser entre 15 à 25 % des coûts énergétiques reliés à la thermorégulation. Certains petits mammifères, tels les lemmings, construisent également des nids sous la neige durant l'hiver. Ces abris formés de végétation leur apportent une protection thermique supplémentaire, à la fois pour eux-mêmes

ainsi que pour leurs jeunes lorsque les conditions leur permettent de se reproduire (Casey 1981, Duchesne et al. 2011a).

Plusieurs petits mammifères demeurent actifs dans cet espace sous nival, creusant des réseaux de tunnels dans la neige afin de trouver un partenaire de reproduction ou des plantes pour se nourrir (Gilg et al. 2012). À l'hiver, l'accessibilité des plantes est réduite pour les petits mammifères (Johnsen et al. 2017). La formation de couches de glace au niveau du sol diminue davantage la quantité de nourriture disponible à l'hiver, ce qui pourrait influencer la survie des petits mammifères (Korslund and Steen 2006, Johnsen et al. 2017).

Déplacements dans le manteau neigeux

Pour se déplacer et rechercher leur nourriture, il est présumé que les lemmings et autres rongeurs utilisent préférentiellement l'espace sous-nival dans le manteau neigeux étant donné la proximité avec la végétation qui se trouve au niveau du sol (Korslund and Steen 2006, Marchand 2013). De façon générale, la densité de la neige basale est plus faible en comparaison aux couches supérieures du manteau neigeux arctique. En plus de la proximité avec la nourriture, il serait donc avantageux pour les petits mammifères de creuser dans cette couche basale de faible densité afin de limiter les dépenses énergétiques reliées à leurs déplacements (Aitchison 2001, Sanecki et al. 2006). Or, mis à part quelques observations anecdotiques (Sutton and Hamilton 1932), peu d'études ont tenté de documenter le creusage des lemmings dans la neige ainsi que l'impact de ses propriétés physiques sur celui-ci. Les observations de Spencer (1984) suggèrent que les campagnols (*Microtus longicaudus*) évitent de creuser dans les couches de neige les plus denses. La dureté et la densité de la neige sont ainsi susceptibles d'influencer le mouvement des lemmings dans le manteau neigeux, mais on ignore encore les détails de cette relation.

Habitat hivernal et importance des combes à neige

Le manteau neigeux est un puissant isolant thermique et son isolation est fonction de son épaisseur totale ainsi que de la cohésion entre les grains de neige qui le compose. Un épais couvert de neige maintien des températures sous-nivales beaucoup plus élevées en limitant l'influence de la température de l'air ambiante et en limitant les pertes de chaleur du sol (Duchesne et al. 2011a, Reid et al. 2012). De ce fait, les lemmings sont davantage portés à

établir leur nid d'hiver dans les combes à neige, où le manteau neigeux y est le plus épais (Duchesne et al. 2011a, Reid et al. 2012, Bilodeau et al. 2013c). L'habitat hivernal le plus utilisé par les lemmings est ainsi associé à des éléments du paysage favorisant une plus grande accumulation de neige comme par exemple les fortes pentes, les dépressions ou les arbustes (Le Vaillant et al. 2018, Schmidt et al. 2021, Von Beckerath et al. 2021). L'épaisseur moyenne de neige semble également être reliée positivement à croissance hivernale des populations de lemmings, tel que suggère l'étude de Bilodeau et al. (2013a).

Un épais manteau neigeux, comme celui retrouvé dans les combes à neige, réduit également les risques de prédation par le renard arctique (Lindström and Hörnfeldt 1994, Bilodeau et al. 2013b). En effet, lorsqu'ils chassent en sautant à travers le manteau neigeux pour capturer leurs proies, les renards sont limités par l'épaisseur de ce dernier (Bilodeau et al. 2013b). L'épaisseur du manteau neigeux semble cependant n'avoir aucun effet sur le taux de prédation par l'hermine puisque celle-ci peut facilement pénétrer dans les tunnels creusés par les lemmings dans la neige (Gilg et al. 2009, Duchesne et al. 2011a). En début d'hiver, la neige s'accumule également plus rapidement dans les combes à neige qu'ailleurs dans la toundra (Pomeroy and Brun 1990). L'utilisation de cet habitat par les petits mammifères leur permettra donc de profiter d'un refuge précoce contre les prédateurs et le commencement des températures froides.

Rôle des micromammifères au sein de l'écosystème arctique

Dans l'Arctique, les micromammifères et en particulier les lemmings (genres *Lemmus* et *Dicrostonyx*) occupent un rôle essentiel au sein du réseau trophique de la toundra (Gauthier et al. 2011, Legagneux et al. 2012). Les lemmings sont les proies principales à la fois d'espèces résidant à l'année dans la toundra comme le renard arctique (*Vulpes lagopus*) et l'hermine (*Mustela erminea*), ainsi que d'espèces migratrices comme le harfang des neiges (*Bubo scandiacus*), le labbe à longue queue (*Stercorarius longicaudus*) et la buse pattue (*Buteo lagopus*) (Fig. 0.1; Gauthier et al. 2011). L'abondance de ces rongeurs influence fortement les populations de ses principaux prédateurs (Gilg et al. 2006, Therrien et al. 2014a, Chevallier et al. 2020). Par exemple, le succès reproducteur des harfangs chute drastiquement lors des déclins des populations de lemmings, tel que documenté à Traill Island au Groenland où la production de jeunes a diminué de plus de 98 % (Schmidt et al. 2012). À l'île Bylot,

dans l'Arctique canadien, les harfangs et buses pattues ne nichent tout simplement pas à ce site lors des années de faible abondance de lemmings (Therrien et al. 2014b, Beardsell et al. 2016).

Un déclin des populations de lemmings peut également entraîner des conséquences indirectes sur des espèces autres que leurs prédateurs (Legagneux et al. 2012). Par exemple, en réponse à une faible densité de lemmings, le renard arctique changera son régime alimentaire et augmentera son taux de prédation sur les nids d'oies des neiges (Bêty et al. 2002, Gauthier et al. 2004). Les limicoles aussi voient une baisse de leur succès de reproduction aux années de faible densité de lemmings, en raison d'une augmentation du taux de prédation, particulièrement par le renard arctique (Lamarre et al. 2017). En effet, lorsque les lemmings sont peu présents dans le paysage, le renard arctique semble parcourir davantage de distance à la recherche de ses proies, ce qui contribuerait à augmenter la probabilité de détecter les nids de ces oiseaux (Beardsell et al. 2021, 2022). Les proies secondaires des renards arctiques et autres prédateurs subiront ainsi une plus grande pression de prédation lorsque les lemmings se trouvent en faible nombre.

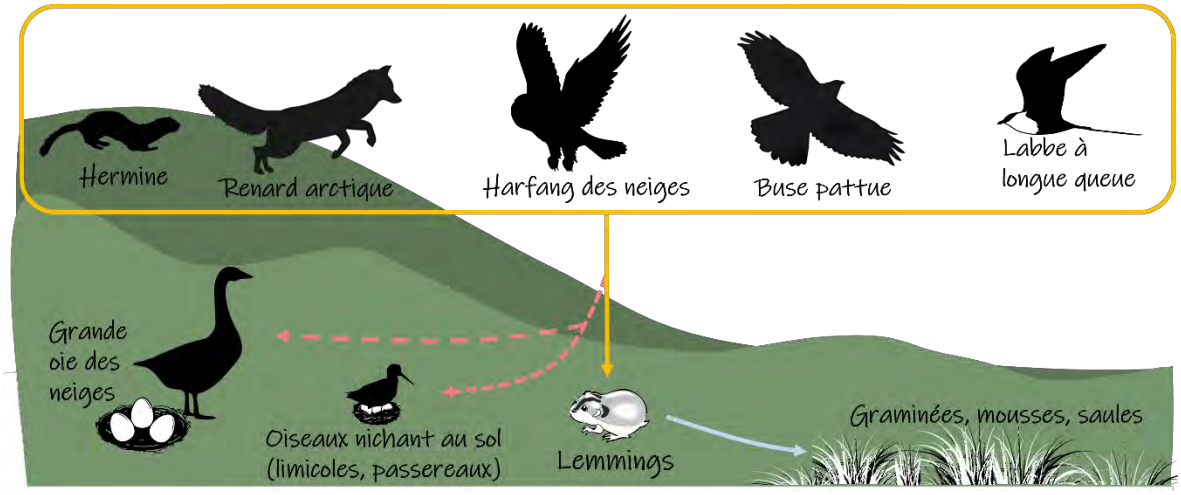

Figure 0.1 Schéma des principales interactions trophiques de l'île Bylot en lien avec les lemmings bruns (*Lemmus trimucronatus*) et les lemmings variables (*Dicrostonyx groenlandicus*), qui se nourrissent principalement de graminées, de mousse et de saules (Soininen et al. 2015, Fauteux et al. 2017). Les prédateurs clés tels que le harfang des neiges, la buse pattue et le labbe à longue queue sont présents uniquement en été, tandis que le renard arctique et l'hermine sont résidant à l'année (Gauthier et al. 2011). La grande oie des neiges et les oiseaux nichant au sol, tels les limicoles et les passereaux, sont des proies alternatives lorsque les lemmings sont moins abondants (Bêty et al. 2002, Lamarre et al. 2017). Les flèches indiquent le sens des interactions trophiques. Les flèches en pointillées indiquent les interactions indirectes.

Cycles de populations de lemmings en Arctique

Les cycles de populations sont un phénomène qui se retrouve chez plusieurs espèces animales et qui fascine bon nombre de chercheurs en dynamique des populations depuis très longtemps (Elton 1924, Korpimäki and Krebs 1996, Cornulier et al. 2013, Myers 2018). Les fluctuations cycliques de populations animales sont connues pour être plus importantes aux hautes latitudes comparativement aux régions tempérées (Hansson and Henttonen 1985). C'est le cas des populations de lemmings en Arctique qui connaissent d'importantes fluctuations cycliques (Krebs 1996, 2011, Fauteux et al. 2015). De façon traditionnelle, ces cycles sont expliqués par des limitations de type *Bottom-up* (c.-à-d. par la nourriture; Oksanen et al. 1981, Turchin et al. 2000) ou de type *Top-down* (c.-à-d. par la prédation; Krebs 1996, Fauteux et al. 2016b). Ces deux hypothèses n'expliquent cependant pas toute la variation dans les populations, suggérant l'intervention d'autres processus, tels que ceux en lien avec les conditions de neige (Fauteux et al. 2015).

Limitations de type Bottom-up

Selon l'hypothèse de contrôle *Bottom-up*, l'abondance ou la qualité de la nourriture déterminerait les cycles de population de petits mammifères (Oksanen et al. 1981, Seldal et al. 1994). Ce type de limitation peut être relié à la taille de la population elle-même (Krebs 2013). En effet, une densité élevée d'individus pourrait entraîner un surpâturage des végétaux, susceptible de causer un déclin des populations dû au manque de nourriture. Le couvert nival présent à l'hiver pourrait également intensifier ce type de limitation comme la végétation devient plus difficile d'accès (Korslund and Steen 2006), en particulier si un événement météorologique entraîne la formation d'une couche de glace au sol (Stien et al. 2012). Ainsi, lorsque les cycles d'abondance en Arctique sont principalement contrôlés par la nourriture, les déclins de populations devraient généralement avoir lieu en hiver lorsque l'accès à la nourriture est à son niveau le plus critique (Fauteux et al. 2015). Toutefois, dans l'Arctique canadien, le broutement hivernal des lemmings a peu d'impact sur la végétation même durant les années de pic d'abondance (Bilodeau et al. 2014), ce qui va à l'encontre d'un contrôle des cycles par la nourriture.

Limitations de type Top-down

Pendant longtemps, la pression de prédation dans la toundra était considérée trop faible pour permettre un contrôle de type *Top-down* en raison de la faible productivité primaire (Oksanen et al. 1981), mais de récentes études ont contredit cette idée (Gilg et al. 2003, Legagneux et al. 2012, 2014, Fauteux et al. 2016). La limitation de type *Top-down* stipule que ce serait principalement la pression de prédation qui contrôlerait les cycles de population des petits mammifères (Legagneux et al. 2012, Fauteux et al. 2016). Selon cette hypothèse, les déclins de population se produiraient à l'été ou à l'automne, soit lorsque l'abondance des prédateurs est la plus forte en raison de la présence de plusieurs espèces migratrices d'oiseaux de proie (Therrien et al. 2014a, Seyer et al. 2020). À l'automne, cette pression de prédation devient d'autant plus importante avec l'atteinte de l'indépendance des jeunes prédateurs qui pourront à leur tour effectuer de la prédation. De plus, au cours de l'été, les lemmings perdent le couvert protecteur offert par la neige, les rendant davantage vulnérables à la prédation (Gilg et al. 2009, Bilodeau et al. 2013b). La limitation de type *Top-down* est densité-dépendant puisque l'augmentation de la taille de la population de lemmings serait en grande partie responsable de l'augmentation du nombre de leurs prédateurs (Fauteux et al. 2016).

La reproduction hivernale

Un autre aspect pouvant avoir une grande influence sur la dynamique des populations de lemmings est la présence de reproduction hivernale (Fauteux et al. 2015). En effet, contrairement à la majorité des petits mammifères, les lemmings ont la capacité de se reproduire sous la neige pendant l'hiver (Millar 2001, Duchesne et al. 2011b). Lorsqu'elle a lieu, la reproduction hivernale permet à plusieurs générations de lemmings d'avoir la chance de maturer au cours de l'année et de se reproduire à leur tour, ce qui favorise une augmentation rapide de la population (Millar 2001, Fauteux et al. 2015). À l'inverse, des conditions rendant difficile, voire impossible, la reproduction des lemmings sous la neige pourraient avoir des conséquences négatives sur leur démographie (MacLean et al. 1974). Il est même avancé que la reproduction hivernale serait indispensable pour le maintien des populations de lemmings en Arctique puisqu'elle permet de compenser la baisse de population estivale due à la forte pression de prédation (Fuller et al. 1975, Gilg 2002). Toutefois, les conditions favorisant la reproduction hivernale des lemmings demeurent peu

connues, une lacune importante considérant que celle-ci pourrait être un élément clé pour expliquer leurs cycles de populations (Domine et al. 2018b).

Les conditions de neige

Dans les dernières décennies, une attention croissante a été portée au rôle des conditions de neige dans la dynamique des populations de micromammifères (Kausrud et al. 2008, Gilg et al. 2009, Bilodeau et al. 2013a, Domine et al. 2018b). Les épisodes de pluie-sur-neige et le durcissement du manteau neigeux qui en résulte ont été identifiés comme des sources de déclin chez les populations de lemmings et de campagnols (Aars and Ims 2002, Kausrud et al. 2008, Stien et al. 2012, Domine et al. 2018b). Des études suggèrent même que les effondrements observés dans les cycles de populations de petits mammifères en Scandinavie et au Groenland seraient reliés à ce durcissement de la neige (Ims et al. 2008, Kausrud et al. 2008, Schmidt et al. 2012). La formation d'une couche de glace au sol bloquant l'accès à la végétation et augmentant la mortalité lors d'événements extrêmes de pluie-sur-neige serait la principale explication de ces effets négatifs (Ims et al. 2008). Par contre, un autre mécanisme pourrait être via le durcissement de la neige lors d'événements plus modérés, ce qui augmenterait la dépense énergétique pour creuser dans la neige et diminuerait l'énergie disponible pour la reproduction hivernale.

Il a également été suggéré que la durée de la période d'enneigement modifierait la période et l'amplitude des cycles de rongeurs (Gilg et al. 2009). Par exemple, une neige tardive en début d'hiver augmenterait l'exposition des lemmings aux prédateurs, diminuant ainsi leur taux de survie (Gilg et al. 2009). Une neige tardive retarderait également la protection thermique qu'assure le manteau neigeux aux lemmings alors que les températures se font déjà froides (Reid and Krebs 1996). Avec les changements climatiques, le régime nival de l'Arctique sera fortement perturbé, soulignant l'importance qui doit être accordée dans l'étude de cette variable sur la dynamique des populations de rongeurs arctiques.

Propriétés physiques du manteau neigeux arctique

La neige est une matière hétérogène donc la composition varie autant à petite qu'à grande échelle spatiale, suivant généralement un gradient latitudinal (Sturm and Benson 2004, Royer et al. 2021). Ses propriétés physiques sont dynamiques et sont largement influencées par les

conditions météorologiques retrouvées en cours d'hiver; le manteau neigeux est ainsi sujet à d'importantes variations interannuelles (Sturm and Benson 2004, Domine et al. 2021a). Une connaissance approfondie des propriétés physiques du manteau neigeux est donc essentielle pour mieux comprendre l'impact de cette neige sur l'écologie hivernale de nombreuses espèces, tel le lemming, ce que peu d'études écologiques ont tenté d'intégrer jusqu'à maintenant.

Le manteau neigeux caractéristique de la toundra arctique est relativement mince, entre 15 – 40 cm, en raison des faibles précipitations et de la forte exposition au vent dans ce paysage dépourvu de végétation haute (Fig 0.2; Domine et al. 2012, Derksen et al. 2014). Les tempêtes de vents fréquentes contribuent à la compaction des grains de neige, formant les couches de neige ventées typiques pouvant atteindre des densités (ρ) très élevées (ρ = 350–488 kg m^{-3}; Domine et al. 2016b). Tout au long de l'hiver, le manteau neigeux arctique se modifie sous l'effet d'un métamorphisme par gradient de température (Marbouty 1980, Colbeck 1982). En raison de ce métamorphisme, les couches du bas perdent de la matière et forment généralement une couche friable nommée givre de profondeur, tandis que les couches supérieures demeurent plus denses (Fig. 0.2, Marbouty 1980).

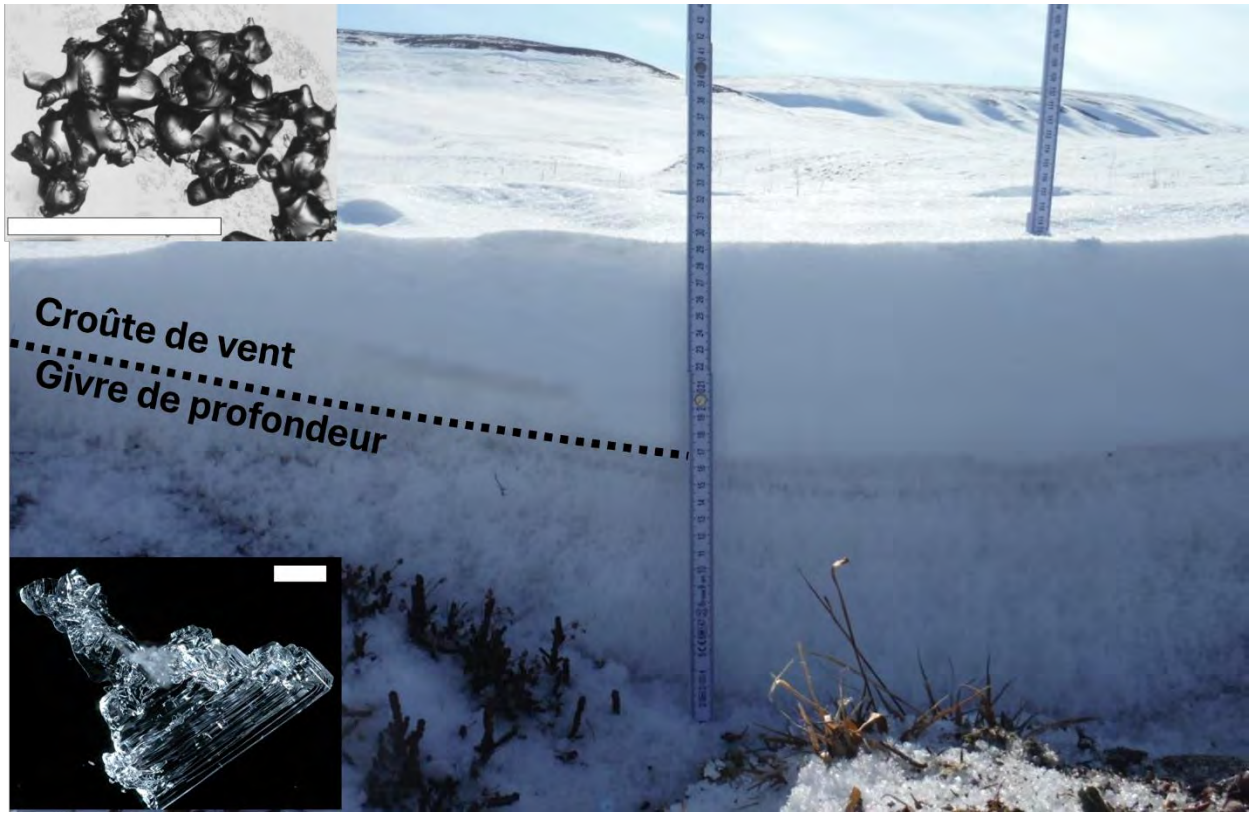

Figure 0.2 Coupe verticale d'un manteau neigeux arctique. Typiquement, la couche basale est formée de givre de profondeur friable, alors que les couches supérieures demeurent durcies. La miniature supérieure représente les grains ronds compactés retrouvés dans la croûte de vent alors que la miniature inférieure représente un exemple de cristal de givre de profondeur, également appelé gobelet. La barre d'échelle est de 1mm. Photos prises par Florent Dominé à l'île Bylot en mai 2015.

Formation du givre de profondeur

La formation du givre de profondeur nécessite la présence d'un gradient vertical de température élevé et durable dans le manteau neigeux (>20 °C/m), tel qu'on le retrouve habituellement dans les manteaux neigeux arctiques (Domine et al. 2018a). Peu après la première accumulation de neige, la température du sol demeure à 0 °C le temps que toute l'eau du sol gèle, alors que la température de l'air chute drastiquement, ce qui crée un gradient de température dans le manteau neigeux (Fig. 0.3a; Sturm and Benson 1997). Ce gradient de température induit un gradient de pression de vapeur d'eau étant donné que la pression de vapeur saturante de la glace augmente exponentiellement avec la température (Fig. 0.3b). Tout gradient provoque un flux, et il s'ensuit donc un flux de vapeur d'eau des couches chaudes, les couches basales du manteau neigeux, vers les couches froides, les couches supérieures (Fig. 0.3c). À l'échelle du grain de neige, le flux est alimenté par la sublimation

de la partie supérieure d'un grain, plus chaud que le grain situé au-dessus de lui, et par la condensation de cette vapeur d'eau sur la partie inférieure de ce dernier grain (Fig. 0.3d). Chaque grain de neige est donc à la fois source (sa partie supérieure) et puits (sa partie inférieure) de vapeur d'eau. Les rapports des flux de sublimation et de condensation sont tels que globalement, il y a un transfert net de vapeur d'eau des couches basales vers les couches supérieures. Ces processus ainsi répétés (c.-à-d. sublimation, diffusion et condensation) résulteront en la formation d'une couche basale de givre de profondeur de faible dureté en comparaison aux couches supérieures (Fig 0.3; Marbouty 1980).

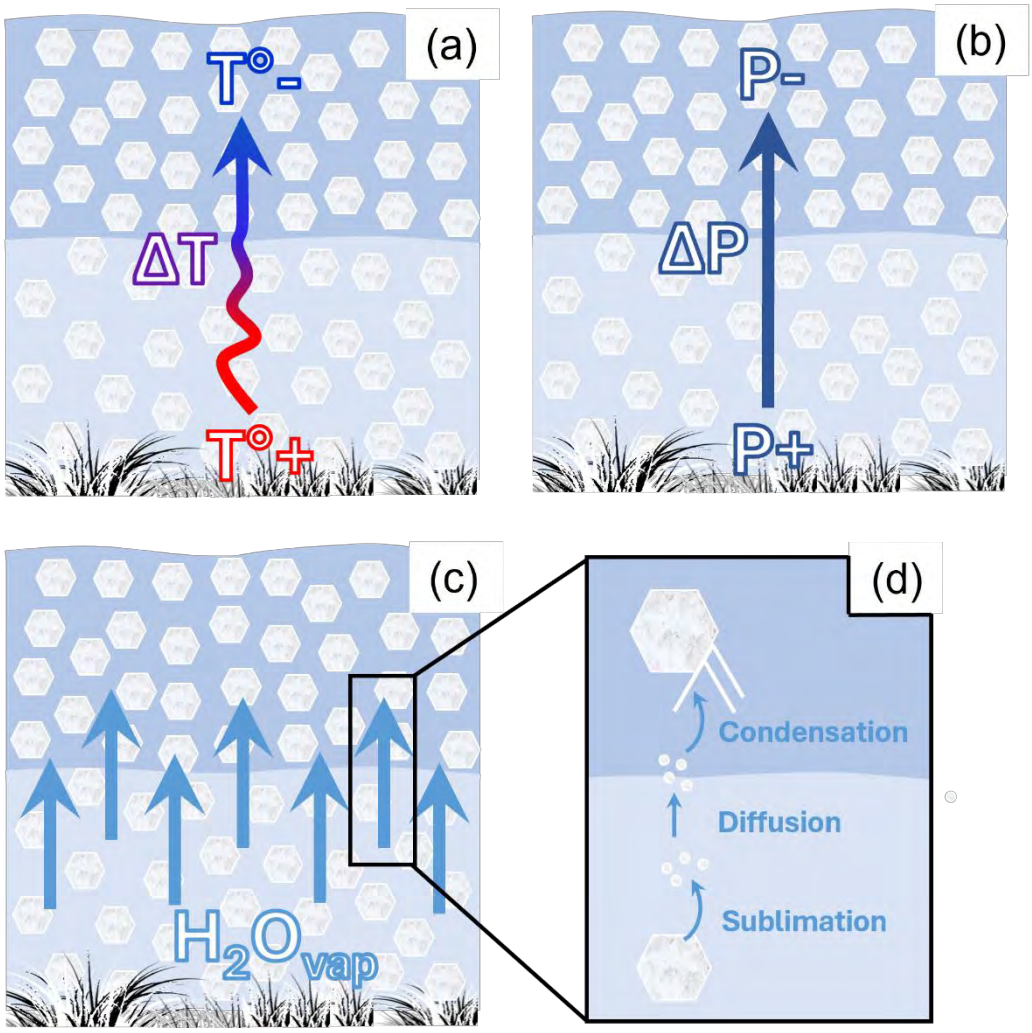

Figure 0.3 Principales étapes menant à la formation du givre de profondeur dans le manteau arctique. (a) Établissement d'un gradient de température dans le manteau neigeux en début d'hiver lorsque la température de l'air est plus froide que la température du sol. (b) Le gradient de température induit un gradient de pression de vapeur d'eau, du bas vers le haut du manteau neigeux. (c) Le gradient de pression de vapeur d'eau provoque un flux de vapeur d'eau du bas vers le haut du manteau neigeux,

c.-à-d. (d) à l'échelle du grain de neige, la sublimation de la partie supérieure des grains de neige, la diffusion verticale de la vapeur d'eau et la condensation sur la partie inférieure des grains de neige.

Propriétés de la couche basale de givre de profondeur

Un mince couvert de neige, une forte humidité du sol et des températures froides de l'air sont des conditions favorisant le gradient de température et ainsi le développement de givre de profondeur (Domine et al. 2018a). De plus, le type de neige dans lequel se formera le givre de profondeur déterminera partiellement la qualité de ce dernier. En effet, si les échanges de vapeur d'eau se produisent dans une couche de neige initialement friable et de faible densité (ρ), le givre de profondeur résultant sera lui aussi de faible densité (ρ = 130-250 kg m^{-3}; Domine et al. 2018a). À l'inverse, si ce processus survient au sein d'une couche plus dure issue d'une neige ventée ou d'une neige fondue-regelée, le givre de profondeur résultant sera induré et plus dur (ρ = 250 à > 350 kg m^{-3}; Domine et al. 2018a). La date d'enneigement influencera également les propriétés du givre de profondeur. En effet, si le sol n'est pas encore gelé lors de la première accumulation permanente, le gradient thermique du manteau neigeux sera amplifié, favorisant le développement d'un givre friable (Sturm and Benson 1997).

La neige possède de bonnes propriétés d'isolation thermique, pouvant isoler 20 fois plus efficacement que le sol (Domine et al. 2016b), et cela est d'autant plus vrai pour la couche de givre de profondeur (Sturm and Benson 1997). Le givre de profondeur est composé de larges cristaux creux ayant une faible cohésion entre eux, formant une couche de neige de faible densité et faible conductivité thermique (k_{eff}) (ρ ~ 200 kg m^{-3}, k_{eff} ~ 0.04 W m^{-1} K^{-1}; Domine et al. 2016b). Ces propriétés physiques confèrent au givre de profondeur une très bonne isolation thermique (Pomeroy and Brun 1990). Isolante et peu cohésive, cette couche de neige constitue ainsi un endroit idéal pour que de petits mammifères s'y abritent et s'y déplacent sans trop dépenser d'énergie (Domine et al. 2016b, Berteaux et al. 2017).

Combes à neige

Les combes à neige sont des zones où la topographie irrégulière (p. ex., bordure de rivière, rupture de pente ou dépression dans le sol) permet à la neige de s'accumuler tôt en saison en grande quantité via le transport et la redistribution de la neige par le vent (Lamare et al. 2023). Cette accumulation hâtive de la neige peut favoriser la formation d'un givre de profondeur

friable via le maintien d'un fort gradient de température vertical si le sol n'a pas encore gelé (Sturm and Benson 1997). Une neige épaisse assure de surcroit une bonne isolation thermique, ce qui en fait un habitat intéressant pour les petits mammifères à la recherche d'un abri contre les froides températures hivernales (Sanecki et al. 2006, Duchesne et al. 2011a, Reid et al. 2012, Von Beckerath et al. 2021). Cependant, un manteau neigeux devenant trop épais entraînerait une réduction du gradient vertical de température et ralentirait donc le développement du givre de profondeur qui pourrait demeurer plus dense (Marbouty 1980). Les combes à neige pourraient donc constituer un habitat idéal pour les lemmings, pour autant que les conditions favorisent le développement d'un givre de profondeur friable (Marbouty 1980, Domine et al. 2018a).

Arbustaies et manteau neigeux

Les régions recouvertes d'arbustes sont reconnues pour favoriser l'accumulation de neige (Domine et al. 2016a, Lamare et al. 2023). Alors que la plupart des végétaux du paysage toundrique sont de petite taille, les arbustes peuvent atteindre quelques dizaines de centimètres de hauteur. Ces arbustes érigés piègent alors la neige soufflée par le vent en plus de la protéger contre l'érosion éolienne (Sturm et al. 2001, Lawrence and Swenson 2011). Les arbustes limiteraient ainsi la compaction de la neige, favorisant la formation d'un givre de profondeur de faible densité en présence d'un gradient de température persistant (Domine et al. 2016a). Les arbustaies sont donc susceptibles de représenter un habitat favorable pour les petits mammifères à l'hiver bien que ceci ait été peu exploré jusqu'à maintenant.

Conditions climatiques en Arctique et changements en cours

Le climat du Haut-Arctique canadien se caractérise par des températures froides en hiver et des précipitations annuelles relativement faibles. Cependant, les études soulèvent déjà les impacts des changements climatiques sur ce vaste territoire, qui a connu un réchauffement quatre fois plus rapide que toute autre région du monde au cours des dernières décennies (IPCC 2022, Rantanen et al. 2022). Le phénomène d'amplification polaire, causé entre autres par la fonte de la glace de mer et le dégel du pergélisol, entraîne des rétroactions positives responsables de cette augmentation rapide de la température aux pôles (Pithan and Mauritsen 2014, Barnes and Polvani 2015).

Impact des changements climatiques sur la cryosphère

Les bouleversements climatiques en cours ont des conséquences sur la cryosphère arctique, telles une diminution de l'étendue du manteau neigeux ainsi qu'une réduction de la durée de neige au sol (Derksen and Brown 2012, AMAP 2017, IPCC 2022). Par exemple, selon l'AMAP (2017), la période d'enneigement en Arctique s'est raccourcie de 2 à 4 jours par décennie au cours des 40 dernières années. De même, la superficie recouverte de neige au printemps a connu une diminution d'environ 18 % par décennie au cours de cette même période (AMAP 2017).

L'augmentation des températures aura également pour conséquence d'augmenter les épisodes de fonte-regel (c.-à-d. la fonte partielle de la neige suivie d'un regel) et de pluie-sur-neige en hiver (Liston and Hiemstra 2011). Dans le Haut-Arctique canadien, le climat très froid et sec limite l'intensité de ces épisodes qui se traduisent généralement en la formation de couches de fonte-regel dans le manteau neigeux (Fig. 0.4a-b). La dureté et l'épaisseur de ces couches de regel dépendent de la quantité d'eau liquide qui se retrouve dans la neige avant de regeler, car la présence d'eau augmente les ponts entre les grains de neige (Liston and Hiemstra 2011). Cependant, dans d'autres régions arctiques où les interactions neige-micromammifères ont été étudiées, le climat est plus doux et ce type d'épisodes peut entraîner la formation de couches de glace au niveau du sol (p. ex. Svalbard et Norvège; Ims et al. 2008, Stien et al. 2012). En effet, une telle couche de glace se forme lorsque d'importantes précipitations liquides surviennent alors que le manteau neigeux est déjà formé et que le sol est déjà gelé. L'eau liquide percolant jusqu'à la base du manteau neigeux gèlera ainsi au contact du sol gelé (Fig. 0.4c-d; Peeters et al. 2019). Les épisodes de pluies verglaçantes, bien que rares pour le moment dans le Haut-Arctique (Roberts and Stewart 2008), pourraient également augmenter en fréquence avec les changements climatiques (Groisman et al. 2016). Ce phénomène survient lorsque des précipitations surfondues gèlent au contact d'une surface gelée, formant instantanément une mince couche de glace (Fig. 0.4e-f).

Rôle de la cryosphère en Arctique

Étant présente au sol pendant la majeure partie de l'année, la neige est une constituante fondamentale de l'écosystème arctique. Le manteau neigeux change complètement la

structure de la toundra et influence considérablement les processus physiques, climatologiques et biologiques à l'échelle de la planète (Callaghan et al. 2011). Par son albédo très élevé, la neige fraîche réfléchit plus de 80 % des rayons du soleil (Gardner and Sharp 2010), influençant ainsi le bilan radiatif de la planète (Atkinson et al. 2006). Puis, en agissant comme un refuge pour certains petits mammifères ou encore comme une barrière à la végétation pour les grands herbivores, la neige est également d'une grande importance pour la faune arctique (Rennert et al. 2009, Bilodeau et al. 2013a, Berteaux et al. 2017). Avec les bouleversements du climat et les conséquences anticipées sur la cryosphère arctique, il est primordial d'approfondir notre compréhension empirique des interactions entre la neige et les composantes biotiques et abiotiques de l'écosystème arctique.

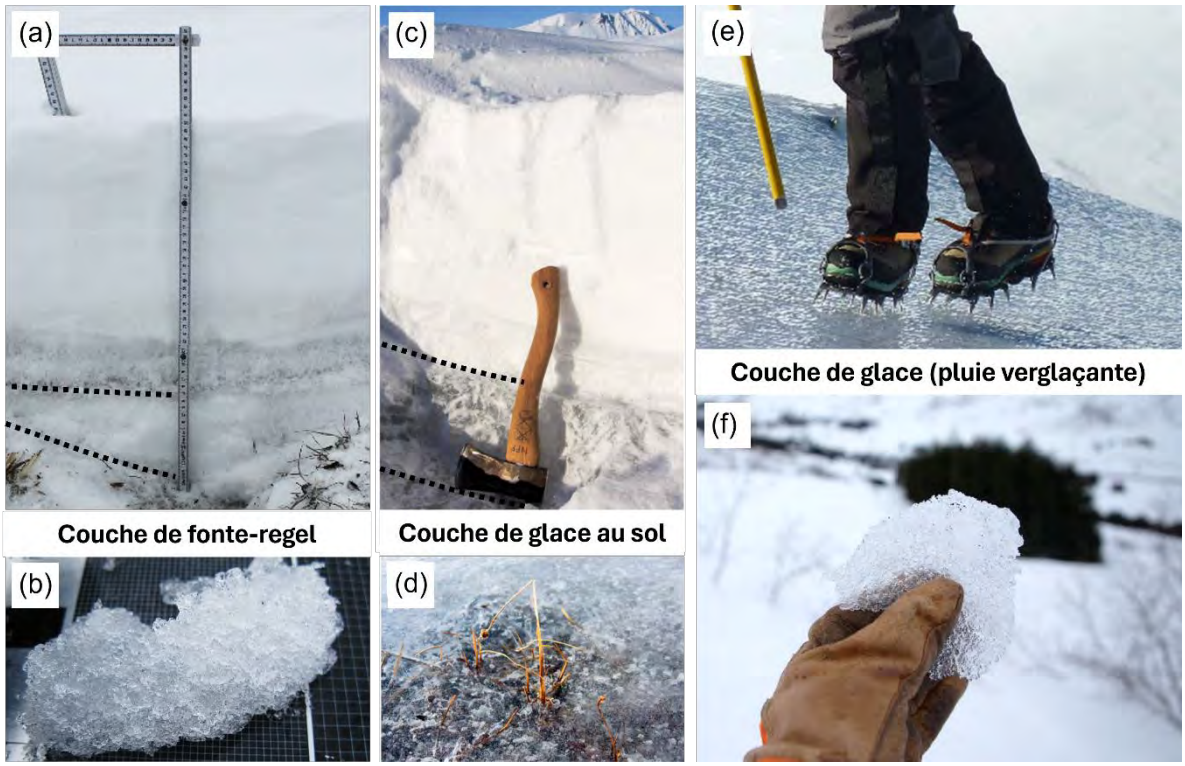

Figure 0.4 Photos de différents types de durcissement de la couche basale de neige. (a-b) Couche de fonte-regel engendrée par un épisode de fonte-regel ou de pluie-sur-neige modéré, typique du climat du Haut-Arctique canadien. (c-d) Couche de glace au sol formée après un important événement de pluie-sur-neige, typique du climat du nord de la Norvège et du Svalbard. (e-f) Couche de glace formée après un important épisode de pluie verglaçante. Photo (a) prise à l'île Bylot au Nunavut en 2017. Photo (b) provenant de la librairie des grains de neige du *CNR Institute of Polar Sciences*. Photos (c-d) prises au Svalbard et modifiées de Peeters et al. (2019). Photo (e) prise en 2012 dans la chaîne de montagnes des Pyrénées et modifiée de Quéno et al. (2018). Photo (f) de *Chugach National Forest Avalanche Information Center*.

Système d'étude

L'île Bylot, situé au Nunavut, est caractérisé par un climat froid et sec typique du Haut Arctique, avec des températures moyennes de -36.7 °C en février et un manteau neigeux d'épaisseur moyenne de 31 cm (Domine et al. 2021b). Deux espèces de lemmings occupent ce site, soit le lemming brun (*Lemmus trimucronatus*) et le lemming variable (*Dicrostonyx groenlandicus*) (Gauthier et al. 2011). Les travaux de Gruyer et al. (2008) ont permis de documenter les fluctuations cycliques de ces deux espèces à ce site. Alors que le lemming variable semble avoir des fluctuations de sa population de faible amplitude, le lemming brun tend à avoir une explosion très rapide, suivie d'une période de déclin de 1 à 3 ans, et ce de façon périodique (Gruyer et al. 2008, Fauteux et al. 2015). Cette différence démographique entre les deux espèces pourrait être reliée au fait que le lemming brun serait plus compétitif et plus agressif par rapport au lemming variable (Morris et al. 2000). De plus, le lemming variable semble être plus vulnérable à la prédation en comparaison avec le lemming brun (Seyer et al. 2020). En période estivale, le lemming brun utilise particulièrement les habitats humides et s'alime de mousses et de graminées, tandis que le lemming variable utilise davantage les habitats secs dominés par les plantes herbacées (Batzli et al. 1983). À l'hiver, il semble y avoir un chevauchement dans le régime alimentaire des deux espèces, puisque toutes deux s'alimentent en grande partie de bourgeons et de racines de saules (Soininen et al. 2015, Fauteux et al. 2017).

Les adaptations à la vie hivernale diffèrent entre les deux espèces. Alors que le lemming brun garde un pelage similaire tout au long de l'année, le lemming variable passe du gris au blanc pour la période hivernale (Zimova et al. 2018). Les pattes du lemming variable s'élargissent également pendant la période hivernale, ce qui semble être une adaptation au creusage dans la neige (Hansen 1957). D'ailleurs, des observations anecdotiques suggèrent que le lemming variable aurait plus de facilité à creuser dans les couches de neige dures en comparaison au lemming brun (Pruitt 1984).

Objectifs de la thèse

Cette thèse a pour but d'examiner l'impact des propriétés physiques de la neige sur les populations de lemmings dans le Haut-Arctique canadien (Fig. 0.5). Nous avons également cherché à vérifier si ces effets diffèrent entre les deux espèces de lemmings. À l'île Bylot,

Nunavut (73°08 N, 80°00 O), un suivi à long terme de près de 30 ans de cet écosystème a permis la création d'un important jeu de données permettant d'élargir nos connaissances de l'écologie arctique (Domine et al. 2021a, Bergeron et al. 2023, Gauthier et al. 2023). Ayant accès à des données à long terme de suivi des populations de lemmings, de variables météorologiques ainsi que des conditions de neige (Gauthier 2020, Domine et al. 2021b, CEN 2022), ce site d'étude nous a semblé idéal pour aborder cette question de recherche.

Comme la plupart de la recherche en Arctique s'effectue à l'été pour des contraintes logistiques, la grande majorité des études sur les lemmings se sont concentrées sur leur écologie estivale (Fauteux et al. 2018, Ehrich et al. 2020). Considérant que les lemmings passent environ les trois quarts de leur vie sous la neige, il nous a semblé nécessaire de pallier le manque de connaissance de leur écologie à l'hiver en documentant cette période critique de leur cycle de vie. De plus, avec le durcissement anticipé du manteau neigeux arctique en réponse aux changements climatiques, il devient encore plus important de mieux comprendre les relations entre les lemmings et leur habitat hivernal. Les lemmings sont un maillon essentiel dans le réseau trophique de l'Arctique et un bouleversement de leurs populations pourrait entraîner des répercussions sur leurs prédateurs ainsi que sur plusieurs autres espèces de l'écosystème (Bêty et al. 2001, Gilg et al. 2006, Lamarre et al. 2017).

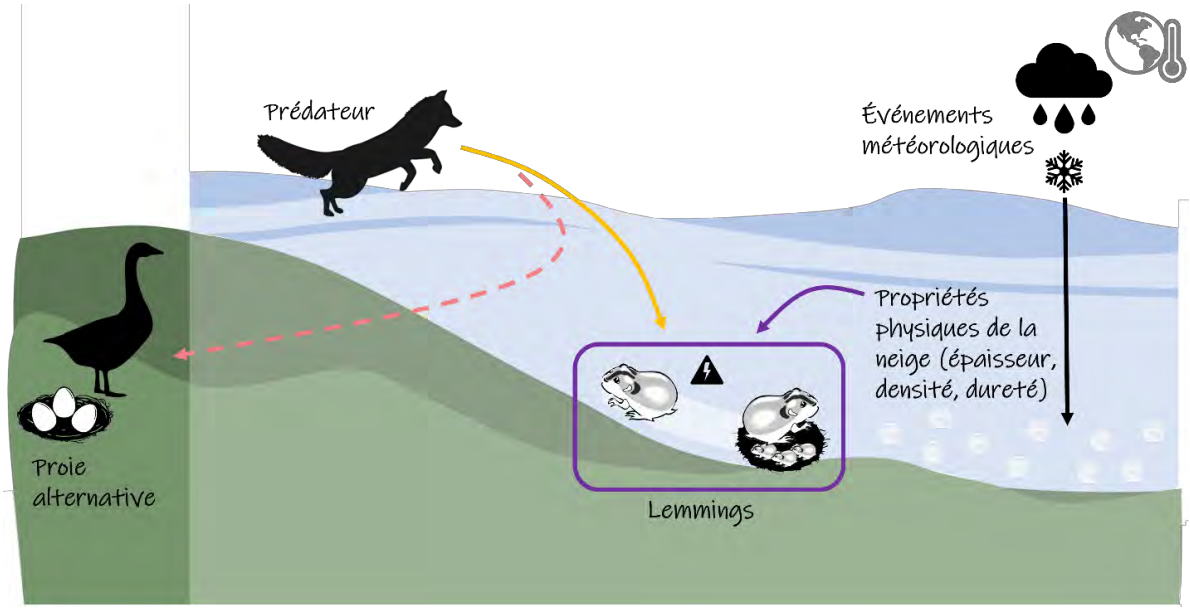

Figure 0.5 Schéma illustrant la problématique abordée dans la thèse. Avec les changements climatiques, de plus en plus d'événements météorologiques pourraient perturber les propriétés physiques de la neige en Arctique (épaisseur du couvert nival, densité et dureté de la neige). Les

lemmings passent l'hiver dans le manteau neigeux, où ils creusent des tunnels pour se déplacer et construisent des nids dans lesquels ils peuvent se reproduire. Des modifications du manteau neigeux pourraient négativement influencer les populations de lemmings. Une diminution des effectifs de lemmings pourrait affecter leurs prédateurs, en plus d'entraîner une hausse de la mortalité chez les proies alternatives aux lemmings. Les flèches indiquent le sens des relations et celle en pointillé indique une relation alternative.

Le premier chapitre de cette thèse a pour objectif de documenter le déplacement des lemmings dans le manteau neigeux. Il était traditionnellement supposé, sans validation empirique, que ces petits mammifères se déplaçaient uniquement dans les couches basales de neige directement au niveau du sol, où se trouve leur nourriture. Nous avons voulu tester cette hypothèse par l'observation et la caractérisation de tunnels de lemmings trouvés à même le manteau neigeux, une démarche qui n'avait jamais été entreprise auparavant. Nous avons également voulu tester l'hypothèse que les lemmings creusent préférentiellement dans la couche basale la plus friable, le givre de profondeur, afin de faciliter les déplacements.

Le second chapitre est une suite au premier et vise à approfondir les connaissances de l'impact des propriétés physiques de la neige sur le comportement de creusage des deux espèces de lemmings dans la neige. Pour ce faire, nous avons exposé des lemmings à des neiges de différentes propriétés physiques afin de mesurer leur réponse comportementale lors d'expériences en conditions contrôlées. Nous avons principalement cherché à vérifier qu'une augmentation de la dureté de la neige impacterait négativement la vitesse de creusage et la longueur des tunnels creusés, et augmenterait l'effort déployé pour le creusage.

Le troisième chapitre a pour objectif de documenter l'utilisation de l'habitat des lemmings à fine échelle spatiale durant l'hiver ainsi que leur reproduction en relation avec les propriétés physiques de la neige. Nous nous sommes intéressés aux variations de la densité de nids d'hiver de lemming et de la proportion de nids avec signes de reproduction dans les quatre principaux habitats retrouvés à notre site d'étude (mésique, humide, riverain et arbustaie) chez les deux espèces de lemmings. Nous voulions vérifier si l'utilisation de l'habitat et le taux de reproduction seraient positivement influencés par l'épaisseur de la neige, puisque cela favorise une meilleure isolation thermique, ainsi que par une couche basale de neige friable, laquelle facilite les déplacements des lemmings dans la neige.

Finalement, le quatrième chapitre documente l'impact des propriétés physiques de la neige sur les paramètres démographiques des lemmings, plus spécifiquement sur leur reproduction hivernale ainsi que sur la croissance de leur population en hiver. Par cette analyse temporelle, nous souhaitions vérifier si les paramètres démographiques des deux espèces de lemmings seraient favorisés par un enneigement hâtif, par un épais manteau neigeux tôt en saison et par une faible fréquence d'épisodes météorologiques menant au durcissement de la couche basale de neige en début d'hiver.

Chapitre 1 – What guides lemming movements through the snowpack?

Référence de la publication :

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

1.1 Résumé

La présence d'un manteau neigeux, qui peut durer jusqu'à 9 mois en Arctique, assure une protection contre le froid pour certains petits mammifères qui s'y abritent pendant l'hiver, tels les lemmings. Cette neige est également susceptible d'affecter leurs mouvements, mais l'endroit exact où les lemmings creusent dans la neige pour se déplacer demeure peu connu. Nous avons donc testé (1) si les lemmings creusent toujours au niveau du sol, près de la végétation dont ils se nourrissent et (2) s'ils choisissent la couche la plus friable pour creuser, reconnue pour être le givre de profondeur dans le manteau neigeux arctique. Nous avons trouvé 33 tunnels de lemmings en 2017 et 2018 en creusant dans la neige à des sites d'attaques de renards sur des lemmings. Nos résultats contredisent notre première hypothèse, car presque tous les tunnels étaient plus haut que le niveau du sol (32/33), probablement en raison de la présence d'obstacles (c.-à-d. couches de fonte-regel et hummocks) dans les couches basales du manteau neigeux. En revanche, nos résultats soutiennent notre deuxième hypothèse puisque les tunnels étaient tous creusés dans le givre de profondeur qui avait une densité plus faible que les couches supérieures et inférieures. Les tunnels de lemmings étaient aussi souvent creusés à la limite supérieure du givre de profondeur, tout juste sous une couche plus dure. Creuser dans la couche de neige la moins dense pourrait être une stratégie des lemmings pour minimiser leurs dépenses énergétiques, ce qui pourrait augmenter leurs chances de survie et de reproduction en hiver.

1.2 Abstract

The presence of a snowpack, which may last up to 9 months in the Arctic, can provide insulation from the cold winter temperature for small mammals living beneath it, such as lemmings. Since lemmings have to move through the snowpack during that period, it is important to better understand how the physical properties of snow affect the way they dig tunnels. Here, we tested 1) whether lemmings systematically dig in the snowpack at the ground level where they can find their food plants, and 2) whether they choose the softest snow layer in which to dig, which is usually the depth hoar layer in the Arctic snowpack. We found 33 lemming tunnels in 2017 and 2018 by digging through the snow at the sites of arctic fox attacks on lemmings. Contrary to our expectation, almost all the tunnels (32/33) were found to be higher than ground level, probably because of the presence of obstacles (i.e., melt-freeze crusts or hummocks) at the base of the snowpack. As predicted, all tunnels were dug in the soft depth hoar layer, which had a lower density than snow layers below and above it. Lemmings also showed a preference to dig their tunnels at the top of the depth hoar, just below a hard snow layer. Systematically digging their tunnels in the lowest-density snow layer, regardless of its height in the snowpack, could be a strategy for lemmings to minimize energy expenditure, which could improve their survival and chances of reproducing in winter.

1.3 Introduction

Winter is a difficult period for arctic and boreal wildlife. During that period, some species enter into a dormant mode or migrate to avoid the lack of food and the cold. Other species remain active all winter long and have to cope with an environment covered by snow for up to 9 months at high latitudes. Indeed, the snow cover dramatically affects all vertebrates during winter, either those living above the snow, such as large herbivores, or those living under it, such as small mammals (Rennert et al. 2009; Bilodeau et al. 2013a; Berteaux et al. 2017).

Lemmings are small mammals that remain active and can even reproduce under the snow throughout the arctic winter (Millar 2001; Duchesne et al. 2011). These species undergo multi-annual cyclic population fluctuations of large amplitude. In the High Arctic, irruptions typically start during the winter (Krebs 2011; Fauteux et al. 2015), suggesting that events occurring during winter can have a strong impact on their population dynamics. Lemmings use tunnels in snow to avoid predators, find mates, and access vegetation for feeding and building nests for shelter and reproduction (MacLean et al. 1974; Stenseth et Ims 1993; Sanecki et al. 2006). In the treeless tundra, lemmings find their food (herbaceous plants, mosses, and prostrate shrubs; Batzli and Jung 1980; Soininen et al. 2015) at the ground level in winter. Some studies have suggested that the physical properties of the snow basal layer could play a role in winter population growth of lemmings in the High Arctic (Bilodeau et al. 2013a; Domine et al. 2018b). The mechanisms behind this are still unclear but we can presume that it is related to the ability of the lemmings to move, access food, and reproduce under the snow. For example, a hard basal snow layer should increase the energy spent to dig tunnels to move around, which could reduce the energy available for reproduction. The snow also plays an important role in thermal insulation and protection against predators, which explains why lemmings usually choose the deepest part of the snowpack to build their nests (Duchesne et al. 2011).

The Arctic snowpack is generally comprised of a hard wind slab layer on top and a soft depth hoar layer at the base (Domine et al. 2002). Depth hoar is formed by the strong vertical temperature gradient present in the snowpack at the beginning of winter (Sturm and Benson 1997; Domine et al. 2018a). When the basal snow layers are not affected by wind-drifting,

depth hoar is composed of large, hollow faceted snow crystals loosely bound together, which form a layer of low density, ρ, and low thermal conductivity, k_{eff}, (ρ = 130 - 250 kg m^{-3}, k_{eff} = 0.025 - 0.1 W m^{-1} K^{-1}; Sturm et al. 1997; Domine et al. 2015, 2016b). However, when basal layers are deposited in the presence of a strong wind, which is frequent on the arctic tundra, those layers transform into a much harder kind of depth hoar, called indurated depth hoar (ρ = 250 to > 350 kg m^{-3}, k_{eff} = 0.05 to > 0.3 W m^{-1} K^{-1}; Domine et al. 2018a). Similarly, temperature oscillations around 0 °C during initial build-up of the snowpack or rain-on-snow events lead to the formation of a hard basal melt-freeze crust (ρ = 360 to > 480 kg m^{-3} and k_{eff} = 0.11 to > 0.4 W m^{-1} K^{-1}; Sturm et al. 1997). The properties of these crusts strongly depend on the amount of liquid water that formed in them and, given sufficiently high temperature gradients, they may transform into indurated depth hoar. Melt-freeze crusts are more likely to form in topographic depressions such as hummock hollows, which are the first to fill with snow in early winter. A soft, low-density depth hoar most likely provides optimal conditions for lemmings to dig a network of tunnels in the snow. Because the depth hoar typically forms near the ground, where lemmings can find their food, it has been assumed that these animals dug in the snowpack at ground level (Berteaux et al. 2017). However, the presence of indurated depth hoar or melt-freeze layers should increase the energy required by lemmings to dig tunnels and result in unfavorable conditions for them (Pruitt 1984).

Several studies have examined the movements of small fossorial mammals in burrows dug into the ground (Vleck 1979; Etienne et al. 1986; Hatough 1990; Kimchi and Terkel 2001). However, almost no study has examined the movements of small mammals in tunnels dug into the snowpack apart from anecdotal observations (Sutton and Hamilton 1932; Pruitt 1984). Yet, this information is critical to better understand how physical properties of snow can affect small mammal population dynamics at high latitudes. In this study, we examined the strategy used by lemmings to dig their tunnels in the snowpack in relation to its physical properties. We tested two hypotheses with respect to the movements of lemmings in the snow. First, we hypothesized that lemmings would dig their tunnels in the snow to maximise energetic intake in winter. Based on this, we predicted that they would predominantly move at the ground level, where they can find their plant food in the tundra. Second, we hypothesized that lemmings would minimize their energetic cost while digging. Based on this, we predicted that most tunnels should be found in the softest layers of the snowpack.

1.4 Methods

1.4.1 Study area

Study site was located in the Qarlikturvik valley of Bylot Island, Nunavut (73°08'N, 80°00'W). Vegetation in the valley consisted of mosses and graminoids in wet lowlands and prostrate shrubs, herbaceous plants and mosses in upland mesic habitat (Gauthier et al. 1996; Duchesne et al. 2011). In the mesic habitat, the ground was characterized by the presence of hummocks that creates a rugged microtopography, which impacts the accumulation pattern of the first snow on the ground (Domine et al. 2016a).

Two species of small mammals are found on the island: the brown lemming (*Lemmus trimucronatus*), which is the most abundant, and the collared lemming (*Dicrostonyx groenlandicus*). Both species are widespread in the Arctic, although the range of collared lemmings extends further north than that of the brown lemming, up to the northernmost arctic landmasses (Jarrell and Fredga 1993). The collared lemming is also considered more apt to dig in hard snow than the brown lemming due to its enlarged fore claw (Sutton and Hamilton 1932; Fuller et al. 1975). Although the brown lemming tends to prefer wet habitats and the collared dry habitats, both species can use the same habitat, especially in mesic tundra. Therefore, there is a high overlap in the diet of the two species at our study site. In winter, both species feed mostly on *Salix* and, in a small proportion, on *Poaceae*; in addition, the brown lemmings also feed on mosses, but the collared lemming does not (Soininen et al. 2015).

Since 1994, instruments have been deployed at our study site to record meteorological data year-round (CEN 2022). In this area, winter lasts for almost 9 months and the mean temperature in February, the coldest month, averages -39.2 °C (Gagnon et al. 2004). The first accumulation of snow on the ground generally takes place in late September−early October (Domine et al. 2018b) and the snowpack lasts until June.

1.4.2 Characterization of lemming tunnels

In early spring 2017 and 2018 (11 to 31 May), before the snow started to melt, we dug snow pits at 13 different sites used by lemmings (10 in 2017, 3 in 2018; the low number in 2018 was due to a crash in lemming populations). We traveled on snowmobiles to find signs of

attacks on lemmings by artic foxes (*Vulpes lagopus*) through the snowpack. Foxes can hear lemmings under the snow and attack them by digging or jumping through the snow (Bilodeau et al. 2013b). Holes left by fox attacks are thus an indicator of the presence of lemmings. All our snow pits, except one, were dug in sites where there was a fox attack. This method could have favored lemming tunnels in shallower snowpacks where fox attacks may be more likely (Lindström and Hörnfeldt 1994; Bilodeau et al. 2013b), but this should not affect our results since we were interested in the relation between tunnels and the basal layers of the snowpack.

We dug snow pits at each site down to the ground level. Snow pits were typically 1 m by 2 m with a mean depth of 51 cm (range: 25–146 cm). We found 30 different lemming tunnels in those pits in 2017 but only three in 2018. One of the three tunnels of 2018 was found after following lemming tracks above the snow. The presence of winter nests was noted and the species using the tunnel was determined based on their feces when present, a highly reliable method (Soininen et al. 2015). Collared lemming feces are dark reddish, about 4–6 mm long, blunt at one end and rather pointed at the other end, whereas brown lemming feces are green, about 6–10 mm long and rounded at both ends (Duchesne et al. 2011). We measured the minimal and maximal heights above the ground of each tunnel, and we determined the snow type in which they were dug. The most common types of snow found in the Arctic snowpack, in their typical decreasing order of hardness, are: wind crust, melt-freeze polycrystals, rounded grains, indurated depth hoar, faceted crystals, and depth hoar (Sturm et al. 1997; Fierz et al. 2009). We measured the maximal height of the snow layer in which the tunnel was dug to determine in which part of this layer the lemming had excavated. When a melt-freeze layer was present at the ground level, the maximal height of this layer was also noted (Fig. 1.1).

Distances between pits ranged from 1 to 4,000 m. In a given pit, several tunnels were often found because lemmings dig tunnel networks. Sometimes, it was possible to observe fox tracks above the snowpack following a lemming under the snow for 1 to 10 m. In that case, several pits were dug to sample different parts of the lemming tunnel network, but these pits were considered to be located at the same site. Thus, a site can be composed of one snow pit or more, and one or several tunnels can be found at a given site.

For two of the three tunnels found in 2018, the pits were enlarged to follow each tunnel longitudinally in the snow to examine spatial variation. These two tunnels were followed for 6 and 10 m in the snow, respectively, and we characterized the tunnels every 0.5 m by measuring the minimal and maximal height of tunnels and of the depth hoar.

1.4.3 Measurement of physical properties of snow

In eight of the 10 different sites sampled in 2017, we measured the physical properties (density and thermal conductivity) of different snow layers for one selected tunnel. Measurements were made in three layers of interest: the layer in which a tunnel was found, the layer immediately below the tunnel layer (when present) and the layer immediately above the tunnel. For both tunnels followed longitudinally in 2018, we measured snow physical properties every 1 m for the same three layers of interest. A visual stratigraphy of the snowpack was done at each site before performing the measurement to delimit all the different snow layers.

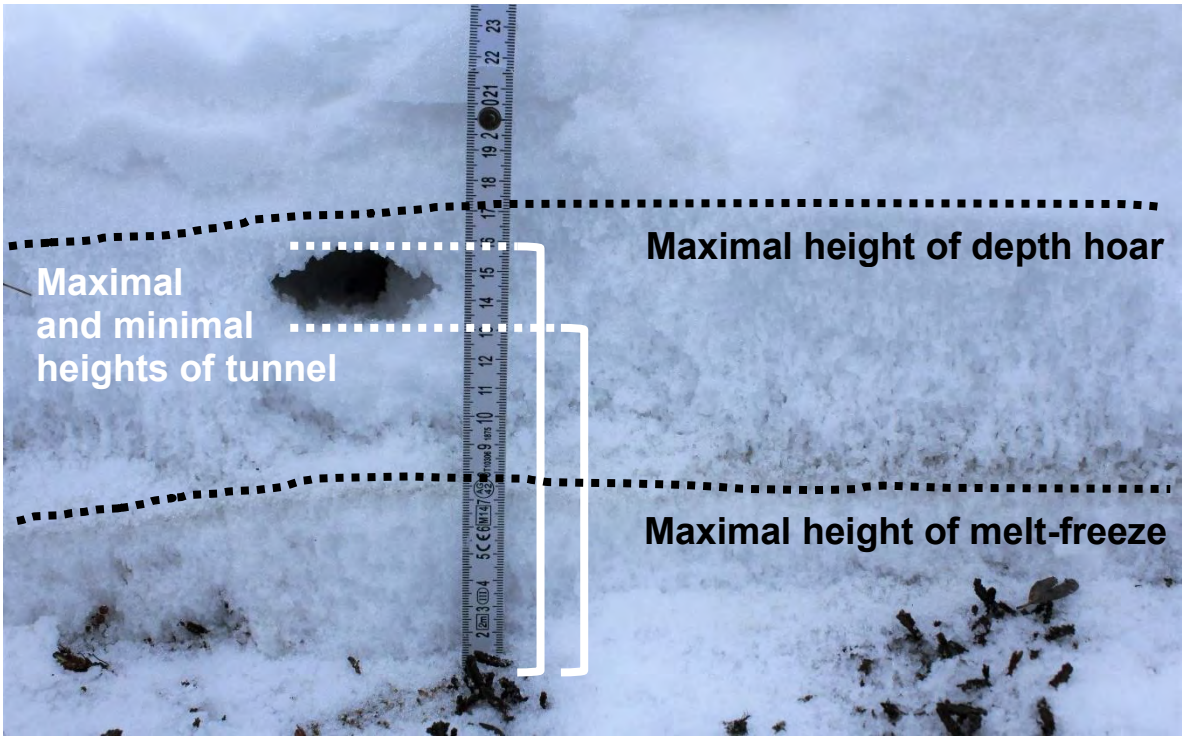

Figure 1.1 Example of measurements taken in a snow pit when a tunnel of lemming was found. Maximal heights of the depth hoar and melt-freeze layers (when present) and maximal and minimal heights of tunnels were taken.

To measure snow density, we sampled a fixed volume of snow with a 100-cm^3 box-cutter (Conger and McClung 2009). We measured snow thermal conductivity with a TP02 heated needle probe from Hukseflux (Hukseflux Thermal Sensors, Delft, The Netherlands), following the method of Domine et al. (2011). Briefly, the needle inserted in the snow was heated with a constant power during 100 s and the temperature at the center of the needle was recorded. Knowing that the rate of heat dissipation depends on the thermal conductivity of the environment, the plot of the temperature in the middle of the needle as a function of the logarithm of time is inversely proportional to the thermal conductivity (Morin et al. 2010; Domine et al. 2011). It is also possible to estimate the shear strength of a snow layer, influenced by its hardness, from its density and thermal conductivity (see calculations in Domine et al. 2011). Density and shear strength are two variables of interest to better understand lemming movements in the snow. The density of a snow layer is representative of the quantity of material to be displaced while shear strength represents the level of difficulty to dig in the layer.

1.4.4 Statistical analyses

To assess how snow layers affect the position of lemming tunnels in the snowpack, we examined the relationships between minimal or maximal height of tunnels and maximal height of melt-freeze (when present) and depth hoar layers. We used both linear and second-degree polynomial relationships to test for the presence of a threshold effect. In our analysis, we assumed there was a dependence between the tunnels that were found in the same site, since they were most likely dug by the same lemming. To account for that, we used linear mixed models with site as random variable. The approximate amount of variation explained by the fixed factors (marginal R^2, R^2_m) and both the fixed and random factors (conditional R^2, R^2_c) in our model was calculated following Nakagawa and Schielzeth (2013). Due to low sample size, we could not perform the statistical analysis separately for each lemming species.

To assess how snow physical properties affect the position of lemming tunnels in the snowpack, we examined differences in snow density, thermal conductivity, and shear strength between the layer used to dig tunnels and layers under or above tunnels. We used paired Student's t tests to take into consideration the spatial variation of snow properties. For

the analysis of shear strength, square root or logarithm transformations were used to improve normality of the data. When data did not conform to normality even with transformations, a Wilcoxon signed-rank test was performed. We only used data from pits sampled in 2017 due to inter-annual differences in physical properties of snow.

To determine spatial variations in physical properties of snow along tunnels, we analysed separately the two tunnels sampled longitudinally in 2018. Differences in density, thermal conductivity, and shear strength between layers were also tested with paired Student's t-tests. Means are presented with standard error (SE) throughout.

1.5 Results

Among the 33 lemming tunnels found in 2017 and 2018, only one was dug at ground level (i.e., a minimal height of 0 cm). Brown lemming feces were found in 13 tunnels, collared lemming feces in 10, and species identification was not possible at 10 others because there were not enough feces. We never found feces of the two species in the same tunnel although both species are known to use the same winter nests occasionally (Duchesne et al. 2011).

Among the eight tunnels where physical properties of snow were measured in 2017, four of them led to a lemming nest made of dead vegetation (see Supplementary Material S1.1 Fig. S1.1 for a picture example). None of the nests were located at the ground level and the minimal height of the base of the nests was 10.3 ± 3.8 cm (n = 4). The snow layers below the nests were hard melt-freeze or indurated depth hoar layers and those above were either a hard melt-freeze or wind slab layers.

1.5.1 Annual variation in physical properties of snow

In 2017, a melt-freeze basal layer was found at some sites due to melt-freeze events that occurred in fall 2016. The mean density of the snow basal layer was 326 ± 10 kg m^{-3} (n = 8) and its mean thermal conductivity 0.071 ± 0.010 W m^{-1} K^{-1} (n = 6; measurements unavailable at two sites due to microtopography).

In 2018, traces of induration in the basal layer were found in one pit but no melt-freeze crust similar to that in 2017 was found. In the first pit sampled, the mean density and thermal conductivity of the basal layer were 231 ± 18 kg m^{-3} and 0.051 ± 0.008 W m^{-1} K^{-1},

respectively (n = 8 longitudinal measurements), and in the second pit sampled, 181 ± 6 kg m^{-3} and 0.038 ± 0.003 W m^{-1} K^{-1} (n = 6). See Supplementary Material S1.1 Figs. S1.2-S1.3 for examples of typical profiles of snow pits from 2017 and 2018.

1.5.2 Relation between tunnels and snow layers

All lemming tunnels monitored (n = 33) were dug horizontally in the depth hoar layer. However, in 2017, we opportunistically found at the same site two collared lemming tunnels that were apparently dug in a layer harder than the soft depth hoar layer: one in a fine-grain layer and the other in an indurated depth hoar layer. Unfortunately, no snow measurements were taken at that site.

In 2018, we followed a lemming track above the snow for 2 km. Along the way, the lemming dug many holes (15 to 20) in the snow that was ~ 40 cm deep in the area, apparently sampling the snowpack. Eventually, the animal reached a snowdrift 80 cm deep where it entered the snowpack and crossed hard snow layers to finally reach the soft depth hoar layer and continue digging a horizontal tunnel through it (Fig. 1.2).

When melt-freeze layers were present at the ground level, we found a strong positive linear relationship between the heights of tunnels in the snowpack and the maximal height of melt-freeze layer (Fig. 1.3A). All tunnels were positioned at or above the 1:1 line on the graph, which indicates that tunnels were always dug above the melt-freeze layer when present, regardless of the thickness of this layer.

Figure 1.2 Left: lemming tracks on the snow followed for ~ 2 km in spring 2018. Right: vertical lemming tunnel at the end of the tracks crossing different snow layers (faceted crystals, rounded grains, wind crust) and continuing horizontally in the soft depth hoar.

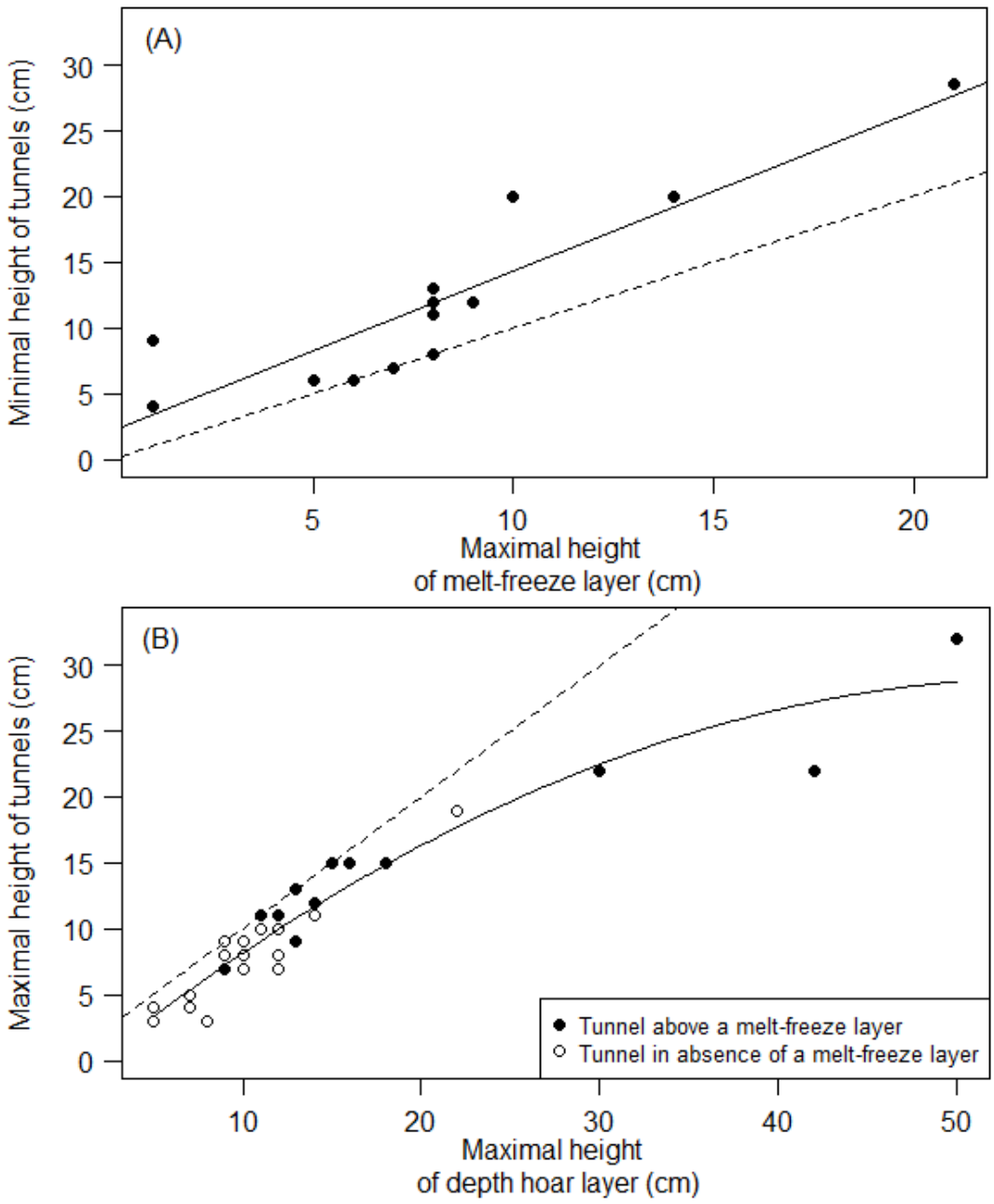

Figure 1.3 Plots of the relationships between height of lemming tunnels in the snowpack and height of specific snow layers. (A) Relationship between the minimal height of tunnels and the maximal height of the melt-freeze layer, when present ($\beta = 1.25$, 95% CI = 0.74 – 1.76, $R^2_m = 0.80$, $R^2_c = 0.90$, n = 14). Dashed line represents the 1:1 ratio and solid line the linear fit. (B) Relationship between maximal height of tunnels and the maximal height of depth hoar layer ($\beta_x = 32.2$, 95% CI = 28.3 – 36.2; $\beta_{x2} = -8.0$, 95% CI = -11.5 – -4.5; $R^2_m = 0.89$, $R^2_c = 0.96$, n = 33). Dashed line represents the 1:1 ratio and solid line the quadratic fit.

We also found a strong positive relationship between the height of tunnels in the snowpack and the maximal height of the depth hoar layer, though in this case the relationship was not linear but rather quadratic (Fig. 1.3B). Up to ~ 20 cm in the snowpack, tunnels were positioned just below the 1:1 line on the graph, which indicates that tunnels were always at the top of the depth hoar layer, just below the harder wind slab layer above (Fig. 1.3B, 1.4). However, lemmings were apparently reluctant to dig tunnels above ~ 20 cm in the snowpack even when the depth hoar was thicker. The tendency of lemmings to dig high in the depth hoar was not influenced by the presence or absence of a basal melt-freeze layer (Fig. 1.3B).

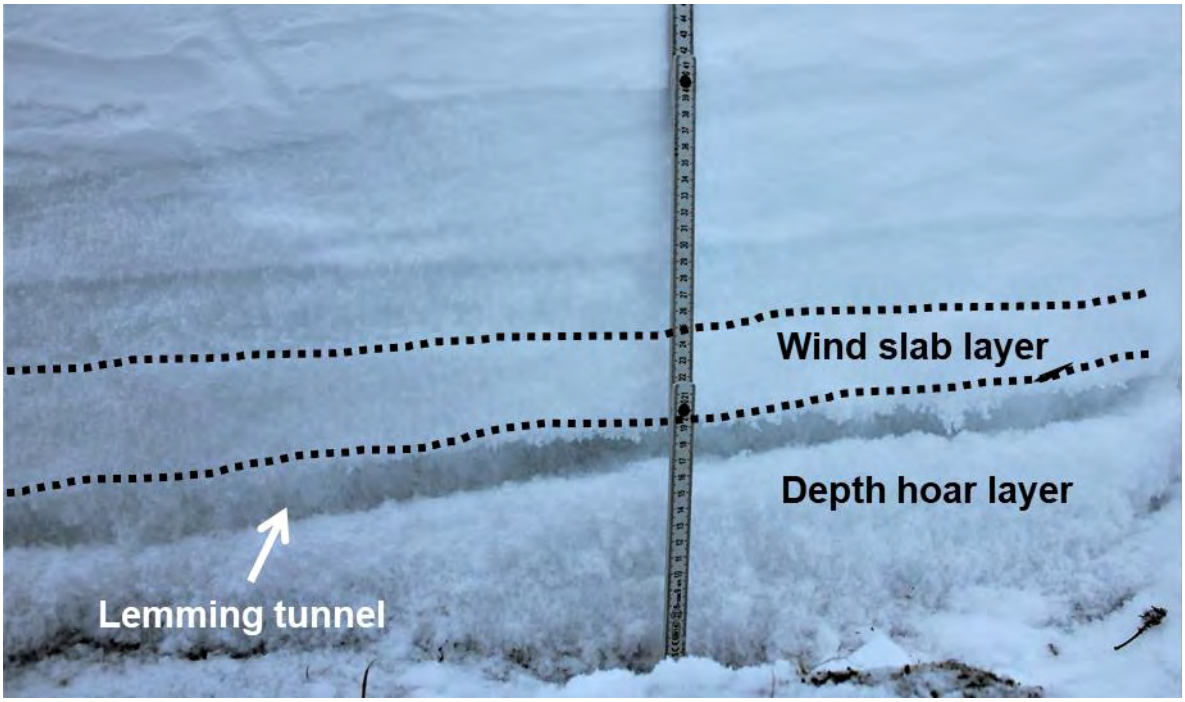

Figure 1.4 Example of a lemming tunnel dug in the upper limit of the basal depth hoar layer, just below a hard wind slab layer.

1.5.3 Differences in physical properties of snow between snow layers

In 2017, the snow density of both layers below and above the lemming tunnels were higher than the density of the tunnel layer (in versus below: $t_7 = -8.14$, $P < 0.01$; in versus above: $t_7 = -6.56$, $P < 0.01$; Fig. 1.5). The thermal conductivity of the tunnel layer was lower than that of layer above the tunnel ($t_6 = -3.67$, $P = 0.01$), but did not differ from that of the layer below the tunnel ($t_5 = -0.73$, $P = 0.50$). Similarly, the shear strength of the tunnel layer was lower than the layer above ($t_6 = -3.41$, $P = 0.01$) but did not differ from that of the layer below the tunnel ($t_5 = 0.28$, $P = 0.79$).

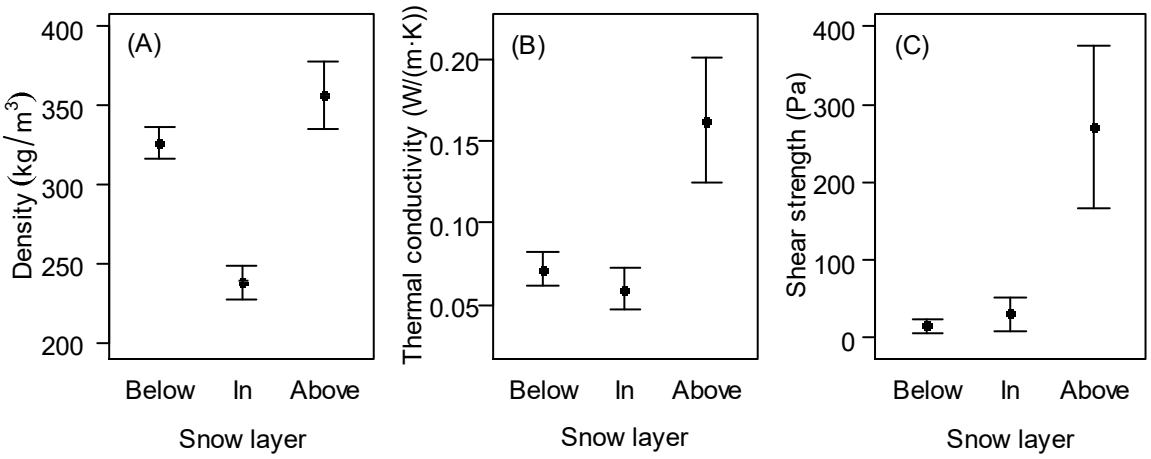

Figure 1.5 Means of density (A), thermal conductivity (B) and shear strength (C) of snow between the layer where lemming tunnels were located (in) and the layers below and above the tunnels in 2017. Error bars represent SE.

In the first pit dug in 2018, snow density along the 10-m-long tunnel layer was lower than for layers below and above the tunnel (in versus below: $t_7 = -2.67$, $P = 0.03$; in versus above: $t_7 = -9.28$, $P < 0.01$; Fig. 1.6). However, there was no significant difference between the tunnel layer and layers below and above the tunnel for thermal conductivity (in versus below: $t_7 = -0.65$, $P = 0.54$; in versus above: $t_7 = -1.95$, $P = 0.09$) or shear strength (in versus below: $t_7 = -0.69$, $P = 0.51$; in versus above: $t_7 = -1.10$, $P = 0.31$).

In the second pit dug in 2018, snow density along the 6-m-long tunnel layer was lower than for the layer above ($t_5 = -13.80$, $P < 0.01$), but not compared to the layer below the tunnel ($t_5 = 0.66$, $P = 0.54$; Fig. 1.6). The thermal conductivity of the tunnel layer was also lower than the layer above ($t_5 = -2.84$, $P = 0.04$), but not compared to the layer below the tunnel ($t_5 = -0.22$, $P = 0.84$). No significant difference in shear strength was found between the tunnel layer and layers below and above the tunnel (in versus below: $t_5 = -0.31$, $P = 0.77$; in versus above: $t_5 = -2.09$, $P = 0.09$).

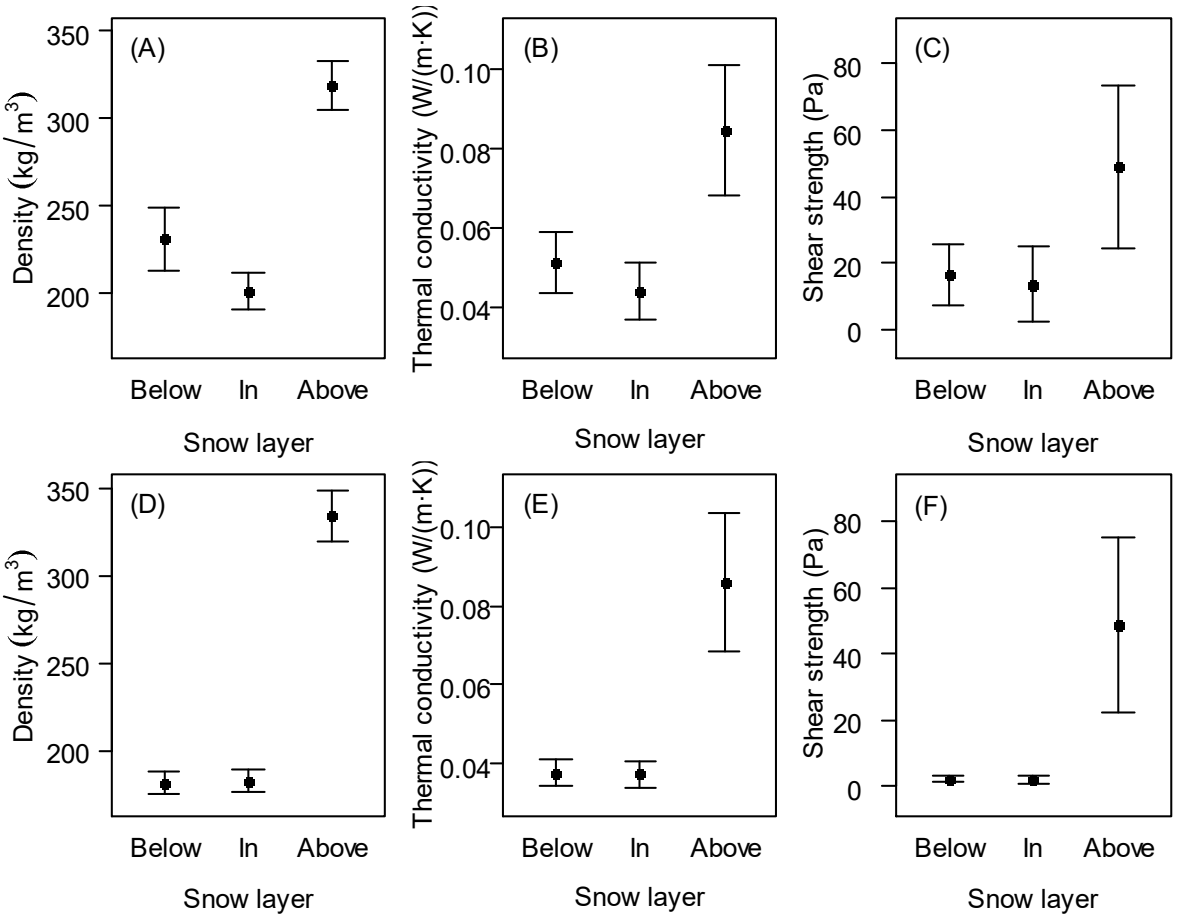

Figure 1.6 Means of density (A, D), thermal conductivity (B, E) and shear strength (C, F) of snow between the layer where lemming tunnels were located (in) and the layers below and above the tunnels in 2018. Pit 1 was dug along a tunnel 10 m long and pit 2 along a tunnel 6 m long. Error bars represent *SE*.

1.6 Discussion

Our results show that lemmings chose to dig in layers of snow with certain attributes. First, lemmings did not usually move in the snow at the ground level, and in fact rarely did so at our study site, contrary to our initial prediction. This was true regardless of the presence or absence of an indurated dense snow layer at the ground level. However, we found strong support for our second prediction as lemmings systematically preferred to dig into the softest snow layer, typically the depth hoar. Moreover, they showed a preference to dig their tunnels at the top of the depth hoar, just below a hard snow layer.

1.6.1 Lemmings dig in the least dense snow layer

The depth hoar layer through which the lemmings dug their tunnel was always the layer that had the lowest density. Snow layers above the tunnel had a higher density and shear strength

than the layer in which the tunnel was dug, which is not surprising since they were mostly wind slab layers with sometime signs of melt-freeze events. Hard wind slab layers in the upper parts of the snowpack are commonly found in the Arctic because of the exposure to high winds (Domine et al. 2002). Lemmings may only dig through these layers to get in or out of the snowpack and our anecdotal evidence (n = 1) suggests that they use the shortest possible route (i.e., going through vertically) until they reach the soft depth hoar layer (Fig. 1.2).

The layer below the tunnels tended to have a higher density than the one used for digging, though not always, probably because properties of the basal layer varied both spatially and between years. Indeed, physical properties of the basal snow layer vary according to the microtopography (e.g., hummocks) and meteorological conditions, especially those at the onset of the snowpack. As shown in Domine et al. (2018b), melt-freeze layers found at our study site, as in 2017, are due to temperature oscillations around 0 °C coupled with rain-on-snow events during the fall-winter transition. We expected that the layer below tunnels should also have higher thermal conductivity and shear strength because of the presence of melt-freeze layers in some sites, but our data did not confirm this. Melt-freeze snow layers can be heterogeneous because they form when liquid water, which accumulates preferentially at grain boundaries (Colbeck 1982), refreezes and increases bond strength between snow crystals (Domine et al. 2011). Also, liquid water from rain-on-snow events can create hard percolation columns in the snowpack (Sturm and Holmgren 1993). When a needle probe is inserted in the snow to measure its conductivity, it naturally avoids hard bounds and hard percolation columns, which may lead to non-representative sampling of the layer. Therefore, measuring thermal conductivity in such heterogeneous layers is more prone to biases than measuring snow density.

Digging in the depth hoar layer, the least dense and softest layer of the snowpack, should be a good strategy for lemmings to reduce their energy expenditure. As shown by Ebensperger and Bozinovic (2000), energy expenditure of the common degu (*Octodon degus*), a fossorial rodent, increases while digging as the density of soil increases. Vleck (1979) also found that soil density was one of the parameters responsible for increased energetic cost while burrowing by the pocket gopher (*Thomomys bottae*). The energy saving provided by digging

in the softest snow layer may be critical during the long arctic winter and could influence the capacity of lemmings to survive and reproduce under the snowpack.

We could not conduct our analyses separately for each lemming species because our sample size was too small. However, since both species were almost equally represented in our samples, our conclusions should apply to both species. Nonetheless, collared lemmings are known to be better adapted to dig in snow because they develop bigger claws on their forelegs during winter compared to brown lemmings (Sutton and Hamilton 1932; Marchand 1996). Two tunnels found opportunistically at the same site were dug in layers other than the soft depth hoar by a collared lemming, which is consistent with the previous statement.

1.6.2 Lemmings dig higher than the ground level in the snowpack

Even in the absence of a melt-freeze basal layer, lemming tunnels were surprisingly not at the ground level where they can reach their food, but higher in the snowpack. In addition, the four nests found were located ~ 10 cm above the ground level. Several hypotheses may explain why those movements happen above the ground level. First, melt-freeze layers are more frequently found in depressions; thus, lemmings may encounter those hard layers more often when digging at the ground level, which could hamper their movements. Second, variations in microtopography (i.e., hummocks) might encourage lemmings to dig higher in the snowpack to avoid constantly changing direction or moving up and down. Digging straight tunnels above the microtopography would allow covering the greatest distance with a minimum of effort.

Because lemmings can reproduce during winter under the snow (Millar 2001), an additional need for males is to move over long distances to find females for reproduction (Brooks 1993). Efficient digging above the ground level could fulfill this need for males. Unfortunately, we could not determine the sex of lemmings that used the tunnels. Lemmings can even move above the snowpack to travel long distance (Fig. 1.2), but they become vulnerable to the extreme cold and predation. Young dispersing from their natal nest may also need to travel long distances.

Digging higher in the snowpack might seem disadvantageous for a lemming to access food, which is present at ground level. However, because of the rugged microtopography and the

preferential location of melt-freeze layers in hollows, digging higher would still allow access to food at the top of hummocks while avoiding hard basal layers (Fig. 1.7). In years when hard basal snow layers are widespread, accessibility to vegetation should decrease and competition for food should increase (Hansen et al. 1999), especially when lemming abundance is high. Under such conditions, lemmings may be forced to travel longer distances to feed and spend more energy to dig tunnels. As the frequency of melt-freeze events is likely to increase with climate changes (Rennert et al. 2009; IPCC 2014; Berteaux et al. 2017), this could have negative impacts on lemming populations.

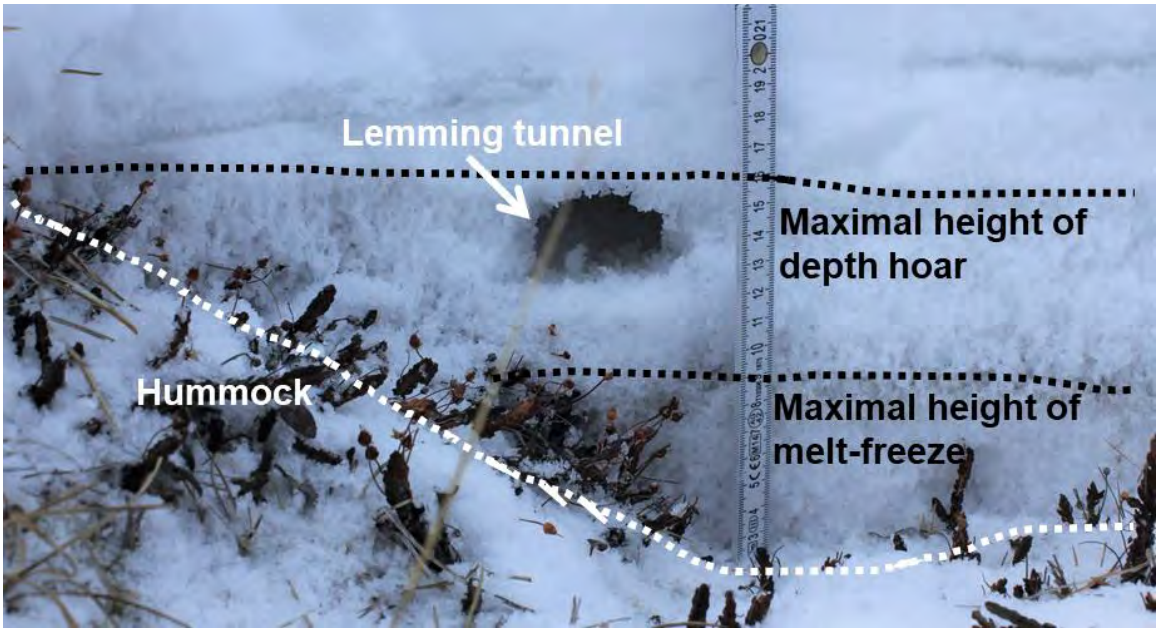

Figure 1.7 Example of a lemming tunnel dug in the depth hoar near a hummock. The base of the hummock is covered by a melt-freeze layer, but its upper part reaches the depth hoar layer. The white stippled line shows the approximate limit of the ground.

1.6.3 Lemmings dig in the upper part of the depth hoar, near a hard snow layer

Most lemming tunnels were located in the top part of the depth hoar layer, near the boundary with the layer right above it. Because this upper layer is hard and dense, we suggest that lemmings may dig right below this snow layer to prevent the collapse of their tunnels. In order for this strategy to be advantageous, tunnels have to be used repeatedly over time. We know very little of the winter behavior of lemmings, but our results suggest that they may maintain a lasting network of tunnels that provide easy travel from their nest to feeding patches or quick escape from a predator (e.g., fox digging through the snow or weasel moving

under the snow). Minimizing tunnel digging and maintenance could further help them to reduce their energy expenditure and perhaps even decrease predation risk by reducing the noise associated with digging.

A potential bias in our inferences of lemming behavior based on the tunnels that we monitored is that they were found at the site of fox attacks in the snow. Therefore, we cannot exclude the possibility that some of these tunnels were actually dug hastily by lemmings trying to escape a fox attack underway. To our knowledge, nobody has studied the speed of snow digging by lemmings, and thus we do not know if an individual could have the time to dig a new tunnel in order to escape a fox attack underway. However, the fact that more than one tunnel was found in the same snow pit, sometimes crisscrossing each other, suggests that these tunnels were present before the fox attacks and were not a response to it.

1.6.4 Conclusions

Our findings show that lemming movements under the snow are strongly guided by physical properties of snow. Lemmings dig in the least dense snow layer (i.e., depth hoar), which could allow them to save energy. Digging above the ground level in the soft depth hoar layer could also be a good strategy to prevent encountering obstacles such as hummocks or melt-freeze patches at the ground level. In addition, lemmings tend to dig at the upper limit of the depth hoar layer, right below a dense snow layer, which could be a strategy to prevent their tunnels from collapsing behind them.

By contradicting the common belief that lemmings predominantly move at ground level under the snow, our results highlight that we know very little about their behavior in the snowpack. For most of their lives, lemmings have to perform their daily activities through the complex Arctic snowpack. We suggest that the amount of energy expended by lemmings to move through the snow may be a key factor affecting their ability to reproduce in winter, which could strongly influence their cyclic fluctuations. Hence, the answer to the mystery of lemming population cycles may be partly hidden in the Arctic snowpack.

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1.8 Supplementary Material

S1.1 – Supplementary material for Chapter 1

1.9 Bibliography

Batzli, G. O., and H.-J. G. Jung. 1980. Nutritional ecology of microtine rodents: resource utilization near Atkasook, Alaska. Arctic and Alpine Research 12:483–499.

Berteaux, D., G. Gauthier, F. Domine, R. Ims, S. Lamoureux, E. Levesque, 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. 2013a. The effect of snow cover on lemming population cycles in the Canadian High Arctic. Oecologia 172:1007–1016.

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

Brooks, R.K. 1993. Dynamics of home range in collared lemmings. Pages 355–386 *in* Stenseth N.C., Ims R.A., editors. The biology of lemmings. Linnean Society of London, Academic Press, London, United Kingdom.

CEN 2018. Climate station data from Bylot Island in Nunavut, Canada, v. 1.9 (1992-2018). Nordicana D2, doi: 10.5885/45039SL-EE76C1BDAADC4890.

Colbeck, S. C. 1982. An overview of seasonal snow metamorphism. Review of Geophysics and Space Physics 20:45–61.

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.

Domine, F., M. Barrere, and S. Morin. 2016a. The growth of shrubs on high Arctic tundra at Bylot Island: impact on snow physical properties and permafrost thermal regime. Biogeosciences 13:6471–6486.

Domine, F., M. Barrere, and D. Sarrazin. 2016b. Seasonal evolution of the effective thermal conductivity of the snow and the soil in high Arctic herb tundra at Bylot Island, Canada. The Cryosphere 10:2573–2588.

Domine, F., M. Barrere, D. Sarrazin, S. Morin, and L. Arnaud. 2015. Automatic monitoring of the effective thermal conductivity of snow in a low-Arctic shrub tundra. The Cryosphere 9:1265–1276.

Domine, F., M. Belke-Brea, D. Sarrazin, L. Arnaud, M. Poirier, and T. Joint. 2018a. Soil moisture , wind speed and depth hoar formation in the Arctic snowpack. Journal of Glaciology 64:990-1002.

Domine, F., J. Bock, S. Morin, and G. Giraud. 2011. Linking the effective thermal

conductivity of snow to its shear strength and density. Journal of Geophysical Research: Earth Surface 116:F04027.
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. 2018b. 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.
Etienne, A. S., R. Maurer, F. Saucy, and E. Teroni. 1986. Short-distance homing in the golden hamster after a passive outward journey. Animal Behaviour 34:696–715.
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.
Fierz, C., R. L. Armstrong, Y. Durand, P. Etchevers, E. Greene, D. M. McClung, K. Nishimura, P. K. Satyawali, and S. A. Sokratov. 2009. The international classification for seasonal snow on the ground. IHP-VII Technical Documents in Hydrology 83:90.
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.
Gagnon, C. A., M.-C. Cadieux, G. Gauthier, E. Lévesque, A. Reed, and D. Berteaux. 2004. Analyses and reporting on 15 years of biological monitoring from Bylot Island, Sirmilik National Park of Canada. Final report, Centre d'études nordiques, Université Laval, Québec, 131 pp.
Gauthier, G., L. Rochefort, and A. Reed. 1996. Exploitation of wetland ecosystems by herbivores on Bylot Island. Geoscience Canada 23:253–259.
Hansen, T. F., N. C. Stenseth, and H. Henttonen. 1999. Multiannual vole cycles and population regulation during long winters: an analysis of seasonal density dependence. The American Naturalist 154:129–139.
Hatough, A. 1990. The burrowing habits of desertic Rodents. Mammalia 54:341–359.
IPCC. 2014. Climate change 2014: Synthesis report. Contribution of working groups I, II and III to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change R.K. Pachauri and L.A. Meyer, editors. Geneva, Switzerland.
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, editor. The biology of lemmings. Linnean Society of London, Academic Press, London, United Kingdom.
Kimchi, T., and J. Terkel. 2001. Spatial learning and memory in the blind mole-rat in comparison with the laboratory rat and Levant vole. Animal Behaviour 61:171–180.
Krebs, C. J. 2011. Of lemmings and snowshoe hares: the ecology of northern Canada. Proceedings of the Royal Society B 278:481–489.
Lindström, E. R., and B. Hörnfeldt. 1994. Vole cycles, snow depth and fox predation. Oikos 70:156–160.
MacLean, S. F., B. M. Fitzgerald, and F. A. Pitelka. 1974. Cycles in arctic lemmings: winter reproduction and predation by weasels. Arctic and Alpine Research 6:1–12.
Marchand, P. J. 1996. Life in the cold : an introduction to winter ecology. University Press

of New England, Hanover.
Millar, J. S. 2001. On reproduction in lemmings. Ecoscience 8:145–150.
Morin, S., F. Domine, L. Arnaud, and G. Picard. 2010. In-situ monitoring of the time evolution of the effective thermal conductivity of snow. Cold Regions Science and Technology 64:73–80.
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.
Pruitt, W. O. 1984. Snow and small mammals. Pages 1–8 *in* J.F. Merritt, editor. Winter ecology of small mammals. Special Publication No.10 Carnegie Museum of Natural History.
Rennert, K. J., G. Roe, J. Putkonen, and C. M. Bitz. 2009. Soil thermal and ecological impacts of rain on snow events in the circumpolar arctic. Journal of Climate 22:2302–2315.
Sanecki, G. M., K. Green, H. Wood, and D. Lindenmayer. 2006. The characteristics and classification of australian snow cover : an ecological perspective. Arctic, Antarctic and Alpine Research 38:429–435.
Soininen, E. M. et al. 2015. Highly overlapping winter diet in two sympatric lemming species revealed by DNA metabarcoding. PLOS ONE 10: e0115335.
Stenseth N.C., Ims R.A. 1993. Population dynamics of lemmings: temporal and spatial variation – an introduction. Pages 61–96 *in* N.C. Stenseth and R.A. Ims, editors. The biology of lemmings. Linnean Society of London, Academic Press, London, United Kingdom.
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.
Sturm, M., and J. Holmgren. 1993. Rain-induced water percolation in snow as detected using heat flux transducers. Water Resources Research 29:2323–2334.
Sturm, M., J. Holmgren, M. König, and K. Morris. 1997. Thermal conductivity of seasonal snow. Journal of Glaciology 43:26–41.
Sutton, G. M., and J. Hamilton. 1932. The mammals of Southampton Island. Pages 1–109 *in* Memoirs of the Carnegie Museum, Pittsburgh.
Vleck, D. 1979. The energy cost of burrowing by the pocket gopher *Thomomys bottae*. Physiological Zoology 52:122–136.

Chapitre 2 – Snow hardness impacts intranivean locomotion of arctic small mammals

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2.1 Résumé

La locomotion des animaux fouisseurs est souvent considérée comme la plus énergivore parmi toutes les formes de locomotions terrestres. Les petits mammifères arctiques, tels que les lemmings, creusent des tunnels à travers le sol, mais aussi à travers le manteau neigeux, présent pendant plus de 8 mois de l'année. Les lemmings creusent généralement dans la couche de neige la plus friable nommée givre de profondeur. Cependant, les événements de fonte-regel et de pluie-sur-neige (ROS) devraient augmenter en fréquence en Arctique, entrainant un durcissement du manteau neigeux. Le but de cette étude était de déterminer les impacts de la dureté de la neige sur la locomotion de deux espèces de lemmings présentant différentes adaptations morphologiques pour le creusage. Nous avons émis l'hypothèse qu'une augmentation de la dureté de la neige entraînerait 1) une diminution des performances des lemmings et 2) un effort accru lors du creusage, mais que ces réponses différeraient entre les espèces de lemmings. Nous avons exposé 4 lemmings bruns (*Lemmus trimucronatus*) et 3 lemmings variables (*Dicrostonyx groenlandicus*) à de la neige de différentes duretés (molle, dure, ROS) lors d'essais de 30 minutes (n = 63 essais) dans une chambre froide et nous avons filmé leur comportement. Nos résultats ont montré que la vitesse de creusage et la longueur des tunnels des deux espèces diminuaient avec la dureté et la densité de la neige, soulignant le rôle crucial des propriétés de la neige sur la performance de creusage des lemmings. Lors des essais avec ROS, le temps passé par les lemmings à creuser a considérablement augmenté et ils utilisaient également leurs incisives pour briser la neige dure, validant notre deuxième hypothèse. Dans l'ensemble, les lemmings variables, qui possèdent davantage d'adaptations morphologiques au creusage, présentaient de meilleures performances de creusage comparativement aux lemmings bruns. Nous concluons que la performance de creusage des lemmings dépend fortement de la dureté du manteau neigeux et que l'augmentation anticipée des événements de ROS pourrait représenter un défi énergétique majeur pour les populations de rongeurs arctiques.

2.2 Abstract

Fossorial locomotion is often considered as the most energetically costly of all terrestrial locomotion. Small arctic rodents, such as lemmings, not only dig tunnels 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, and that those responses would differ between lemming species. We exposed 4 brown lemmings (*Lemmus trimucronatus*) and 3 collared lemmings (*Dicrostonyx groenlandicus*) to snow of different hardness (soft, hard, ROS) during 30-minute 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.

2.3 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 not only dig 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. 2011a). Lemmings are divided in 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. 2013b). 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. 2018b).

A recent study 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 mammals 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 increase 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*.

2.4 Method

2.4.1 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 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 4 brown and 3 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 16h on August 16 to 3h 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).

2.4.2 Experimental setup

To collect snow samples and perform the experiment, we built two narrow observation boxes (100 x 31 x 8 cm, length x height x width) with windows on each vertical side to see lemmings while digging in the snow (see Supplementary Material S2.1 Fig. S1.1 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 heterogenous (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.

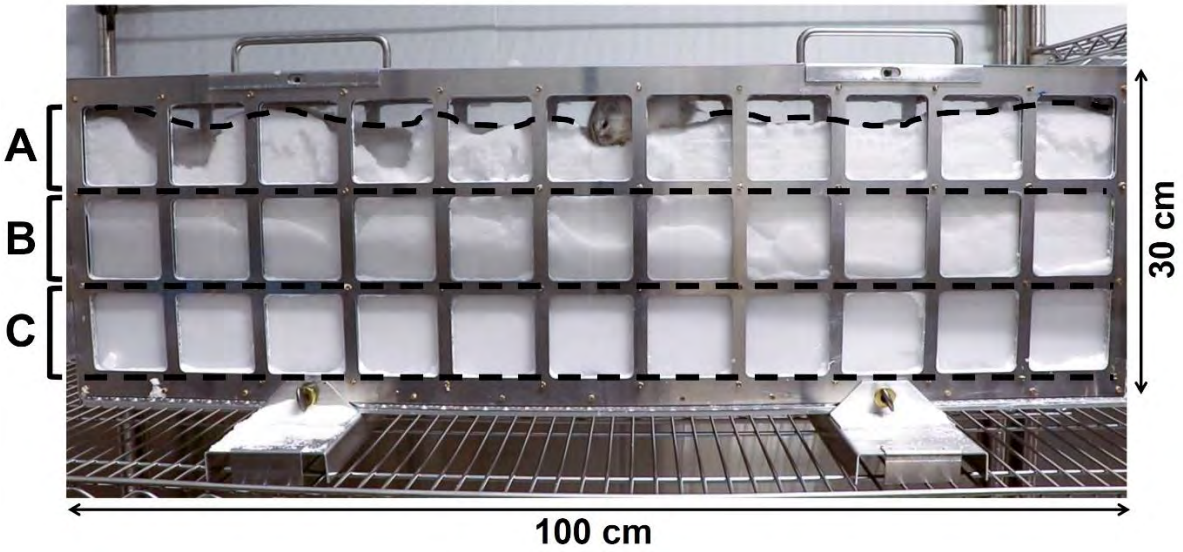

Figure 2.1 Observation box used to collect snow samples and conduct digging trials. The sampled snowpack was divided in 3 different snow layers (A, B, C) based on visual stratigraphy (see Supplementary Material S2 Fig. S2.2) and on differences in hardness and density (see Fig. 2.2). Here a trial with a collared lemming (located at the surface of the snow) is presented.

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. 2.1). 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 force indicated by the instrument (N, Newton), but it can easily be converted to pressure (Pa, Pascal) by dividing the value by $1.4x10^{-4}$ 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 2-3 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 sec. Second, we added a thin snow layer of about 1 cm. Third, we heated again for 5-10 sec. Fourth, we sprayed a small amount of warm water. We repeated steps 2 to 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.

2.4.3 Course of the experiment

The digging experiment was conducted in the last 2 weeks of November 2019. Each trial lasted 30 minutes and started by introducing a captive lemming on top of a snow sample in the observation box (see Supplementary Material S2.2 Video S2.1). Each lemming (n = 7) was tested on each snow type (soft, hard and ROS) three times (a different snow sample 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 4 were reused ROS samples. A total of 37 snow samples were collected in the field.

2.4.4 Video analysis

During the video analysis, we continuously recorded the lemming behavior using the 8 categories defined in Table 2.1 (behaviors lasting < 2 sec were ignored). When needed, we used the zoom to enlarge the image.

Table 2.1 Description of the eight main behaviors of lemmings identified during the trials (see Supplementary Material S2.2 Video S2.2).

Behavior	Description
Digging	Efficient – Continuous digging with front and hind legs in the snow for > 2 sec and progression in the snowpack.
	Inefficient – Continuous digging with front and hind legs in the snow for > 2 sec and without progression in the snowpack.
Scratching	Scratching at the surface of the snow with only the front legs for < 2 sec at the same spot but constantly changing spot.
Exploring	Walking on top of the snow, looking around and standing on its hind legs.
Travelling	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).

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

- Time elapsed since the beginning of the trial before reaching snow layer B for the first time (i.e., layer A had been crossed).

- 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).
- Time spent under the snow.
- Time spent using their teeth while digging or scratching the snow.
- 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 sec to a maximum of 13 sec) during which we measured the distance travelled and divided it by the sequence duration to obtain speed (cm s^{-1}). 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 travelled.

2.4.5 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, 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; see above). We therefore examined the link between behavioral variables and the snow type (soft, hard, 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 effect 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 analysing 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 modelled using linear mixed effect model, and travelling behavior and time spent under snow, which were modelled 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. 2020). 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).

2.5 Results

2.5.1 Snow physical properties

We found strong variations in hardness and density between snow types (soft, hard, ROS) and between layers that we visually determined within snow types (Fig. 2.2; see Appendix S2.1 Fig. S2.2 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 ($\beta_{hard\text{-}soft}$ = 5.92, CI = [5.24, 6.60]; $\beta_{ROS\text{-}hard}$ = 2.70, CI = [2.02, 3.38]). Density showed a similar trend, being denser in the top layer of hard snow compared to soft snow ($\beta_{hard\text{-}soft}$ = 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. 2.2; Appendix S2.1: Table S2.1). Snow density and hardness were positively related although hardness increased rapidly only when snow density exceeded ~300 kg m^{-3} (Appendix S2.1: Fig. S2.3).

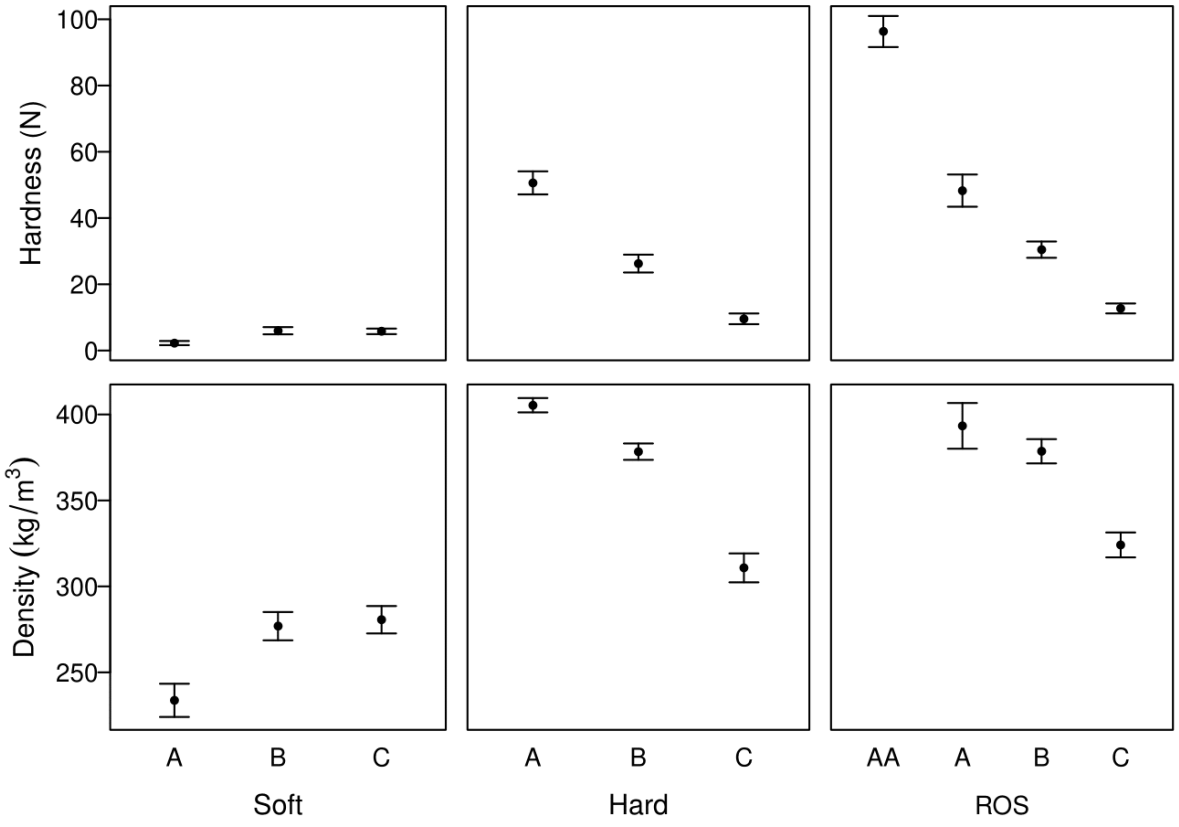

Figure 2.2 Mean hardness (top) and density (bottom) of the different layers of the three types of snow (ROS = rain-on-snow) in which lemmings dug, n = 21 measurements per layer and type of snow. Error bars represent SE. AA = surface layer hardened by experimental rain-on-snow (~2 - 3 cm); A = top layer; B = middle layer; C = bottom layer. It was impossible to measure snow density of the AA layer.

2.5.2 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 ($\beta_{density\text{^}2}$ = -3.40E-06, CI = [-4.28E-06, -2.52E-06]) and hardness ($\beta_{hardness\text{^}0.5}$ = -0.06, CI = [-0.08, -0.04]; Fig. 3; Appendix S1 Table S2.2). Digging speed started to decline more rapidly when snow density was above ~275 kg m^{-3} (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. 2.3).

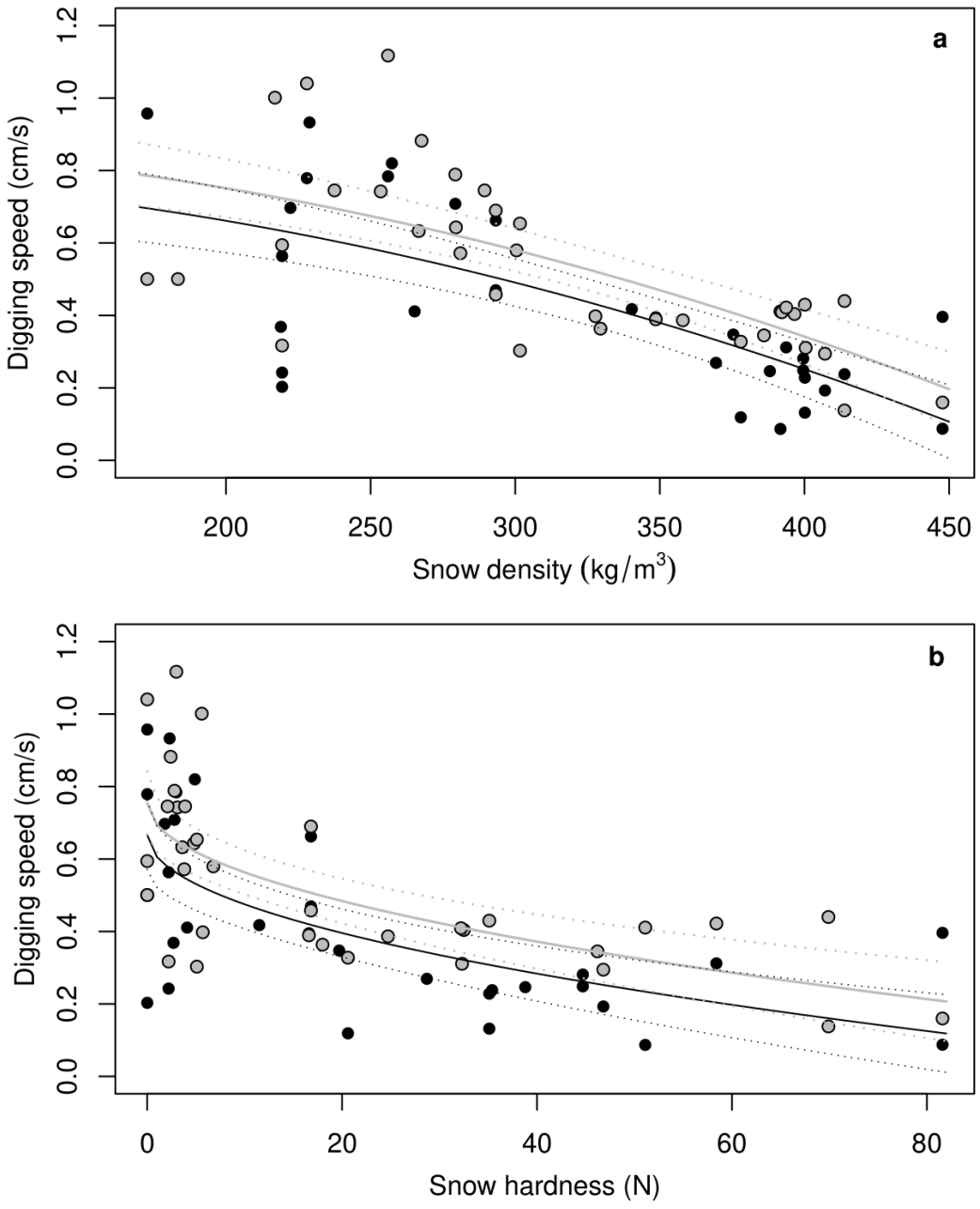

Figure 2.3 Relationship between lemming digging speed and (a) snow density and (b) snow hardness. Black circles/lines = brown lemming, grey circles/lines = collared lemming. Dotted lines are 95% CI.

2.5.3 Behavior

We found several behavioral differences between lemming species and snow types (soft, hard or ROS; Fig. 2.4). 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 ($\beta = 0.42$, CI = [0.10, 0.74]). Inefficient digging almost never occurred in soft or hard snow, but it was common in ROS (50 to 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 travelling 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 to soft snow in brown lemmings ($\beta = -0.55$, CI = [-0.88, -0.22]) but resting increased in hard and ROS snow types compared to soft snow in collared lemmings ($\beta_{hard} = 0.87$, CI = [0.34, 1.40]; $\beta_{ROS} = 1.09$, CI = [0.56, 1.62]).

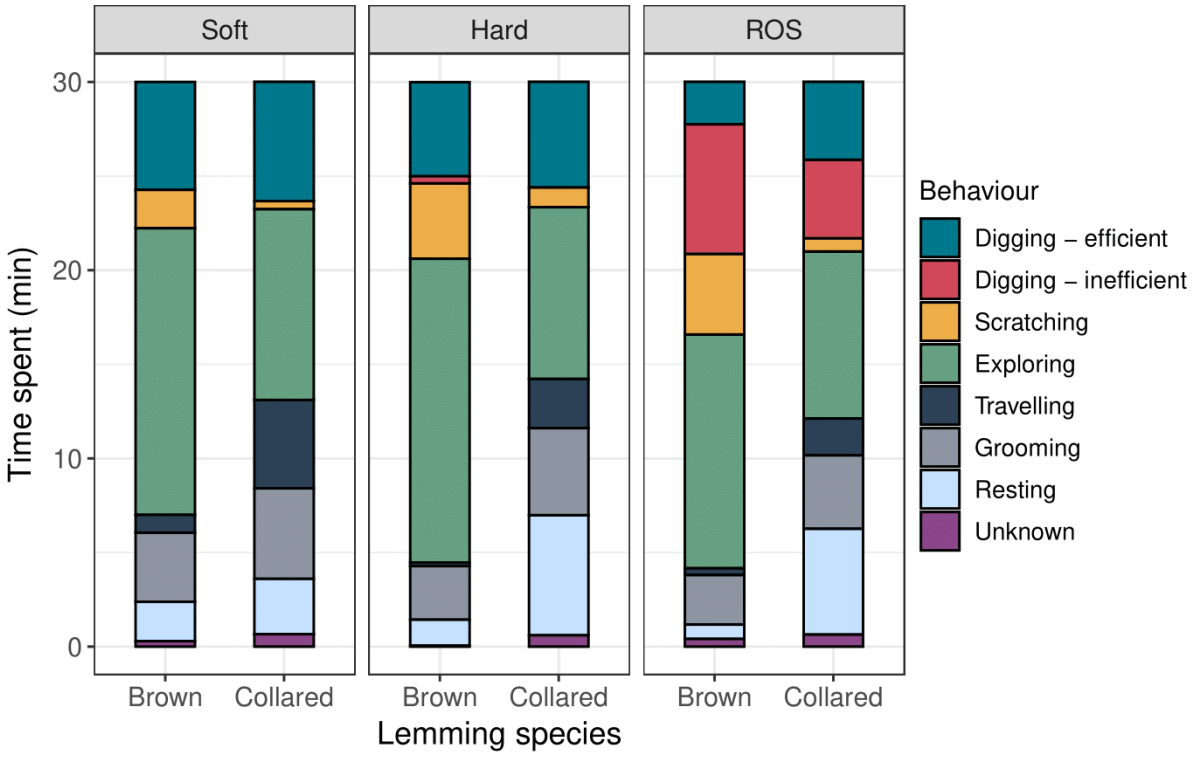

Figure 2.4 Proportion of the time lemmings spent in different behaviors during the 30-minute trials in each snow type (soft, hard, ROS) ($n_{brown} = 36$, $n_{collared} = 27$).

2.5.4 Tunnel length and time spent within the snow

Tunnel length of lemmings decreased in hard and ROS snow types compared with soft snow (β_{hard} = -1.07, CI = [-1.56, -0.58]; β_{ROS} = -1.40, CI = [-1.91, -0.89]; Fig. 2.5) but did not differ between species (β = 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 (β = 12.07, CI = [7.82, 16.32]), but did not differ between snow type (β_{hard} = 1.93, CI = [-1.62, 5.48]; β_{ROS} = 1.48, CI = [-1.50, 4.46]; Fig. 2.6).

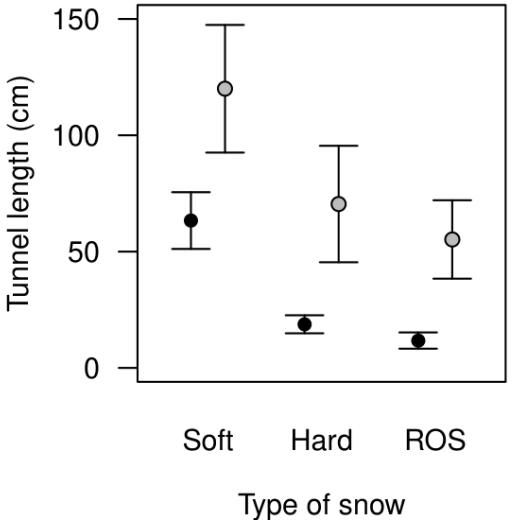

Figure 2.5 Mean length of tunnels dug by lemmings in each snow type (soft, hard, ROS). Black = brown lemmings (n = 36), grey = collared lemmings (n = 27). Error bars represent SE.

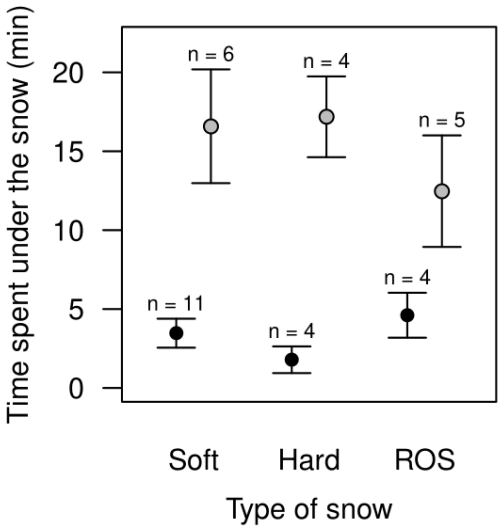

Figure 2.6 Mean time spent within the snow by lemmings in each snow type. Black = brown lemmings, grey = collared lemmings. Error bars represent SE. The number above the bars indicate the number of trials where lemmings went in the snow.

2.5.5 Vertical movement

The probability of reaching layer B was lower in hard and ROS snow types than in soft snow (β_{hard} = -2.23, CI = [0.54, 3.92]; β_{ROS} = -1.96, CI = [-3.59, -0.33]), but did not differ between species (Fig. 2.7a). 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. 2.7b). Lemmings took more time to reach layer B or C in ROS snow than in soft snow (β = 0.87, CI = [0.01, 1.73] and β = 0.74, CI = [0.19, 1.29], respectively; Fig. 2.8). Collared lemmings took less time than brown lemmings to reach layer C (β = -0.90, CI = [-1.37, -0.43]) but no difference was found for layer B (Fig. 2.8).

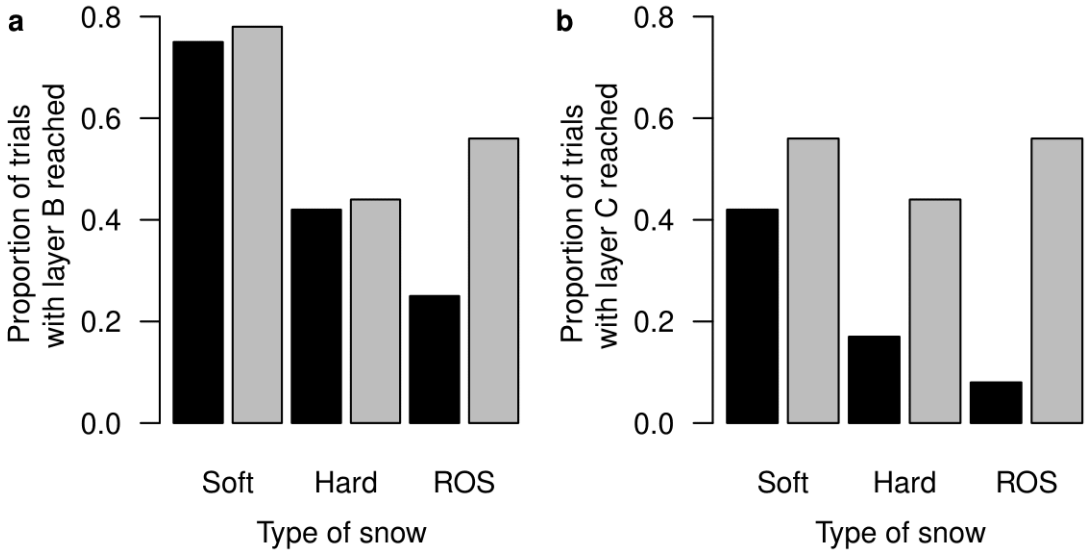

Figure 2.7 Proportion of trials where lemmings reached layer B (a) and layer C (b) in each snow type. Black = brown lemmings (n = 36), grey = collared lemmings (n = 27).

2.5.6 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 Supplementary Material S2.2 Video S2.3 for example of the two digging techniques). In soft snow, lemmings never used their incisors to dig and rarely 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.

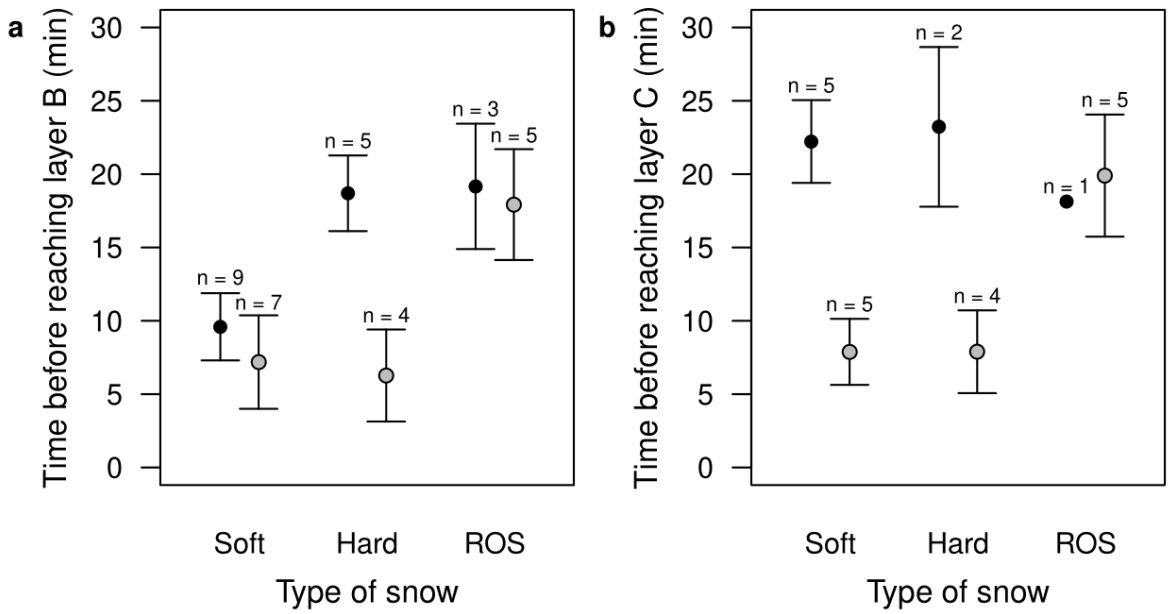

Figure 2.8 Mean time taken by lemmings to reach layer B (a) and layer C (b) in each snow type. Black = brown lemming, grey = collared lemming. Error bars represent SE.

2.6 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 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 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 reduce the digging performance of lemmings and affect their behavior.

2.6.1 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 of inefficient digging in ROS suggests that speed may be very low and close to 0 cm^{-1} 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 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).

2.6.2 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 (Fuller, Martell, Smith, & Speller, 1975; Hansen, 1957). 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 to arctic or subarctic regions (Royer et al., 2021). Therefore, the greater efficiency of collared lemmings to dig in hard snow compared to brown lemmings may partly explain their more northerly distribution where a denser snow type is more prevalent.

2.6.3 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. 2016a, 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 (Hansen et al., 2013; Stien et al., 2012). 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).

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2.8 Supplementary Material

S2.1 – Supplementary material for Chapter 2

S2.2 – Videos of the experiment

2.9 Bibliography

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, MA.

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 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. 2020. lme4: linear mixed-effects models. R package version 1.1-26.

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 13:6471–6486.

Domine, F., M. Belke-Brea, D. Sarrazin, L. Arnaud, M. Poirier, and T. Joint. 2018a. Soil moisture , wind speed and depth hoar formation in the Arctic snowpack. Journal of Glaciology 64:990–1002.

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. 2018b. 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., V. Grøtan, R. Aanes, B. Sæther, E. Fuglei, R. A. Ims, N. G. Yoccoz, Å. Ø. Pedersen, A. Wikner, N. Mait, E. Abbe, J. Jose, L. Chan, A. Phys, S. Jose, and M. Nichols. 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, editor. The biology of lemmings. Linnean Society of London, Academic Press, London, United Kingdom.
Kausrud, K. L., A. Mysterud, H. Steen, J. O. Vik, E. Østbye, B. Cazelles, E. Framstad, A. M. Eikeset, I. Mysterud, T. Solhøy, and N. C. Stenseth. 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 278:481–489.
Langlois, A., C. A. Johnson, B. Montpetit, A. Royer, E. A. Blukacz-Richards, E. Neave, C. Dolant, A. Roy, G. Arhonditsis, D. K. Kim, S. Kaluskar, and L. Brucker. 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.
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.
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 and London.
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.
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.
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.
Stien, A., R. A. Ims, S. D. Albon, E. Fuglei, R. J. Irvine, E. Ropstad, O. Halvorsen, R. Langvatn, L. E. Loe, V. Veiberg, and N. G. Yoccoz. 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 Memoirs of Carnegie Museum.
Vleck, D. 1979. The energy cost of burrowing by the pocket gopher *Thomomys bottae*. Physiological Zoology 52:122–136.
Zimova, M., K. Hackl, J. M. Good, C. Paulo, 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.

Chapitre 3 – Lemming winter habitat: the quest for warm and soft snow

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3.1 Résumé

Pendant le long hiver arctique, les petits mammifères tels que les lemmings se réfugient à l'intérieur du manteau neigeux afin de garder leur chaleur. Ils y creusent des réseaux de tunnels dans la couche basale de neige, habituellement formée de givre de profondeur friable, afin de trouver la végétation dont ils se nourrissent. Le manteau neigeux est toutefois un milieu hétérogène et les lemmings devraient utiliser davantage les habitats où les propriétés de la neige favorisent leur survie et leur reproduction hivernale. Nous avons ainsi déterminé l'impact des propriétés physiques de la neige sur l'utilisation de l'habitat et sur la reproduction hivernale des lemmings. Pour ce faire, nous avons échantillonné leurs nids d'hiver sur une période de 13 ans ainsi que les propriétés physiques de la neige pendant 6 ans dans 4 habitats différents (mésique, riverain, arbustaie, humide) à l'île Bylot dans le Haut-Arctique canadien. Nous avons trouvé que les lemmings utilisent plus intensément l'habitat riverain étant donné que la neige s'y accumule rapidement, que la neige y est la plus épaisse et que la température de la couche basale de neige est la plus élevée dans cet habitat. Cependant, dans les manteaux neigeux les plus épais, la couche basale de givre de profondeur était plus dense et moins développée comparativement aux habitats avec un manteau neigeux plus mince. Cette couche basale plus dense était négativement reliée à la reproduction hivernale des lemmings. Les arbustaies semblaient être un habitat de qualité intermédiaire pour les lemmings, car ils favorisent une couche basale de faible densité et un épais couvert de neige comparativement aux habitats mésique et humide. Cependant, les conditions de neige dans cet habitat dépendent grandement des conditions météorologiques en début d'hiver. Avec les changements climatiques en cours, un durcissement de la couche basale de neige ainsi qu'un retard dans les dates d'établissement du manteau neigeux sont à prévoir, ce qui pourrait avoir un impact négatif sur l'habitat hivernal des lemmings et nuire à leurs populations.

3.2 Abstract

During the cold arctic winter, small mammals like lemmings seek refuge inside the snowpack to keep warm and they dig tunnels in the basal snow layer, usually formed of a soft depth hoar, to find vegetation on which they feed. The snowpack, however, is a heterogenous medium and lemmings should use habitats where snow properties favor their survival and winter reproduction. We determined the impact of snow physical properties on lemming habitat use and reproduction in winter by sampling their winter nests for 13 years and snow properties for 6 years across 4 different habitats (mesic, riparian, shrubland, and wetland) on Bylot Island in the Canadian High Arctic. We found that lemmings use riparian habitat most intensively because snow accumulates more rapidly, the snowpack is the deepest and temperature of the basal snow layer is the highest in this habitat. However, in the deepest snowpacks, the basal depth hoar layer was denser and less developed than in habitats with shallower snowpacks, and those conditions were negatively related to lemming reproduction in winter. Shrubland appeared a habitat of moderate quality for lemmings as it favored a soft basal snow layer and a deep snowpack compared with mesic and wetland, but snow conditions in this habitat critically depend on weather conditions at the beginning of the winter. With climate change, a hardening of the basal layer of the snowpack and a delay in snow accumulation are expected, which could negatively affect the winter habitat of lemmings and be detrimental to their populations.

3.3 Introduction

The arrival of below-zero temperatures and of a snow-covered landscape in autumn marks the beginning of a challenging period for boreal and arctic species. Snow, depending on its properties, can either be an ally or a foe for animals living in these environments. For instance, willow ptarmigans (*Lagopus lagopus*) can benefit from deep snow accumulation as it allows them to browse buds higher up on shrubs and increase their food intake (St-Georges et al. 1995). For other herbivores such as reindeer (*Rangifer tarandus*) and muskoxen (*Ovibos moschatus*), hard snow or ice crusts resulting from rain-on-snow events can reduce access to ground vegetation and lead to population-wide reduction in survival (Rennert et al. 2009, Hansen et al. 2011). Snow properties vary from year to year but also within the landscape. Depending on their specific needs and characteristics, each species should theoretically use the habitat in a way that maximizes snow attributes favoring them. For instance, mammals like red foxes (*Vulpes vulpes*) or mule deer (*Odocoileus hemionus*) minimize travelling in deep and soft snow, probably to reduce their energy expenditure for locomotion (Halpin and Bissonette 1988, Coe et al. 2018).

Lemmings are small arctic rodents that benefit from the snowpack for thermoregulation and protection against predators (Duchesne et al. 2011a). These small mammals are the main prey of many predators and these interactions likely lead to their cyclic population fluctuation (Gilg et al. 2003, Fauteux et al. 2016). In winter, lemmings stay active in the snowpack where they dig a network of tunnels to find plants on which they feed or to disperse. They build nests for warmth where they can also reproduce if they have enough energy (Millar 2001, Duchesne et al. 2011a). Lemmings typically build their nest within a deep snowpack (60 cm or more) where subnivean temperatures reach an optimum (Duchesne et al. 2011a, Reid et al. 2012). However, in a collared lemming (*Dicrostonyx groenlandicus*) population in Greenland, use of shallower snowpacks increased as the population density increased, suggesting density-dependent habitat selection resulting from resource competition (Schmidt et al. 2021). Most studies have focused on snow depth to explain lemming distribution in the landscape, but other snow properties could also influence their habitat use in winter. For instance, it has been shown that lemmings predominantly use the soft, low-density basal snow

layer to move through the snowpack (Poirier et al. 2019), which can vary at the landscape level.

The High Arctic snowpack is shallow, typically 25 cm thick, but often as little as 15 cm (Sturm and Benson 2004, Domine et al. 2012) and is generally comprised of two main layers: a basal soft, fragile layer of low density snow topped by a hard dense wind slab (see Figure 1 of Domine et al. 2018a). It should be noted that this description excludes arctic regions strongly affected by oceanic currents. The basal layer mostly forms at the beginning of winter, when the high temperature gradient between the ground that is still warm and the cold polar air generates strong upward water vapor fluxes that lead to the formation of large, loosely bonded cup-shaped crystals called depth hoar (Marbouty 1980). The decrease in temperature gradient throughout the winter subsequently limits further depth hoar formation and snow evolution is instead governed by wind effects. A greater depth hoar fraction in the snowpack is therefore favored by greater soil moisture that delays freezing, a shallow snowpack, and low wind exposure (Domine et al. 2018a). In areas with a heterogeneous topography (e.g., hummocks, river banks), snow accumulation is greater due to wind redistribution (Pomeroy and Brun 1990). The presence of shrubs can also increase snow accumulation and depth hoar fraction (Sturm et al. 2001) because branches trap wind-blown snow and limit erosion by strong winds (Domine et al. 2016a).

Several variables characterize the quality of the different snow layers, as relevant to lemming habitat. Snow density (ρ) is the mass/volume ratio of a snow layer (Conger and McClung 2009). Snow thermal conductivity (k_{eff}) is inversely proportional to the thermal insulation properties of the snow and is positively correlated to both density and hardness (Domine et al. 2011). Snow specific surface area (SSA) is a measure of the surface/volume or surface/mass ratio of sampled snow grains and is inversely related to grain size (Gallet et al. 2009). The basal depth hoar is usually relatively soft (ρ = 130-250 kg m^{-3}, k_{eff} = 0.025-0.1 W m^{-1} K^{-1}, SSA = 9-11 m^2 kg^{-1}; Sturm and Benson 1997, Domine et al. 2018). However, when temperature increases above 0 °C, partial melting and subsequent refreezing of the snow, or a rain-on-snow event, can occur and create hard melt-freeze layers (ρ = 364-480 kg m^{-3}, k_{eff} = 0.11-0.39 W m^{-1} K^{-1}, SSA = ~3 m^2 kg^{-1}; Sturm et al. 1997, Domine et al. 2009). Although such layers can subsequently metamorphize into depth hoar, it will be fairly hard.

In regions where the climate is wetter and milder, melt-freeze layers are more frequent, and warmer air temperature and deeper snowpack will slow down the depth hoar metamorphism (Marbouty 1980, Sturm et al. 1995). Another mode of formation of hard depth hoar is when a wind slab forms early in the season. A wind slab is usually dense and hard (ρ = 350-488 kg m^{-3}, k_{eff} = 0.16-0.45 W m^{-1} K^{-1}, SSA = 20-30 m^2 kg^{-1}; Sturm et al. 1997; Domine 2016) but when formed early in the season and subjected to a high temperature gradient, it will also metamorphize into hard depth hoar. Hard depth hoar, formed from either refrozen layers or a wind slab, is called indurated depth hoar (ρ = 250 to >350 kg m^{-3}, k_{eff} = 0.05 to > 0.30 W m^{-1} K^{-1}; Domine et al. 2018). Depth hoar with a SSA in the lower range (~8 m^2 kg^{-1}) usually indicates formation from a melt-freeze layer while a SSA value ~12 m^2 kg^{-1} usually indicates formation from a wind slab layer (Domine et al. 2009).

With climate change, a delayed onset of the snowpack is expected (Liston and Hiemstra 2011) and may reduce the period when lemmings can benefit from it (Gilg et al. 2009). Global warming also threatens to increase the frequency of rain-on-snow events, leading to a hardening of the snowpack (Liston and Hiemstra 2011, Hansen et al. 2014). As lemmings have greater difficulty digging in harder snow (Poirier et al. 2021), this could have population-wide impacts by increasing their energy expenditure and reducing their chances of reproduction. Some studies already reported negative consequences of rain-on-snow on lemming and vole populations (Ims et al. 2008, Kausrud et al. 2008, Domine et al. 2018b), but a better understanding of their winter habitat use is necessary to assess their vulnerability to future snow conditions.

In this study, we examined winter habitat use and the impact of habitat and snow properties on the probability of reproduction of the brown (*Lemmus trimucronatus*) and northern collared lemming in the High Arctic. Habitat use was determined by comparing density of lemming winter nests among four habitats (mesic, riparian, shrubland and wetland) and their reproductive activity by comparing the proportion of reproduction in those nests over 13 years. We hypothesized that habitat use and reproduction rates of lemmings would be higher in habitats where snow conditions are expected to facilitate their thermoregulation and locomotion. We predicted that winter nest density and proportion of nests with reproduction would be higher (1) in habitats with a deep snowpack and early snow accumulation because

these conditions should offer good thermal insulation, and (2) where the basal snow layer is characterized by a soft and well-developed depth hoar layer because it facilitates locomotion through the snow. We also hypothesized that winter nest density would increase in less favorable habitats in years of high lemming abundance due to a density-dependent spillover effect. Finally, we hypothesized that brown and collared lemmings would use winter habitats differently because collared lemmings are more efficient at digging into the snow than brown lemmings (Poirier et al. 2021).

3.4 Method

3.4.1 Study area

This study took place in the Qarlikturvik valley of Bylot Island, Nunavut (73°08'N, 80°00'W), from 2007 to 2019 (Supplementary Material S3.1 Fig. S3.1). Winter, which is defined here as the period with snow cover, typically starts in early October and ends in early June (Domine et al. 2021a). The coldest month is February with a mean temperature of -36.7 °C (Domine et al. 2021a). Climate in this area is typical of cold and dry Arctic regions unaffected by oceanic currents. For this study, we separated the study area (~51 km^2) in four main habitats for lemmings in winter, namely, mesic (67 %), wetland (17 %), riparian (10 %) and shrubland (6 %) (Supplementary Material S3.1 Figs. S3.1-S3.2). The mesic habitat is mostly found upland, in sites with moderate to good drainage. It is characterized by hummocky tundra and the main plant species encountered are *Salix arctica*, *Cassiope tetragona*, graminoids and mosses (Audet et al. 2007). Wetland habitat (wet) is found in low-lying areas close to sea-level and is characterized by shallow ponds and polygon tundra created by the growth of ice wedges in the permafrost. The vegetation mostly consists of graminoids, such as *Carex aquatilis*, *Eriophorum sheuchzeri* and *Dupontia fisheri* growing through an extensive moss cover (Gauthier et al. 2011). Riparian habitat is restricted to the area along streams or gullies with steep slopes on either side (i.e., 10-30 m from them), running mostly through the mesic habitat or along hills, which allow the formation of snowdrifts in winter (Pomeroy and Brun 1990). This habitat has a similar vegetation composition to mesic, but near the center of gullies, vegetation becomes more similar to wetland due to higher ground humidity. Finally, shrubland habitat (shrub) resembles mesic but is the only habitat with erect vegetation, primarily *Salix richardsonii*, rising 10 to 40 cm

above the ground (Domine et al. 2016a). This habitat is very limited spatially and mostly occurs in the most inland part of the valley, at the base of alluvial fans, which provide abundant water supply by channeling snowmelt water.

3.4.2 Lemming demographic parameters

Lemming winter nests were sampled along 20 permanent transects of 500 m each in mesic, riparian and wet habitats between 2007 and 2019 (total of 60 transects each year; Supplementary Material S3.1 Fig S3.1). For the shrub habitat, the sampling took place between 2017 and 2019 along 25 transects of 200 m (transects were shorter because that habitat occurred in small-size patches). These transects were randomly positioned in the landscape from predetermined coordinates and had a predominantly N-S orientation to avoid transects crossing each other. Most of them were spaced by at least 200 m, which ensured spatial independence considering the small home range of lemmings (Banks et al. 1975, Predavec and Krebs 2000). We walked all transects soon after complete snow melt and noted every winter nest detected from the transect line. We measured the perpendicular distance between each nest and the transect and destroyed them so only new nests could be sampled the next year. We identified the lemming species that occupied every nest found based on the size, shape and color of feces (MacLean et al. 1974, Soininen et al. 2015). Feces were easy to identify because we only sampled fresh nests from the year. In some cases (about 5 %), feces from both brown and collared lemmings were found, suggesting a mixed occupation. In those cases, we duplicated the nest in our dataset so it would be considered twice in the analysis, once for each species.

We estimated nest density of each species separately in each habitat and year with the distance sampling method (Miller et al. 2019). Data from all transects were pooled within each habitat to obtain a single estimate of nest density per habitat annually. We assumed that detection probabilities decreased with distance separating the nest from the transect. For each habitat and year, we modeled the detection probability with different probability distribution functions (half normal, hazard rate, uniform; Buckland et al. 2004). It was also possible to specify an adjustment factor (i.e., cosine, Hermite polynomial, or simple polynomial) to improve the fit of the model. We used the second-order Akaike criterion (AIC_c) to determine which probability distribution function provided the best fit for each dataset. The model

estimated the effective area surveyed by the observer as well as the number of undetected nests based on the detection probability function. Nest density was obtained by the sum of detected and undetected nests, divided by the effective area surveyed in each habitat. Those analyses were performed with the *Distance* package version 1.0.3. (Miller et al. 2019) implemented in the R software version 4.1.0 (R Core Team 2021). When models could not be run or performed poorly due to low sample size (about 25 % of the time), we obtained a nest density by dividing the number of nests found in the habitat by the total area surveyed assuming a perfect detection 5 m on either side of the transect.

For each lemming nest, we determined the occurrence of reproduction based on the presence of a high number of small-size feces (i.e., at least one third of all feces), which indicates that juveniles once occupied the nest (Duchesne et al. 2011b). In cases of mixed nest occupation, the layering order of feces in the nest indicated which species had reproduced. We estimated the proportion of nests with reproduction for each species, year and habitat by dividing the number of nests with presence of reproduction by the total number of nests found. In years of low lemming densities, the number of winter nests found along transects was very low, which reduced the precision of the proportions of nests with reproduction. In those years, we increased sample size by including winter nests found opportunistically in the field. Opportunistic nests were found while observers conducted other field activities across the study area and were considered randomly sampled. The habitat where opportunistic nests were found was assigned in the field and they were analyzed in the same way as those found along transects. However, they were not used in the density estimation.

3.4.3 Snow physical properties

We sampled snow physical properties in the four habitats by digging snow pits in May before snow melt from 2014 to 2019 except in 2016 due to logistical constraints. We dug between 1 to 11 snow pits in every habitat each year. It was not possible to perform snow pits at the exact same location than the winter nests transects, but we selected sites with similar habitat characteristics within the area covered by our transects (Supplementary Material S3.1 Fig. S3.1). In every snow pit, we sampled physical properties of the basal layer of snow between 0 to 5 cm from the ground level. We measured snow density by weighing a fixed volume of snow with a 100 cm^3 box-cutter (Conger and McClung 2009). As a proxy for snow hardness,

we measured the thermal conductivity of snow (k_{eff}) with a TP02 heated needle probe (Hukseflux Thermal Sensors, Delft, The Netherlands). A needle was inserted in the basal snow layer, avoiding touching the ground, heated with a constant power during 100 s and the temperature at the center of the needle was recorded. The relationship between temperature at the center of the needle and time (on a log-scale) depends on heat dissipation in the environment and can be used to calculate thermal conductivity (Morin et al. 2010, Domine et al. 2011). We used the DUFISSS instrument (Dual Frequency Integrating Sphere for Snow SSA measurement) to measure the snow specific surface area (SSA), which is the surface area per unit of mass (Gallet et al. 2009). The idea consists in illuminating a given volume of snow with a laser diode at 1310 nm to measure the reflected light with a photodiode, and to convert the reflectance measurement into SSA (more details in Gallet et al. 2009, Domine et al. 2012). Finally, we visually determined the depth hoar layer in the snowpack, and we measured the maximal height of this layer and the total height of the snow pit.

We measured mean snow depth in each habitat in mid-May, which is usually the period of maximum snow depth. In mesic, shrub and wet habitats, this was measured using a snow probe along 4 random transects positioned in a square shape, totaling 100 to 200 points per habitat spaced out by 2 m. For riparian habitat, because the snow depth varies considerably at the meter scale within snow drifts, we used the maximum depth recorded in May at three permanent poles centrally located in selected snowdrifts.

From 2016 to 2021, three automated stations (one per habitat) monitored snow temperature with thermistors in riparian, shrub and wet habitats throughout the winter. Since the snow depth is similar between wet and mesic habitats, we assumed that their thermal profiles are also relatively similar even though we recognize that differences in slope, aspect, soil properties and vegetation may affect them. The thermistors were installed at different heights in the snowpack between 0 and 35 cm. We used the temperature at 2 cm above the ground, obtained either from direct measurement at that height or from linear interpolation using the nearest 2 thermistors. We obtained the daily temperature as well as the daily temperature fluctuation (i.e., maximal – minimal daily temperature) of the basal snow layer. Due to malfunction of the equipment in some years, we could only compare the three habitats over three winters (2016-17, 2019-20 and 2020-21). Air temperature was measured at two

automated stations (shrub, wet) with a ventilated sensor at 2.3 m height (Domine et al. 2021a).

We obtained dates of permanent snow onset from 2017 to 2021 using automatic cameras (Reconyx®) that recorded daily photographs of a representative area of each habitat. One camera positioned about 10 m above the ground took pictures in mesic, riparian and wet habitats simultaneously, and a second camera recorded pictures in the shrub habitat. Snow onset was defined as the first day in autumn when snow cover reached or exceeded 80 % of the area and did not return below 50 %. Note that throughout the paper, the year of a given winter is referred to by the year of the spring when most measurements were taken (e.g., winter 2016-2017 is referred to as winter 2017).

3.4.4 Statistical analyses

We analyzed lemming winter nest density with linear mixed effect models to assess the influence of either habitat or snow parameters, lemming species and their interactions when relevant. The sampling unit used in this analysis was annual nest density estimated in each habitat with the distance sampling method (see *Lemming demographic parameters* above). We log-transformed (natural log) nest densities to meet normality and homoscedasticity assumptions. The temporal autocorrelation in model residuals caused by the cyclic dynamics of these rodents was removed by adding year as a random factor. To test for a density-dependent effect on habitat use, we repeated the global model with data divided into years of low and high nest density and compared the effect size and significance of the habitat covariates. The threshold used to separate low and high density was the 2.9 nests/ha, which corresponds to the median of yearly nest density for brown and collared lemmings combined (Supplementary Material S3.1 Fig. S3.4). For datasets including the shrub habitat (available only for 2017-2019), we could not test for a density-dependent effect due to the short time series. To test the influence of snow physical properties on nest densities (2014-2019), we used different combinations of additive parameters (i.e., density and thermal conductivity of the basal snow layer, maximal height of depth hoar, snow depth) and we evaluated the strength of support of each model using the second-order Akaike criterion (AIC_c). We used model-averaging when several had reasonable statistical support ($\Delta AIC_c < 4$).

We analyzed the proportion of winter nests with reproduction with binomial models to examine the influence of habitat and species. For the longest time series (2007-2019), we used generalized linear mixed quasi-binomial models to overcome overdispersion in the data (MASS package version 7.3-57.1; Ripley et al. 2022), with year included as random factor. For the dataset including shrub (2017-2019), we used binomial models without year as a random effect due to the small dataset. Similarly, we used binomial models to test for influence of species and snow parameters on proportion of nests with reproduction (2014-2019). We evaluated the strength of support of each model using ΔAICc and determined significance of relationships based on the 95 % confidence interval of slope parameters.

To establish potential differences in snow properties between the four habitats, we used linear mixed effect models with habitat as the fixed effect and year as a random effect (2014-2019). Response variables were density, thermal conductivity and specific surface area (SSA) of the basal snow layer, snow depth and maximal height of the depth hoar. We also examined the differences in temperature (with and without correcting for differences in air temperature) and daily temperature fluctuation of the basal snow layer between habitats with data from the automated stations. To avoid autocorrelation problems of repeated measures, we used mean monthly temperatures and mean of daily fluctuations in temperature calculated over 15-day intervals (time intervals were determined to minimize autocorrelation in the data and to maximize sample size). For the snow onset date, we examined the difference only between the wet and riparian habitats because dates were the same for mesic and wet habitats and almost the same for riparian and shrub habitats. In some models we had to perform a natural log, inverse or square-root transformation of the response variable to improve normality and homoscedasticity. Due to the different scales of variables, we could not use the same transformation consistently. As a complementary analysis, we explored the degree of association amongst snow variables through a principal component analysis (PCA) and examined variations in PC scores between habitats (see details in Supplementary Material S3.2).

When relevant, the proportion of variation explained by the models was calculated with the MuMIn package version 1.47.1 (Barton 2022) following Nakagawa and Schielzeth 2013, with R^2_m being the amount of variation explained by fixed factors and R^2_c by both fixed and

random factors. In tables, slope parameters (β) are presented with their 95 % CI and differences between groups are calculated with the Tukey's Honestly Significant Difference test (HSD). When log-transformed data were used in the models, we obtained the mean estimates on the linear scale by applying an exponential transformation of the sum of the estimate and half of the variance (Feng et al. 2014) and we calculated the approximate 95% CI with the Cox's method (Chami et al. 2007).

3.5 Results

3.5.1 Winter nest density

Nest density of both lemming species varied considerably among years, as expected based on their known cyclic population fluctuations, and between habitats (Supplementary Material S3.1 Figs. S3.3- S3.4). We found evidence that nest densities were highest in the riparian habitat, lowest in the wet habitat and intermediate in the mesic habitat (Fig. 3.1, Table 3.1a). Nest densities of collared lemmings were also 2.6 times lower than that of brown lemmings (β = -0.96, CI = [-1.38, -0.54]) and a model with an interaction between lemming species and habitat had less support (ΔAICc = 1.2). We did not find evidence of density-dependent effects in habitat use since models where years were separated in low and high density yielded similar results (i.e., similar slopes) to the global model (Supplementary Material S3.1 Fig. S3.5, Table S3.1). Results of the analysis using years with shrub habitat data were very consistent with the previous analysis despite the smaller dataset (Table 3.1a). Nest density in the shrub habitat was 1.2 and 3.7 times higher than in the mesic and wet habitats, respectively but 3.8 times lower than in the riparian habitat (Fig. 3.1 c-d, Table 3.1a).

When examining the influence of snow parameters on nest density, we found support for a positive effect of snow depth and maximal height of depth hoar on nest density and slightly lower nest densities of collared than brown lemmings (Fig. 3.2, Table 3.2a, Supplementary Material S3.1 Table S3.2). A model with an inverse transformation of snow depth had less support, providing little evidence of a threshold effect of snow depth on lemming nest density.

3.5.2 Winter reproduction

The proportion of lemming winter nests with signs of reproduction also varied considerably among years and habitats (Supplementary Material S1 Fig. S3.6). We found evidence that proportion of nests with reproduction was 1.2 and 3.3 times higher in riparian compared to mesic and wet habitats, respectively (Table 3.1b), and was twice higher in collared than in brown lemmings ($\beta = 0.69$, CI = [0.45, 0.94]; Fig. 3.3a). Results from the years when data from the shrub habitat was available revealed the same trends and suggested a low reproductive activity in shrubs, although no significant difference was found, probably due to small sample size (Table 3.1b, Fig. 3.3b). However, reproductive rate was still 2 times higher in collared lemmings than in brown lemmings in this time series ($\beta = 0.70$, CI = [0.11, 1.29]).

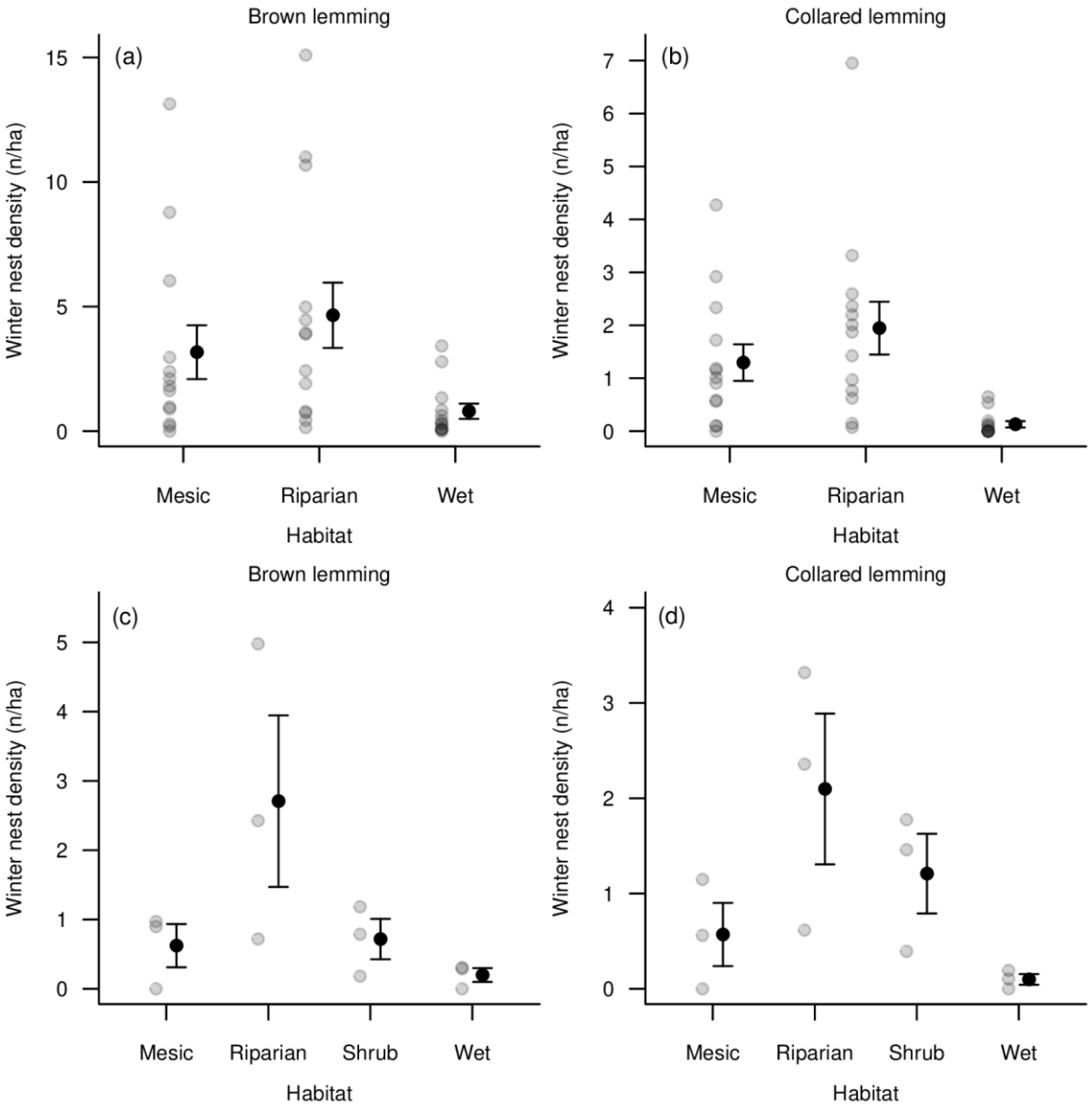

Figure 3.1 Lemming winter nest density in three different habitats (2007 – 2019) for (a) brown lemming (n_{mesic} = 431, $n_{riparian}$ = 718, n_{wet} = 139; total number of nests found) and (b) collared lemming (n_{mesic} = 200, $n_{riparian}$ = 282, n_{wet} = 23), and in four different habitats (2017 – 2019) for (c) brown lemming (n_{mesic} = 30, $n_{riparian}$ = 70, n_{shrub} = 9, n_{wet} = 9) and (d) collared lemming (n_{mesic} = 31, $n_{riparian}$ = 58, n_{shrub} = 16, n_{wet} = 5) at Bylot Island. Gray circles are individual years, black circles are the mean and error bars represent SE.

Table 3.1 (a) Coefficients of the models examining the influence of three (2007-2019) or four habitats (2017-2019) on lemming nest density (ln-transformed). (b) Coefficients of the models examining the influence of three (2007-2019) or four habitats (2017-2019) on proportion of nests with reproduction. Year was used as a random effect except for the reproduction rate analysis of the 2017-2019 dataset. Estimates in bold indicate that the 95% confidence interval did not include 0.

a) Nest density

Years	Habitat comparisons	β[1]	95% CI	R^2_m	R^2_c
2007 - 2019	**riparian - mesic**	**0.57**	**[0.07, 1.07]**	0.41	0.72
	wet - mesic	**-1.78**	**[-2.29, -1.28]**		
	wet - riparian	**-2.36**	**[-2.86, -1.85]**		
2017 - 2019	**riparian - mesic**	**1.71**	**[1.02, 2.41]**	0.51	0.80
	shrub - mesic	**0.85**	**[0.16, 1.54]**		
	wet- mesic	**-0.84**	**[-1.54, -0.15]**		
	shrub - riparian	**-0.86**	**[-1.56, -0.17]**		
	wet - riparian	**-2.56**	**[-3.25, -1.86]**		
	wet - shrub	**-1.69**	**[-2.39, -1.00]**		

b) Proportion of nests with reproduction

Years	Habitat comparisons	β[1]	95% CI	R^2_m	R^2_c
2007 - 2019	**riparian - mesic**	**0.44**	**[0.22, 0.67]**	0.36	0.67
	wet - mesic	-0.17	[-0.53, 0.19]		
	wet - riparian	**-0.61**	**[-0.96, -0.27]**		
2017 - 2019	riparian - mesic	0.42	[-0.24, 1.08]	R^2 = 0.32	
	shrub - mesic	-0.50	[-1.71, 0.70]		
	wet - mesic	-0.16	[-1.27, 0.96]		
	shrub - riparian	-0.92	[-2.08, 0.23]		
	wet - riparian	-0.58	[-1.64, 0.48]		
	wet - shrub	0.35	[-1.12, 1.81]		

[1] Coefficients are calculated from Tukey's HSD test.

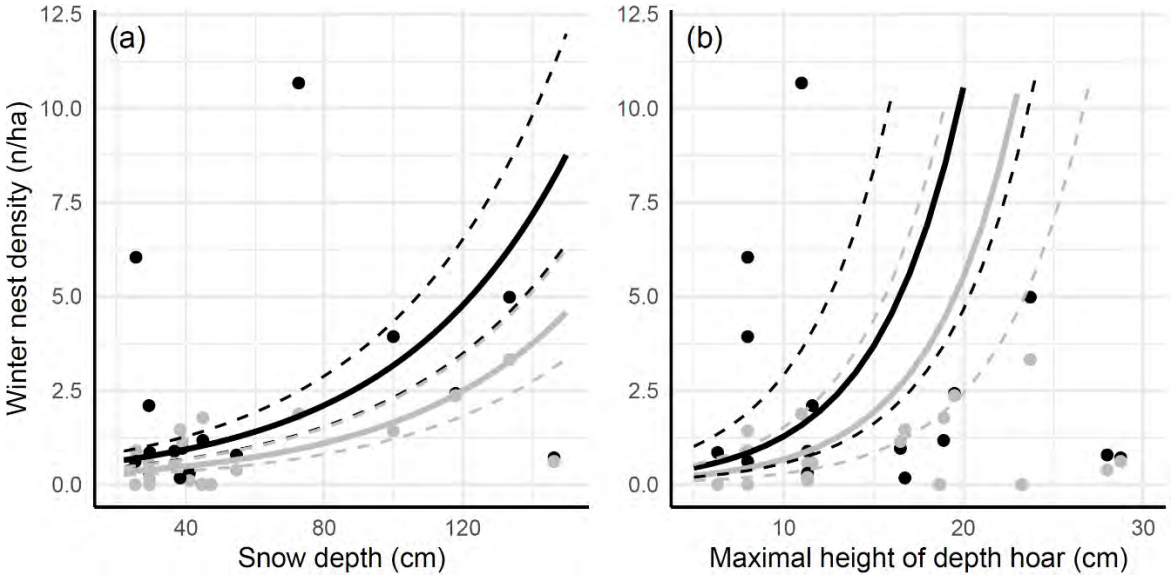

Figure 3.2 Relationship between winter nest density and (a) snow depth (R^2_m = 0.29, R^2_c = 0.55) and (b) maximal height of depth hoar (R^2_m = 0.34, R^2_c = 0.86) for brown lemming (black circles) and collared lemming (grey circle) at Bylot Island, 2014-2019. Top models were used (i.e., no model averaging) and dashed lines are the 95% CI of the relationships. Outlier points showing high brown lemming density at low values of snow depth and maximal height of depth hoar all belong to the peak year of 2014.

Table 3.2 Model-averaged coefficient estimates of the effect of various snow parameters on (a) lemming nest density and (b) proportion of lemming nests with of reproduction (see models on Table S3.2). Estimates in bold indicate that the 95% confidence interval did not include 0.

a) Nest density

Parameter	β	95% CI
snow depth	**0.02**	**[0.01, 0.03]**
max height depth hoar	**0.14**	**[0.02, 0.26]**
basal k_{eff}	2.43	[-20.39, 25.26]
basal density	0	[-0.02, 0.02]
collared lemming	**-0.65**	**[-1.3, 0]**

b) Proportion of nests with reproduction

Parameter	β	95% CI
snow depth^{-1}	**-24.22**	**[-42.77, -5.68]**
max height depth hoar	-0.05	[-0.08, 0.02]
basal density	**-0.01**	**[-0.01, 0]**
basal k_{eff}	**-19.5**	**[-35.01, -3.98]**
collared lemming	**0.73**	**[0.34, 1.12]**

When examining the influence of snow parameters on lemming reproduction, we found support for an increase in reproduction with greater snow depth and a reduction in reproduction as maximal height of depth hoar increased (Table 3.2b, Fig. 3.4a-b, Supplementary Material S3.1 Table S3.2). A relationship with the inverse of snow depth was preferred over a linear one (ΔAICc = 1.8), suggesting a positive effect on reproduction until ~60 cm, after which there was little change (Fig. 3.4a). We also found evidence of a decrease in reproduction with an increase in density and thermal conductivity of the basal snow layer (Fig. 3.4c-d; Table 3.2b).

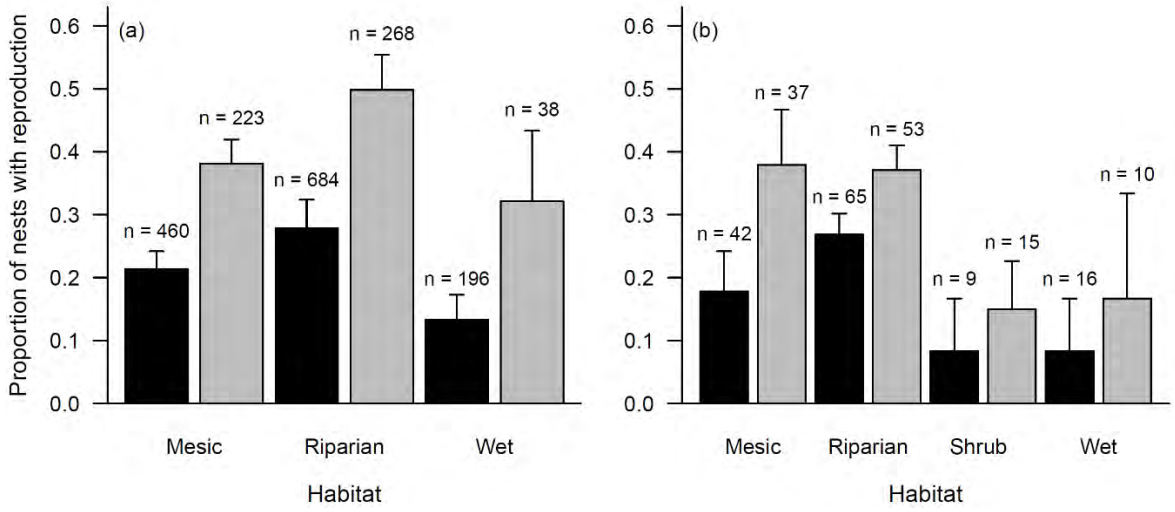

Figure 3.3 Proportion of winter nests with reproduction (mean + SE) in brown lemmings (black) and collared lemmings (gray) in (a) three different habitats (2007 – 2019) and (b) four different habitats (2017 – 2019) at Bylot Island. n = number of nests used to calculate the proportion, all years confounded.

3.5.3 Variation in snow physical properties across habitats

The density of the basal snow layer was highest in riparian habitat, lowest in shrub, and intermediate in the other two habitats (Fig. 3.5a; coefficients of all models are shown in Supplementary Material S3.1 Table S3.3). We did not find any evidence of differences in the snow thermal conductivity (k_{eff}) across habitats, but we note a high residual variability of the random variable ($SD_{residual}$ = 8.77), suggesting large variations within years (Fig. 3.5b). Snow SSA was 1.2 to 1.4 times lower in the riparian habitat compared with the others (Fig. 3.5c). Snow depth differed between all habitats and, as expected, it was 2.8 to 3.1 times deeper in riparian habitat compared to the other three habitats (Fig. 3.5d). Maximal height of depth

hoar was lowest in the wet habitat and highest in riparian and shrub habitats (Fig. 3.5e). Finally, snow onset dates in the riparian habitat were almost two weeks earlier than in the wet habitat (Fig. 3.5f).

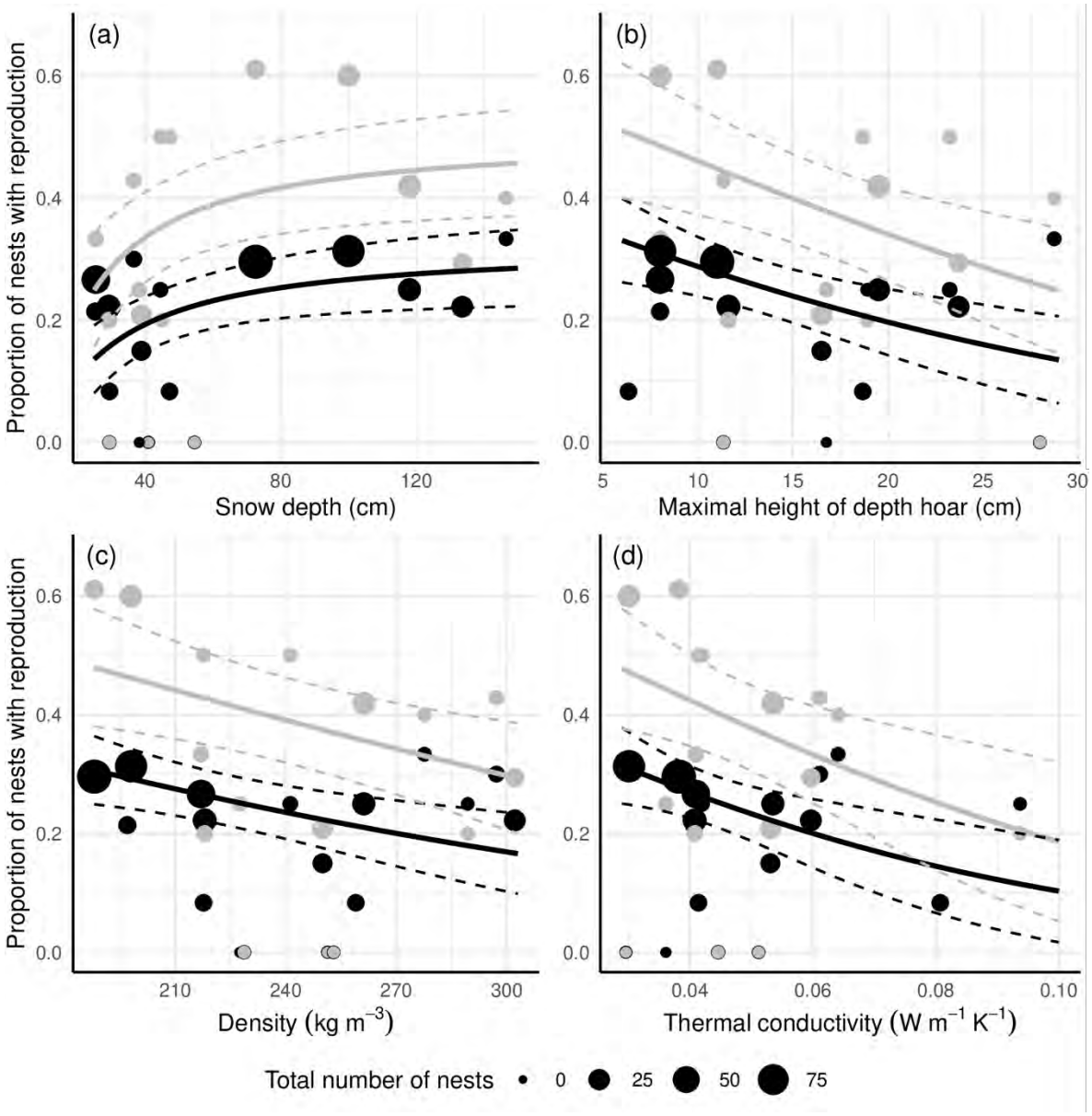

Figure 3.4 Relationships between the proportion of winter nests with reproduction and (a) snow depth, (b) maximal height of the depth hoar, (c) density of the basal snow layer and (d) thermal conductivity (k_{eff}) of the basal snow layer in brown lemming (black circles) and collared lemming (gray circles) at Bylot Island, 2014 – 2019. Top models were used (i.e., no model averaging) and dashed lines are the 95% CI of the relationships.

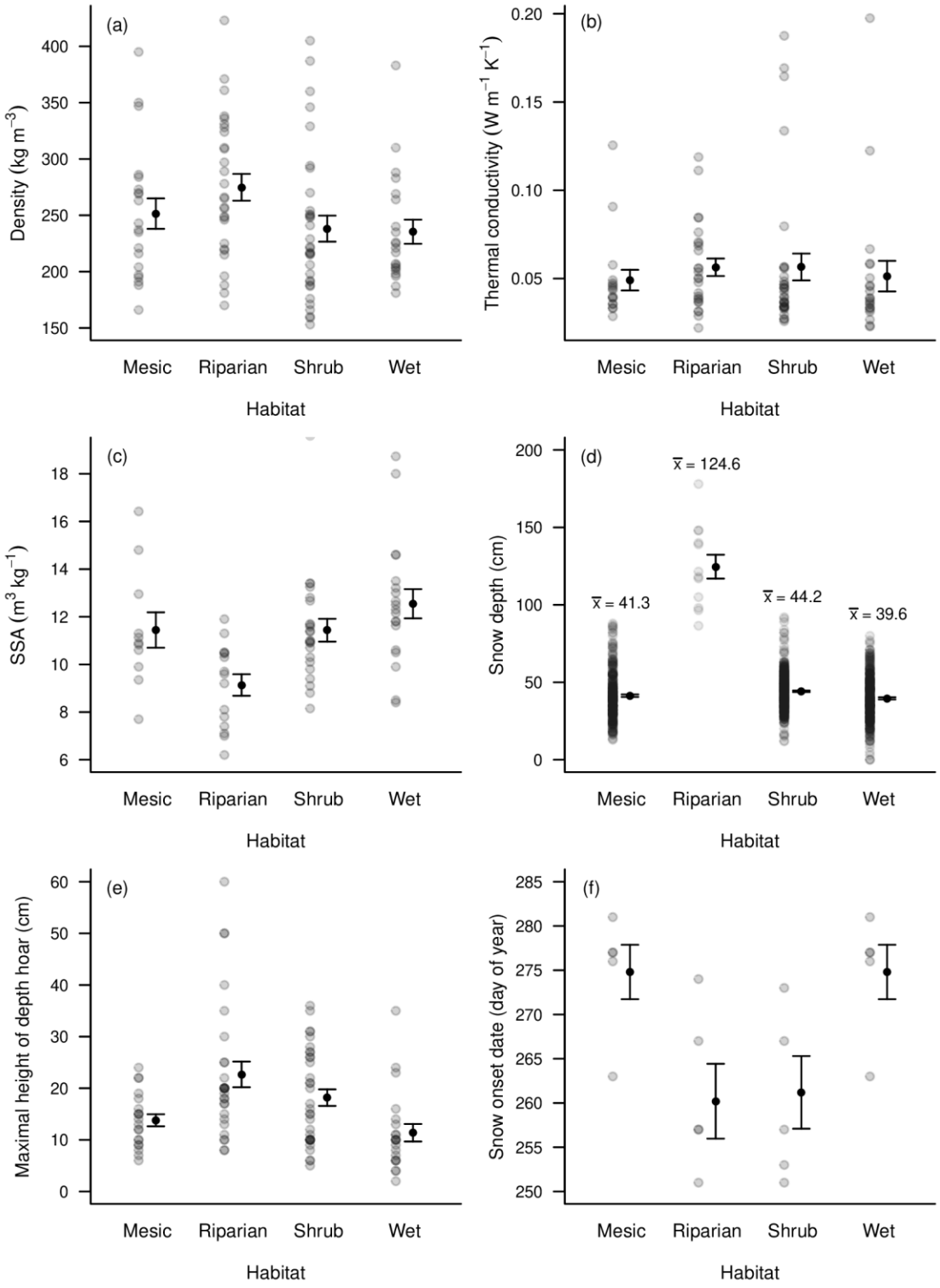

Figure 3.5 Snow properties of four winter habitats used by lemmings at Bylot Island, 2014 – 2019. (a) basal density, (b) basal thermal conductivity (k_{eff}), (c) basal snow specific surface area (SSA), (d) snow depth (n_{mesic} = 342, $n_{riparian}$ = 12, n_{shrub} = 527, n_{wet} = 397), (e) maximal height of depth hoar, and (f) date of permanent snow onset (n_{mesic} = 5, $n_{riparian}$ = 5, n_{shrub} = 5, n_{wet} = 5). For a, b, c and e; n_{mesic} = 20, $n_{riparian}$ = 28, n_{shrub} = 33, n_{wet} = 21. Gray circles represent individual measurements, black circles are the mean and error bars represent SE.

We found strong evidence that temperature of the basal snow layer was warmest in the riparian habitat, coldest in wet and intermediate in shrub ($\beta_{riparian\text{-}shrub}$ = 5.01, CI = [1.7, 8.32]; $\beta_{shrub\text{-}wet}$ = 4.53, CI = [1.21, 7.85]; n = 72; Fig 3.6a, Supplementary Material S3.1 Table S3.3, Fig S3.7). Similarly, we found that daily temperature fluctuations were lowest in riparian habitat, highest in wet and intermediate in shrub, suggesting a more insulative snowpack in riparian and shrub ($\beta_{riparian\text{-}shrub}$ = -1.70, CI = [-2.03, -1.37]; $\beta_{shrub\text{-}wet}$ = -1.04, CI = [-1.36, -0.71]; n = 144; Fig 3.6b, Supplementary Material S3.1 Table S3.3, Fig. S3.8). When correcting for the slight difference in air temperature between the shrub and other habitats (1 °C warmer in shrubs on average), we found similar results (Supplementary Material S3.1 Fig. S3.9).

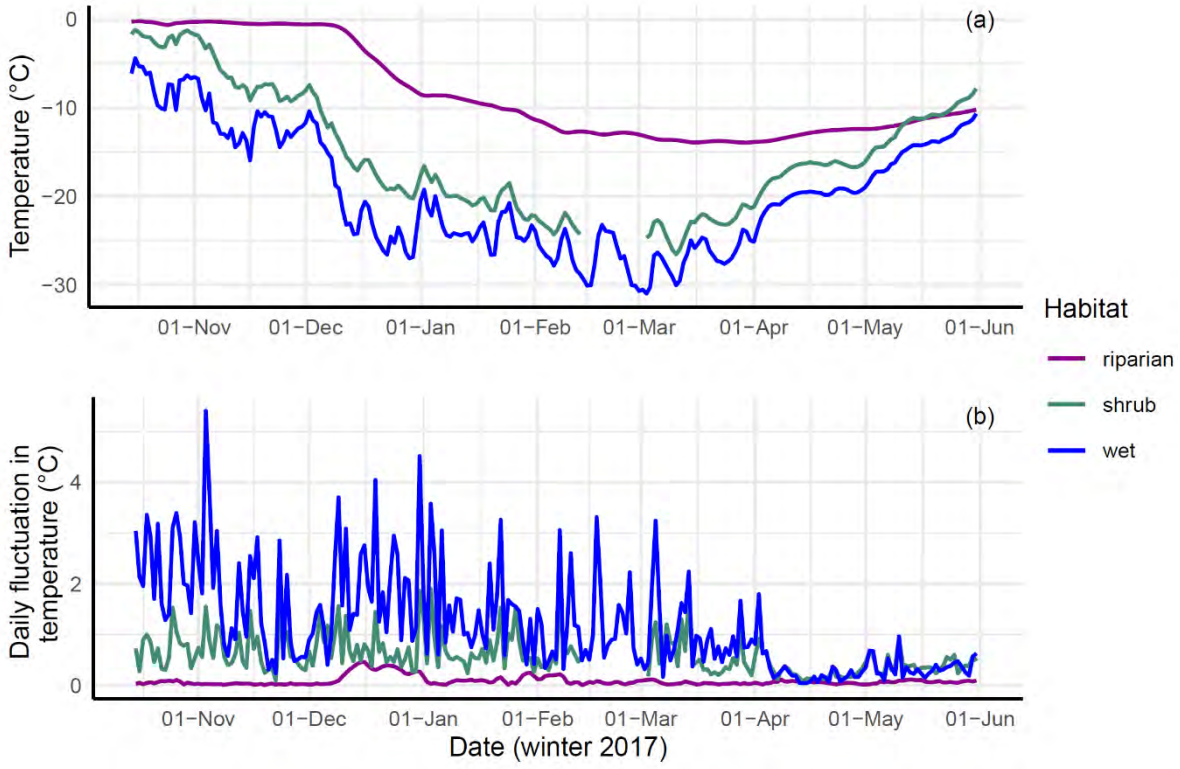

Figure 3.6 (a) Daily temperature and (b) daily temperature fluctuations in the basal snow layer over the winter 2017 in three winter habitats used by lemmings at Bylot Island. There is a data gap for shrub between February 14 and March 2. Winters 2020 and 2021 are presented in Supplementary Material S3.1 Fig. S3.7.

The principal component analysis (PCA) revealed an association between deep snow cover, thick depth hoar and high density of the basal layer, for which riparian habitat globally had higher scores than the other three habitats (Supplementary Material S3.2, Table S3.4, Fig.

S3.11). There was also an association between thermal conductivity and SSA, and scores of the riparian habitat on this axis indicated a negative association with these variables (see Supplementary Material S3.2 for more details on the results).

3.6 Discussion

Our results show that habitat use by lemmings in winter is not random and that snow properties can explain some of the observed patterns. Reproductive activity also differs among habitats and can also be partly explained by spatial variations in snow properties. Overall, riparian habitat was the one with the highest quality in winter as revealed by the highest nest density and reproductive rate, followed by shrub being intermediate, and wetland and mesic habitats being the lowest quality. These patterns were broadly similar for both lemming species despite some differences, and they did not change with population density.

3.6.1 On the importance of a warm and soft snowpack

The first weeks of the winter are thought to be a critical period for lemmings since temperature drops rapidly and the thin, heterogenous snowpack does not provide a significant protection from cold temperatures. Thus, lemming may seek habitats where snow accumulates first, as is the case in riparian and shrub habitats. The riparian habitat also had the deepest snowpack and the thickest depth hoar, two snow characteristics known to offer good insulating properties (Zhang 2005). Indeed, we observed more stable and warmer temperature in the basal snow layer of riparian compared with other habitats (up to 17 °C warmer compared to wetland in the coldest months). These conditions should decrease thermoregulatory costs for lemmings (Chappell 1980a) and could therefore explain why riparian habitat had the highest use and reproductive activity. These observations are consistent with previous studies highlighting the importance of snow depth in lemming habitat use (Batzli et al. 1983, Duchesne et al. 2011a, Schmidt et al. 2021, Von Beckerath et al. 2021), but also in other mammal species like wolverine (*Gulo gulo*; Glass et al. 2021) or brown bear (*Ursus arctos*; Sorum et al. 2019).

Use of the riparian habitat could nonetheless come with a cost as we found evidence for higher snow density in its basal layer compared to other habitats. Since thermal conductivity and density are correlated (Domine et al. 2011), we were surprised that thermal conductivity

was not higher in the riparian habitat, but this might be related to technical difficulties when taking this measurement manually in friable depth hoar layers (Fourteau et al. 2022). We did find smaller SSA values in this habitat, suggesting a greater extent of indurated depth hoar formed in melt-freeze layers, which is consistent with our observations. As snow accumulates early in the riparian habitat, this makes it more susceptible to melting episodes in early winter when temperatures are fluctuating around 0 °C. Furthermore, the vertical temperature gradient is reduced in deeper snowpacks, which slows down depth hoar formation and leads to a denser and less developed depth hoar layer (Marbouty 1980). Therefore, the dense and relatively hard basal layer found in deep snow could explain the reduced reproduction that we observed.

For lemmings, staying inside their nests in winter offers an energetic advantage (Chappell 1980a), so their foraging trips should be as quick and efficient as possible. Digging in hard and dense snow increases their energy expenditure but also decreases their digging speed (Poirier et al. 2021), which may increase the time spent outside the nest and thus thermoregulatory costs. Our results suggest that the complex spatial variability in snow properties may impose tradeoffs on lemmings because even if deep snow areas provide the most favorable thermal environment, they may not offer the best conditions to minimize travel costs. Ultimately, this may reduce their energy available for reproduction. In the boreal forest, a similar tradeoff was observed in the Pacific marten (*Martes caurina*), which prefers habitats with deep snow as a shelter against the cold despite the increased locomotion costs associated with this type of habitat (Martin et al. 2020).

Despite the known preference of brown lemmings for wet habitats in summer (Batzli et al. 1983), our study shows that it is the least used habitat in winter, likely due to its thin snowpack and high daily temperature fluctuations (Duchesne et al. 2011a). Nonetheless, this summer preference could explain the trend for a greater use of this habitat by brown compared to collared lemmings in winter. In addition, considering that lemmings favor horizontal movements over vertical ones when digging tunnels in the snow (Poirier et al. 2019), the presence of sharp mounds surrounding polygons in the wet habitat (Fig. S3.1) may impede lemming movements.

Our results suggest that the shrub is a relatively good habitat for lemmings in winter. Shrubs not only favor early and relatively deep snow accumulation, but they also reduce densification due to overburden compaction, therefore providing optimal conditions for the development of soft depth hoar where movement is facilitated (Domine et al. 2016a). In addition, food resources such as willow buds may encourage lemmings to use this habitat (Soininen et al. 2015, Fauteux et al. 2017). We did not find evidence for a greater reproductive activity in this habitat, but this may be related to the relatively small number of nests found during the 3 years of sampling the shrub habitat. Nonetheless, the favorable snow conditions offered by this habitat will strongly depend on the weather at the beginning of the winter. Indeed, if early winter warm spells lead to the formation of a hard melt-freeze snow layer, this will preclude snow from drifting, preventing the accumulation of a deep snow cover around shrubs (Barrere et al. 2018). It is worth noting that the favorable subnivean temperature found in this habitat was enhanced by the slightly warmer air temperature in that area of the study site compared to the other sites due to the reduced cool katabatic flow (Domine et al. 2022). Moreover, because this habitat is spatially limited in the High Arctic, it is difficult to extrapolate our results in this habitat to other systems.

It is also worth noting that our study focused only on snow properties but other factors such as vegetation or soil characteristics could also influence lemming distribution and reproduction in winter (Duchesne et al. 2011a). Nonetheless, experimental studies showed that snow per se is a strong factor affecting lemming distribution independently of other landscape features (Reid et al. 2012).

3.6.2 Interspecific differences and density dependence

We did not find any difference in habitat use between the two lemming species during winter despite known differences in their summer habitat use (Batzli et al. 1983). One reason could be that both lemmings have a relatively similar winter diet at our study site dominated by dicotyledons, which are mainly found in riparian, shrub and mesic habitats (Soininen et al. 2015). We found a higher winter reproductive activity in collared lemmings compared to brown lemmings, independently of the habitat. Collared lemmings are thought to be better adapted to the extreme conditions of the High Arctic (Fuller et al. 1975) and to be more efficient at digging in hard snow compared to brown lemmings (Poirier et al. 2021), which

might help them save energy for winter reproduction. Considering that winter reproduction is generally a key determinant of lemming outbreaks (Millar 2001, Fauteux et la. 2015), it is surprising that it is the brown and not the collared lemming that reaches the highest density at our study site in those years (Gauthier et al. 2013). This suggests that other demographic factors such as mortality may limit population growth in collared lemmings. This species is known to be more vulnerable to avian predators compared to brown lemmings during the summer (Seyer et al. 2020), and a high reproductive activity may increase predation rate in winter nests (Fauteux and Gauthier 2022).

Contrary to Schmidt et al. (2021), we did not find evidence of density dependence in habitat use. This suggests that when conditions are favorable for the development of a high-quality basal snow layer (Domine et al. 2018), there may be enough refuges and resources to support both lemming species even in peak years at our study site. Nonetheless, brown lemmings are thought to be dominant over collared lemmings during competitive interactions and can force them to use sub-optimal habitats (Morris et al. 2000). Brown lemmings may sometimes take over collared lemming nests and even perform infanticide if young are present (M. Poirier, pers. obs.). Therefore, considering the large overlap in habitat use in winter, we cannot exclude that more subtle differences due to competitive interactions may still exist between the two species. We should also bear in mind that this study focuses on habitats that act as shelter for lemmings (i.e., where they build their nests), which could differ in some cases from the habitats where they forage.

3.6.3 Conclusion

Understanding the winter ecology of arctic species is a huge challenge, especially those living within the snowpack. Our study differs from previous ones by directly assessing the links between snow properties and lemming habitat use instead of relying on proxies of snow conditions, like topographic features or habitat classes (Le Vaillant et al. 2018, Schmidt et al. 2021, Von Beckerath et al. 2021). We showed that spatial variation in snow properties can affect lemming habitat use and reproduction, and thus could affect their demography, as previously shown for annual variations in snow conditions (Bilodeau et al. 2013a, Domine et al. 2018b). Moreover, our results highlight the complex links between snow properties and the ecology of animals living in this medium as we found that habitats offering the most

favorable microclimate (deep snow) may not offer the best conditions for reproduction due to the presence of harder snow. The Arctic snowpack is expected to be strongly affected by climate change as rain-on-snow and melt-freeze events should increase at higher latitudes and cause a hardening of the basal snow layer, especially in critical habitats where snow accumulates early in winter (Hansen et al. 2014). Arctic regions exposed to oceanic currents and with milder and wetter climate are especially exposed to such events (Boonstra et al. 2016). In the worst cases, basal ice crust could encapsulate vegetation and deprive herbivores from their food (Berteaux et al. 2017), leading to massive mortality as was observed in reindeer populations (Stien et al. 2012, Langlois et al. 2017, Dolant et al. 2018). On the other hand, warming of the Arctic will lead to shrub expansion (Tape et al. 2006), which could provide favorable habitats for small mammals in winter. Researchers should aim to monitor snow properties in the long-term, but also at a fine spatial scale to better assess the determinants of the population dynamics of Arctic mammals.

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3.8 Supplementary Material

S3.1 – Supplementary material for Chapter 3

S3.2 – Supplementary analysis: principal component analysis (PCA)

3.9 Bibliography

Audet, B., G. Gauthier, and E. Lévesque. 2007. Feeding ecology of greater snow goose goslings in mesic tundra on Bylot Island, Nunavut, Canada. Condor 109:361–376.

Banks, E. M., R. J. Brooks, and J. Schnell. 1975. A radiotracking study of home range and activity of the brown lemming (*Lemmus trimucronatus*). Journal of Mammalogy 56:888–901.

Barrere, M., F. Domine, M. Belke-Brea, and D. Sarrazin. 2018. Snowmelt events in autumn can reduce or cancel the soil warming effect of snow-vegetation interactions in the arctic. Journal of Climate 31:9507–9518.

Barton, K. 2022. Package MuMIn: Multi-model inference.

Batzli, G. O., F. A. Pitelka, and G. N. Cameron. 1983. Habitat use by lemming near Barrow, Alaska. Holarctic Ecology 6:255–262.

Von Beckerath, X., G. Benadi, O. Gilg, B. Sittler, G. Yannic, A.-M. Klein, and B. Eitzinger. 2021. Long-term monitoring reveals topographical features and vegetation explain winter habitat use of an arctic rodent. Arctic Science 8:349–361.

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 lemming population cycles in the Canadian High Arctic. Oecologia 172:1007–1016.

Boonstra, R., H. P. Andreassen, S. Boutin, J. Hušek, R. A. Ims, C. J. Krebs, C. Skarpe, and P. Wabakken. 2016. Why do the boreal forest ecosystems of Northwestern Europe differ from those of Western North America? BioScience 66:722–734.

Buckland, S. T., D. R. Anderson, K. P. Burnham, J. L. Laake, D. L. Borchers, and L. Thomas. 2004. Advanced distance sampling: estimating abundance of biological populations. Page Oxford University Press, London.

Chami, P., R. Antoine, and A. Sahai. 2007. On efficient confidence intervals for the log-normal mean. Journal of Applied Sciences 7:1790–1794.

Chappell, M. A. 1980. Thermal energetics and thermoregulatory costs of small arctic mammals. Journal of Mammalogy 61:278–291.

Coe, P. K., D. A. Clark, R. M. Nielson, S. C. Gregory, J. B. Cupples, M. J. Hedrick, B. K. Johnson, and D. H. Jackson. 2018. Multiscale models of habitat use by mule deer in winter. Journal of Wildlife Management 82:1285–1299.

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.

Dolant, C., B. Montpetit, A. Langlois, L. Brucker, O. Zolina, C. A. Johnson, A. Royer, and P. Smith. 2018. Assessment of the Barren Ground caribou die-off during winter 2015–2016 using passive microwave observations. Geophysical Research Letters 45:4908–4916.

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 13:6471–6486.

Domine, F., M. Belke-Brea, D. Sarrazin, L. Arnaud, M. Poirier, and T. Joint. 2018a. Soil moisture , wind speed and depth hoar formation in the Arctic snowpack. Journal of Glaciology 64:990–1002.

Domine, F., J. Bock, S. Morin, and G. Giraud. 2011. Linking the effective thermal

conductivity of snow to its shear strength and density. Journal of Geophysical Research: Earth Surface 116:1–10.
Domine, F., K. Fourteau, G. Picard, G. Lackner, D. Sarrazin, and M. Poirier. 2022. Permafrost cooled in winter by thermal bridging through snow-covered shrub branches. Nature geoscience 15:554–560.
Domine, F., J. C. Gallet, J. Bock, and S. Morin. 2012. Structure, specific surface area and thermal conductivity of the snowpack around Barrow, Alaska. Journal of Geophysical Research Atmospheres 117:D00R14.
Domine, F., G. Gauthier, V. Vionnet, D. Fauteux, M. Dumont, and M. Barrere. 2018b. Snow physical properties may be a significant determinant of lemming population dynamics in the high Arctic. Arctic Science 4:813–826.
Domine, F., G. Lackner, D. Sarrazin, M. Poirier, and M. Belke-Brea. 2021. Meteorological, snow and soil data (2013-2019) from a herb tundra permafrost site at Bylot Island, Canadian high Arctic, for driving and testing snow and land surface models. Earth System Science Data 13:4331–4348.
Domine, F., A. S. Taillandier, A. Cabanes, T. A. Douglas, and M. Sturm. 2009. Three examples where the specific surface area of snow increased over time. Cryosphere 3:31–39.
Duchesne, D., G. Gauthier, and D. Berteaux. 2011a. Habitat selection, reproduction and predation of wintering lemmings in the Arctic. Oecologia 167:967–980.
Duchesne, D., G. Gauthier, and D. Berteaux. 2011b. Evaluation of a method to determine the breeding activity of lemmings in their winter nests. Journal of Mammalogy 92:511–516.
Fauteux, D., and G. Gauthier. 2022. Density-dependent demography and movements in a cyclic brown lemming population. Ecology and Evolution 12:e9055.
Fauteux, D., G. Gauthier, and D. Berteaux. 2016. Top-down limitation of lemmings revealed by experimental reduction of predators. Ecology 97:3231–3241.
Fauteux, D., G. Slevan-Tremblay, G. Gauthier, and D. Berteaux. 2017. Feeding preference of brown lemmings (*Lemmus trimucronatus*) for plant parts of Arctic willow (*Salix arctica*). Polar Biology 40:2329–2334.
Feng, C., H. Wang, N. Lu, T. Chen, H. He, Y. Lu, and X. M. Tu. 2014. Log-transformation and its implications for data analysis. Shanghai Archives of Psychiatry 26:105–109.
Fourteau, K., P. Hagenmuller, J. Roulle, and F. Domine. 2022. On the use of heated needle probes for measuring snow thermal conductivity. Journal of Glaciology 68:705–719.
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.
Gallet, J.-C. C., F. Domine, C. S. Zender, and G. Picard. 2009. Measurement of the specific surface area of snow using infrared reflectance in an integrating sphere at 1310 and 1550 nm. The Cryosphere 3:167–182.
Gauthier, G., D. Berteaux, J. Bêty, A. Tarroux, J.-F. Therrien, L. McKinnon, P. Legagneux, and M.-C. Cadieux. 2011. The tundra food web of Bylot Island in a changing climate and the role of exchanges between ecosystems. Ecoscience 18:223–235.
Gauthier, G., J. Bêty, M.-C. Cadieux, P. Legagneux, M. Doiron, C. Chevallier, S. Lai, A. Tarroux, and D. Berteaux. 2013. Long-term monitoring at multiple trophic levels suggests heterogeneity in responses to climate change in the Canadian Arctic tundra. Philosophical transactions of the Royal Society of London. Series B, Biological sciences 368:20120482.
Gilg, O., I. Hanski, and B. Sittler. 2003. Cyclic dynamics in a simple vertebrate predator-

prey community. Science (New York, N.Y.) 302:866–868.
Gilg, O., B. Sittler, and I. Hanski. 2009. Climate change and cyclic predator-prey population dynamics in the high Arctic. Global Change Biology 15:2634–2652.
Glass, T. W., G. A. Breed, G. E. Liston, A. K. Reinking, M. D. Robards, and K. Kielland. 2021. Spatiotemporally variable snow properties drive habitat use of an Arctic mesopredator. Oecologia 195:887–899.
Halpin, M. A., and J. A. Bissonette. 1988. Influence of snow depth on prey availability and habitat use by red fox. Canadian Journal of Zoology 66:587–592.
Hansen, B. B., R. Aanes, I. Herfindal, J. Kohler, and B.-E. Seather. 2011. Climate, icing, and wild arctic reindeer: past relationships and future prospects. Ecology 92:1917–1923.
Hansen, B. B., K. Isaksen, R. E. Benestad, J. Kohler, Å. Pedersen, L. E. Loe, S. J. Coulson, J. O. Larsen, and Ø. Varpe. 2014. Warmer and wetter winters: characteristics and implications of an extreme weather event in the High Arctic. Environmental Research Letters 9:114021.
Ims, R. A., J. A. Henden, and S. T. Killengreen. 2008. Collapsing population cycles. Trends in Ecology and Evolution 23:79–86.
Kausrud, K. L., A. Mysterud, H. Steen, J. O. Vik, E. Østbye, B. Cazelles, E. Framstad, A. M. Eikeset, I. Mysterud, T. Solhøy, and N. C. Stenseth. 2008. Linking climate change to lemming cycles. Nature 456:93–97.
Langlois, A., C. A. Johnson, B. Montpetit, A. Royer, E. A. Blukacz-Richards, E. Neave, C. Dolant, A. Roy, G. Arhonditsis, D. K. Kim, S. Kaluskar, and L. Brucker. 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.
Liston, G. E., and C. A. Hiemstra. 2011. The changing cryosphere: pan-Arctic snow trends (1979-2009). Journal of Climate 24:5691–5712.
MacLean, S. F., B. M. Fitzgerald, and F. A. Pitelka. 1974. Cycles in arctic lemmings: winter reproduction and predation by weasels. Arctic and Alpine Research 6:1–12.
Marbouty, D. 1980. An experimental study of temperature-gradient metamorphism. Journal of Glaciology 26:303–312.
Martin, M. E., K. M. Moriarty, and J. N. Pauli. 2020. Forest structure and snow depth alter the movement patterns and subsequent expenditures of a forest carnivore, the Pacific marten. Oikos 129:356–366.
Millar, J. S. 2001. On reproduction in lemmings. Ecoscience 8:145–150.
Miller, D. L., E. Rexstad, L. Thomas, J. L. Laake, and L. Marshall. 2019. Distance sampling in R. Journal of Statistical Software 89:1–28.
Morris, D. W., D. L. Davidson, and C. J. Krebs. 2000. Measuring the ghost of competition: Insights from density-dependent habitat selection on the co-existence and dynamics of lemmings. Evolutionary Ecology Research 2:41–67.
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.
Poirier, M., D. Fauteux, G. Gauthier, F. Domine, and J. F. Lamarre. 2021. Snow hardness impacts intranivean locomotion of arctic small mammals. Ecosphere 12:e03835.
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. Pages 45-118 *in* H.G. Jones, editor. Snow ecology: An interdisciplinary examination of snow-covered

ecosystems. Cambridge University Press.
Predavec, M., and C. J. Krebs. 2000. Microhabitat utilisation, home ranges, and movement patterns of the collared lemming (*Dicrostonyx groenlandicus*) in the central Canadian Arctic. Canadian Journal of Zoology 78:1885–1890.
R Core Team. 2021. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.
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.
Rennert, K. J., G. Roe, J. Putkonen, and C. M. Bitz. 2009. Soil thermal and ecological impacts of rain on snow events in the circumpolar arctic. Journal of Climate 22:2302–2315.
Ripley, B., B. Venables, D. M. Bates, K. Hornik, A. Gebhardt, and D. Firth. 2022. Package ' MASS ' version 7.3-58.
Schmidt, N. M., F. M. Van Beest, A. Dupuch, L. H. Hansen, J. Pierre, and D. W. Morris. 2021. Long-term patterns in winter habitat selection, breeding and predation in a density-fluctuating, high Arctic lemming population. Oecologia 195:927–935.
Seyer, Y., G. Gauthier, D. Fauteux, and J. F. Therrien. 2020. Resource partitioning among avian predators of the Arctic tundra. Journal of Animal Ecology 89:2934–2945.
Soininen, E. M., G. Gauthier, F. Bilodeau, D. Berteaux, L. Gielly, P. Taberlet, G. Gussarova, E. Bellemain, K. Hassel, H. K. Stenøien, L. Epp, A. Schrøder-Nielsen, C. Brochmann, and N. G. Yoccoz. 2015. Highly overlapping winter diet in two sympatric lemming species revealed by DNA metabarcoding. PLOS ONE 10:e0115335.
Sorum, M. S., K. Joly, A. G. Wells, M. D. Cameron, G. V. Hilderbrand, and D. D. Gustine. 2019. Den-site characteristics and selection by brown bears (*Ursus arctos*) in the central Brooks Range of Alaska. Ecosphere 10:e02822.
St-georges, M., S. Nadeau, and D. Lambert. 1995. Winter habitat use by ptarmigan, snowshoe hares, red foxes, and river otters in the boreal forest - tundra transition zone of western Quebec. Canadian Journal of Zoology 73:755–764.
Stien, A., R. A. Ims, S. D. Albon, E. Fuglei, R. J. Irvine, E. Ropstad, O. Halvorsen, R. Langvatn, L. E. Loe, V. Veiberg, and N. G. Yoccoz. 2012. Congruent responses to weather variability in high arctic herbivores. Biology Letters 8:1002–1005.
Sturm, M., and C. Benson. 2004. Scales of spatial heterogeneity for perennial and seasonal snow layers. Annals of Glaciology 38:253–260.
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.
Sturm, M., J. Holmgren, M. König, and K. Morris. 1997. Thermal conductivity of seasonal snow. Journal of Glaciology 43:26–41.
Sturm, M., J. Holmgren, and G. E. Liston. 1995. A seasonal snow cover classification system for local to global applications. Journal of Climate 8:1261–1283.
Sturm, M., J. P. McFadden, G. E. Liston, S. Chapin III, C. H. Racine, and J. Holmgren. 2001. Snow–shrub interactions in arctic tundra: a hypothesis with climatic implications. Journal of Climate 14:336–344.
Tape, K., M. Sturm, and C. Racine. 2006. The evidence for shrub expansion in Northern Alaska and the Pan-Arctic. Global Change Biology 12:686–702.
Le Vaillant, M., R. Erlandsson, B. Elmhagen, B. Hörnfeldt, N. E. Eide, and A. Angerbjörn. 2018. Spatial distribution in Norwegian lemming *Lemmus lemmus* in relation to the phase of the cycle. Polar Biology 41:1391–1403.

Venables, W. N., and B. D. Ripley. 2002. Modern applied statistics with S. Fourth Edi. Springer-Verlag.
Zhang, T. 2005. Influence of the seasonal snow cover on the ground thermal regime: an overview. Reviews of Geophysics 43:RG4002.

Chapitre 4 – Demography of high Arctic lemmings in response to snow physical properties

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4.1 Résumé

L'hiver est une période difficile pour plusieurs espèces arctiques, dont les lemmings. Pour éviter les températures froides, les lemmings se réfugient sous d'épais couverts de neige où ils construisent des nids à l'intérieur desquels ils peuvent se reproduire si les conditions sont favorables. La présence d'un givre de profondeur friable assure un creusage efficace et facilite le mouvement des lemmings dans la neige, mais de telles conditions favorables dépendent fortement des conditions météorologiques en début d'hiver. En utilisant des séries temporelles de 17 ans, nous avons évalué l'impact des propriétés physiques de la neige sur la reproduction hivernale des lemmings et la croissance hivernale de leur population à l'île Bylot, dans le Haut-Arctique canadien. Notre étude s'est concentrée sur la date d'établissement du manteau neigeux, l'épaisseur de neige et les événements météorologiques menant au durcissement de la couche basale de neige (pluie verglaçante, fonte-regel et pluie-sur-neige) en début d'hiver. Nous avons également vérifié s'il y avait des différences entre les deux espèces de lemmings présentes à notre site d'étude, le lemming brun (*Lemmus tricmucronatus*) et le lemming variable (*Dicrostonyx groenlandicus*), ce dernier montrant de meilleures adaptations morphologiques pour la vie en hiver. Nous avons trouvé que la reproduction hivernale et la croissance des populations des deux espèces étaient négativement reliées aux épisodes modérés de pluie-sur-neige et de fonte-regel. Nous avons également mis en évidence une diminution de la reproduction hivernale avec les épisodes de pluie verglaçante. Contrairement à nos attentes, nous n'avons pas observé de relation entre la démographie des lemmings et la date d'établissement du manteau neigeux ou l'épaisseur de neige. Nous avons trouvé un plus grand taux de reproduction chez le lemming variable en comparaison au lemming brun, suggérant une stratégie plus efficace pour économiser de l'énergie en vue de la reproduction. Globalement, cette étude montre que même des épisodes météorologiques modérés menant au durcissement du manteau neigeux peuvent affecter la démographie des lemmings, probablement en influençant leur capacité à se reproduire dans le manteau neigeux. Avec les changements climatiques, l'augmentation attendue de tels événements météorologiques pourrait menacer les populations de lemmings du Haut-Arctique ainsi que les prédateurs qui en dépendent.

4.2 Abstract

Winter poses major challenges for many arctic species such as lemmings. To avoid cold temperature, lemmings seek refuge in areas with deep snowpack where they build nests in which they can reproduce if conditions are favorable. Presence of a soft depth hoar ensures efficient digging and facilitates lemming movement in the snow but such favorable conditions are highly dependent on weather conditions at the beginning of winter. Using 17-year time series, we assessed the impact of snow physical properties on lemming winter reproduction and winter population growth on Bylot Island in the Canadian High Arctic, a site characterized by a cold and dry Arctic climate. We focused on snow onset date, snow depth and weather events leading to a hardening of the snow basal layer (i.e., freezing rain, melt-freeze, and rain-on-snow) at the beginning of winter. We also examined possible differences between the two lemming species found at our study site, the brown lemming (*Lemmus trimucronatus*) and collared lemming (*Dycrostonyx groenlandicus*), the latter presenting better morphological adaptation to winter life. We found that winter reproduction and population growth of both species were negatively related to moderate rain-on-snow and melt-freeze events. We also found evidence for a decrease in their winter reproduction in presence of freezing rain. Contrary to our expectation, no relationship was found between lemming demography and snow onset date or snow depth. We found a higher reproductive rate in collared than in brown lemming, suggesting a more effective strategy to save energy for winter reproduction in the former species. Overall, this study shows that even moderate weather events leading to snow hardening can impact lemming population growth in winter, likely by influencing their capacity to reproduce beneath the snowpack. The expected increase in such weather events with climate change may threaten lemming populations even in the High Arctic, as well as predators depending upon them.

4.3 Introduction

Seasonality can produce temporary but essential habitats for many species that evolved with its recurrent climatic pattern. For instance, vernal pools created during rainy seasons support the development of numerous organisms including insects and amphibians (Zedler 2003). Similarly, in northern environments, the formation of an annual snowpack creates a temporary habitat for a multitude of resident animals, such as brown bears (*Ursus arctos*), willow ptarmigans (*Lagopus lagopus*), wolverines (*Gulo gulo*) and several small mammals (Andreev 1991, Reid et al. 2012, Sorum et al. 2019, Glass et al. 2021a). For animals living under the snowpack, the insulating properties of snow makes it a good shelter against cold and also offers protection against predators (Duchesne et al. 2011a, Bilodeau et al. 2013b). Nevertheless, physical characteristics of snow can change drastically from year to year depending on prevailing weather conditions and this can have a profound impact on animals using this habitat.

Lemmings of the *Lemmus* and *Dicrostonyx* genera are small mammals found in the Arctic that have adapted to the long and harsh winter by living within the snowpack for up to 9 months. They seek deep snowpack to build their nests made of dry vegetation, which provide warmth and can even support reproduction under the right conditions (Duchesne et al. 2011a, Reid et al. 2012, Poirier et al. 2023). The capacity to reproduce under the snowpack allows for rapid population growth during the winter period. To find food or mate, lemmings dig a network of tunnels in the softest snow layer, called the depth hoar, typically located at the base of the snowpack (Sturm and Benson 1997, Poirier et al. 2019). Their ability to thrive in this habitat is a key factor allowing for the persistence of their populations and can explain why they have become a vital prey for most tundra predators (Gauthier et al. 2011, Schmidt et la. 2012). Despite these adaptations, many lemming populations go through large amplitude multi-annual cyclic fluctuations, mostly due to density-dependent changes in predator pressure (Fauteux et al. 2016, Fauteux and Gauthier 2022, Bergeron et al. 2023). However, recent literature highlighted the role of other factors, including snow properties, which could play a role in affecting and in some case dampening these cyclic fluctuations (Kausrud et al. 2008, Bilodeau et al. 2013a, Domine et al. 2018b).

The changing climate will inevitably modify characteristics of the snowpack, particularly in the Arctic where temperatures have already increased almost four times faster than the global average (Rantanen et al. 2022). As a result, delayed snow onset and increased precipitation are anticipated (Liston and Hiemstra 2011). Moreover, temperatures are more prone to rise above the freezing point after snow onset, leading to the formation of liquid water due to melting in the snowpack, or to input of liquid water during rain-on-snow events (Liston and Hiemstra 2011). Subsequent refreezing of this water forms hard melt-freeze layers within the snowpack, and rain-on-snow events form the hardest and thickest refrozen layers (Domine et al. 2018b). When occurring at the beginning of winter, these melt-freeze layers compromise the formation of a soft depth hoar layer (Domine et al. 2009), which can have a long-lasting effect and be detrimental to lemmings (Berteaux et al. 2017, Domine et al. 2018b). Freezing rain can also lead to glazed ice on top of the snow and, although it is typically rare in the High Arctic (Roberts and Stewart 2008), it could become more frequent with global warming (Groisman et al. 2016).

Hardening of the snowpack, mainly induced by rain-on-snow events, has been shown to threaten populations of herbivores such as caribous (*Rangifer tarandus*), rock ptarmigans (*Lagopus muta*) and east European voles (*Microtus levis*) (Stien et al. 2012, Hansen et al. 2013). In addition to hampering animal movements through the snow (Poirier et al. 2021), severe rain-on-snow events can encapsulate vegetation and deprive animals from their food source (Hansen et al. 2014, Sokolov et al. 2016). The fading out of small mammal population fluctuations and persistent low population in some regions of the Arctic has been linked to change in the snow regime, such as an increase in snow hardness (Hörnfeldt et al. 2005, Ims and Fuglei 2005, Kausrud et al. 2008). Winter reproduction is considered a crucial factor in lemming population outbreaks (Ims et al. 2011), but snow characteristics can modulate their ability to reproduce (Domine et al. 2018b). Indeed, in presence of hard snow, lemmings increase their digging efforts (Poirier et al. 2021), which likely reduce the energy available for reproduction. However, all lemming species may not be affected equally. For instance, the collared lemming (*Dicrostonyx groenlandicus*) appears to be better adapted to life in the snow than the brown lemming (*Lemmus trimucronatus*) with its white fur color, the growth of large bifid claws in winter, and its overall better performance when digging in hard snow (Hansen 1957, Zimova et al. 2018, Poirier et al. 2021).

In this study, we assessed the impact of specific snow conditions on lemming winter demography under the cold and dry climate of the High Arctic. First, we hypothesized that lemming exposure to predation and thermoregulatory costs should increase with a delayed or shallow snow cover (Gilg et al. 2009). Accordingly, we predicted that a late snow onset and a shallow snow accumulation at the beginning of winter should reduce lemming winter reproduction and population growth. Second, we hypothesized that a hard basal snow layer induced by extreme weather events increases lemming energetic costs to dig (Poirier et al. 2021) and negatively impacts their demography. Therefore, we predicted that melt-freeze, rain-on-snow and freezing rain events occurring at the beginning of winter should also reduce lemming winter reproduction and population growth. Third, we hypothesized that the effects of these specific snow properties on lemming demography should be exacerbated (1) by the presence of ermines (*Mustela richardsonii*), the only predator that can efficiently hunt lemmings under the snow (Bilodeau et al. 2013b), and (2) at high lemming density due to increased competition for food. Finally, we hypothesized that demographic responses to snow conditions will differ between lemming species due to differential adaptation to the winter environment. More specifically, winter reproduction and population growth of collared lemmings should be less impacted by hard snow compared to brown lemmings.

4.4 Methods

4.4.1 Study area

The study took place in the Qarlikturvik valley of Bylot Island (73°08'N, 80°00'W) between 2004 and 2021. This site is characterized by a cold and dry High Arctic climate with a mean temperature of -36.7 °C during the coldest month in February and a mean snow depth of 31 cm in flat terrains at the end of winter (Domine et al. 2021b). Snow usually sets in early October and ends in early June. The 51 km^2 study area is mainly characterized by a mosaic of mesic, wetland and riparian habitats. The mesic habitat is dominated by herbaceous plants, prostrate shrubs and mosses (Audet et al. 2007) whereas the wetland habitat is dominated by mosses and graminoids (Gauthier et al. 2011). The riparian habitat is defined as the tundra next to streams including slopes on either side, which favors deep snow accumulation (i.e., snowdrifts) due to wind deposition. Vegetation in riparian habitat is a mix of mesic and

wetland, following an increasing humidity gradient from the top to the bottom of slopes (Poirier et al. 2023).

4.4.2 Lemming demographic parameters

We determined lemming winter reproduction annually between 2007 and 2022 from winter nests sampled along forty 500 m long permanent transects, equally and randomly distributed in the mesic and riparian habitats. The wetland habitat was not sampled since it is little used by lemmings in winter, likely due to the low quality of the snow cover (Poirier et al. 2023). Soon after snow melt, we slowly walked each transect and dissected every nest detected. We identified the species that occupied it (brown or collared) based on size, shape and color of feces (MacLean et al. 1974), a reliable method (Soininen et al. 2015). We also noted the occurrence of reproduction, which was determined when at least one third of all feces present were of distinctively small size, an indication that juveniles occupied the nest (Duchesne et al. 2011b). When feces of both species were found in the nest (about 5 % of the time), we duplicated the nest in our dataset and considered it as a double occupation. When reproduction was detected in these nests, layering order of feces indicated which species had reproduced. We estimated the proportion of reproductive nests for each species by dividing the number of nests with reproduction by the total number of nests found each year. In years of low lemming density, we could not find enough nests along the transects to accurately estimate proportions, so we included in the analysis nests found opportunistically in mesic and riparian habitats. Observers found nests opportunistically while conducting other activities in the field and such sampling was considered random. Due to covid-19 travel restrictions, we could not collect nests in early summer 2021, and no nest at all in 2020.

We obtained summer lemming densities from live-trapping in two 11-ha square grids located in mesic and wet habitats (one each). Each grid had 144 Longworth traps (100 from 2004 to 2006) spaced out at 30-m intervals. Traps were baited with a small piece of apple and peanut butter and stuffing was added to help animals keep their warmth. Trapping was performed in mid-June, mid-July and mid-August every year since 2004, but not in 2020 and only in August 2021 due to covid-19. Traps were checked twice a day for 3 or 4 consecutive days during each trapping session. All animals trapped were identified to species, marked, and released (see Fauteux et al. 2015 for details). We obtained density estimates from spatially

explicit capture-recapture models using the secr package version 4.6.0 (Efford 2023) implemented in the R software version 4.1.0 (R Core Team 2021) for each species, grid and trapping session. We averaged density of both grids to obtain density by species and by month (June, July, August).

We determined winter growth of lemmings between 2004 and 2021 from the natural log of the ratio between density in June and density in August of the previous year. Each winter is referred to by the year when it ended (e.g., winter 2003–2004 is referred to as winter 2004). Due to some zero values, we added to all densities (in lemmings/ha) 0.01, which is half of the smallest value (0.02) that could be determined on our trapping grids, i.e., if only one individual was captured. In 2010, we used mean June-July lemming density because persistent snow led to an underestimation of lemming density in June. For winter 2004, density in August of the previous year (2003) was estimated from snap trapping data (Gruyer et al. 2008) based on the equations of Fauteux et al. (2018) because live-trapping only started in 2004.

4.4.3 Snow and weather data

Since 1993, an automated weather station located in our study area (BYLCAMP) records several snow and weather variables such as snow depth, air temperature, relative humidity and wind velocity et hourly interval (CEN 2022). We obtained mean snow depth during the month of November with a SR50 acoustic gauge. In 2010 and between 2014-2017, no snow depth data were recorded due to a malfunction of the station. For 2014-2017, we used environmental data from another automated weather station located 1.7 km away in the study area. We adjusted data between the two stations using the 2018 and 2019 data, which were available at both stations (average snow depth difference: 0.83 cm, $R^2 = 0.92$).

The snow onset date corresponds to the first date of the season when snow covered more than 80 % of our study area without returning below 50 % cover at a later date during the season. To determine this value, we first obtained an interval of snow onset date using MODIS images (Moderate Resolution Imaging Spectroradiometer; extracted from https://modis.gsfc.nasa.gov/). This satellite provides one image daily (500 m resolution) in which we detected the presence of snow on the ground with the normalized-difference snow

index (NDSI; Riggs and Hall 2015), allowing us to calculate a percentage of snow cover over the study area (see Supplementary Material S4.1 for details). However, images were often not usable due to presence of clouds, leading to data gaps of up to 18 days. Having a more accurate snow onset date was crucial because it influences partial melting processes we wished to determine in this study. Therefore, we refined snow onset dates by using other methods including pictures of the study area taken daily by automated cameras (from 2016 to 2021 only) and hourly weather data recorded at our study site and in Mittimatalik (Pond Inlet), a town located about 90 km from our study site (see Supplementary Material S4.1 Figs. S4.1-S4.22). In Supplementary Material S4.1 Table S4.1, we summarized how each data source was used to determine the snow onset date each year.

To evaluate the impact of rain-on-snow, melt-freeze and freezing rain events on lemming demography, we scored the occurrence and intensity of each of these events as follows. Scores were calculated between the snow onset date and November 30 because we were interested in events occurring at the beginning of winter when most of the depth hoar is formed. The rain-on-snow score was obtained by summing the number of hours with positive temperatures and a relative humidity >95 %. Under these conditions, it is safe to assume that precipitations were most likely rain rather than snow, as the precipitation phase is a function of relative humidity (Jennings et al. 2018). The melt-freeze score was obtained by summing the number of hours with positive temperatures and a relative humidity <95 %. Chances of liquid precipitation are less than 50 % below this humidity level (Jennings et al. 2018) and 0 °C is the temperature at which snow grains start thawing and forming clusters when refreezing (Colbeck 1982). Finally, we based our freezing rain score on categorical freezing rain reanalysis data, which estimates the presence/absence of freezing rain events every 6h (NCEP North American Regional Reanalysis (NARR), extracted from https://psl.noaa.gov/). This reanalysis model combines observational data, satellite data and output from numerical weather prediction models to estimate atmospheric conditions that favor the occurrence of a freezing rain event during a 6h period with a 32 km resolution. We summed the number of freezing rain events detected within a radius of 80 km from the center of our study site and multiplied this value by 6 to obtain hourly scores.

Between 2014 and 2022, we also measured snow basal density (i.e., the lowest 5 cm of snow) in riparian and mesic habitat with a box cutter (Conger and McClung 2009). These measurements were performed in May before snow melt except in 2016 due to logistical constraints. Between 1 to 11 snow pits were dug in each habitat annually, from which the snow basal density measurements were taken.

4.4.4 Statistical analysis

We assessed the influence of snow properties (snow onset, snow depth in November) and weather events (rain-on-snow, melt-freeze, freezing rain) on the proportion of winter nests with reproduction using generalized linear models with the logit link and the quasibinomial distribution to account for overdispersion problems (glm function, Venables and Ripley (2002). Lemming species, density dependence and ermine abundance were added to the models as additive or interactive terms. We used lemming density in August of the previous year to test for density-dependence and index of abundance obtained during the preceding summer for the ermine. This latter estimation of abundance was derived from testimonials of observations from the field because no ermine densities were available (see Bolduc et al. (2023) for more details). We log-transformed weather events variables to better fit the data distribution since visual inspection of the data suggested that relationships were not linear. We evaluated how our models fitted the data with the adjusted R^2 and retained the model with the highest R^2 for interpretation as it is not possible to obtain ΔAICc with quasibinomial models (Venables and Ripley 2002). This method is particularly useful when the number of parameters is low and slightly varies among models (±2 parameters), which was the case here.

We also assessed the effect of snow properties (snow onset, snow depth in November) and weather events (rain-on-snow, melt-freeze, freezing rain) on winter growth of lemming populations using linear models. Lemming species, density-dependence and ermine abundance were added to the models as additive or interactive terms as previously described. We evaluated the strength of support of each model using adjusted R^2.

The evidence of the relationships was determined based on the 95% confidence intervals around the slope parameters, and robust standard errors (SE) were used in linear models with

homoscedasticity problems (hccm function of the car package version 3.1-2; Freedman 2006).

As a complementary analysis, we examined the direct effect of snow basal density on winter reproduction and population growth using linear and binomial models, respectively. We could not compare these analyses with the previous ones due to the shorter time series (2014-2021).

4.5 Results

4.5.1 Occurrence of specific weather events

During winters 2004 to 2022, the compilation of weather data allowed us to document six years with rain-on-snow events of various intensities from snow onset date to end of November on Bylot Island (Fig. 4.1). Melt-freeze events were more common and occurred every year but with a highly variable intensity (scores between 4 to 140; Fig. 4.1). Finally, we detected seven years with freezing rain events near our study site (Fig. 4.1).

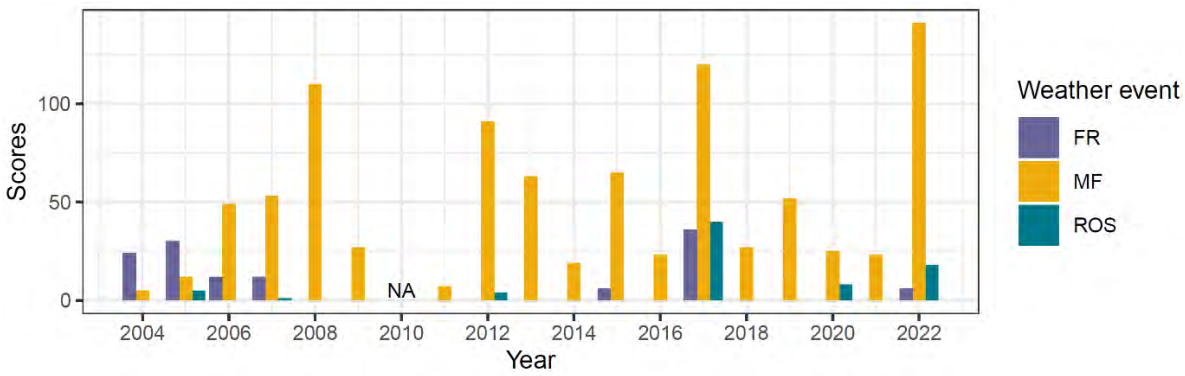

Figure 4.1 Scores of the different weather events occurring at the beginning of winter (from snow onset to the end of November) on Bylot Island over the period 2004 to 2022 (each winter is referred to by the year when it ended). No measurement is available for 2010 (NA). Freezing rain (FR) is the sum of hours with freezing rain events, melt-freeze (MF) score is the sum of positive temperature recorded every hour with humidity < 95%, and rain-on-snow (ROS) is the sum of positive temperature recorded every hour with humidity > 95% (see methods for details).

4.5.2 Determinants of winter reproduction

From 2007 to 2022, the proportion of winter nests with signs of reproduction was 1.7 times greater on average in collared compared to brown lemmings (Table 4.1, Supplementary Material S4.2 Fig. S4.23). We found evidence for a negative influence of rain-on-snow, melt-freeze and freezing rain on lemming winter reproduction (Fig. 4.2, Table 4.1). On average,

the proportion of winter nests with reproduction was reduced by 47 % by rain-on-snow, 43 % by melt-freeze and 37 % by freezing rain over the range of scores encountered for each of these variables on Bylot Island. We also found weak evidence for a slight positive relationship between winter reproduction and lemming density (Table 4.1), but no evidence for an interaction with snow variables. We did not find evidence for an influence of snow onset date and snow depth in November on winter reproduction (Supplementary Material S4.2 Table S4.2, Figs. S4.24, S4.25). We also did not find support for interactive effects between snow variables and ermine abundance, as well as no influence of ermine alone (Table 4.1, Supplementary Material S4.2 Table S4.2).

Table 4.1 Coefficients of the models with the greatest strength of support examining the influence of snow parameters (rain-on-snow (ros), melt-freeze (melt), freezing rain (fr), snow depth in November and snow onset) on annual proportion of lemming winter nests with reproduction with additive or interactive effects of lemming species, lemming density in August of the previous year (density) and ermine abundance of the previous summer on Bylot Island, 2007 – 2022. The slope estimate (β), its 95% confidence interval (CI), the dispersion parameter (φ), the number of parameters in the model (k), and the adjusted R^2 are presented. Models appear in decreasing order of strength of support based on R^2. Conclusive fixed effects are in bold. See Supplementary Material S4.2 Table S4.2 for the exhaustive model list.

Model	Parameter	β	95% CI	φ	k	R^2
ros + density + species	(Intercept)	-1.00	[-1.20, -0.76]	1.91	4	0.43
	log(ros)	**-0.23**	**[-0.38, -0.08]**			
	log(density)	**0.09**	**[0.00, 0.18]**			
	collared	**0.76**	**[0.40, 1.12]**			
ros + ermine + species	(Intercept)	-1.16	[-1.44, -1.76]	1.96	4	0.41
	log(ros)	**-0.26**	**[-0.42, -0.09]**			
	ermine	0.20	[-0.02, 0.43]			
	collared	**0.64**	**[0.31, 0.97]**			
ros*density + species	(Intercept)	-1.01	[-1.22, -0.76]	1.99	5	0.4
	log(ros)	**-0.23**	**[-0.39, -0.07]**			
	log(density)	**0.10**	**[0.00, 0.20]**			
	collared	**0.77**	**[0.39, 1.15]**			
	log(ros):log(density)	0.02	[-0.08, 0.11]			
fr + density + species	(Intercept)	-0.47	[-0.85, -4.76]	2.04	4	0.39
	log(fr)	**-0.32**	**[-0.56, -0.09]**			
	log(density)	**0.10**	**[0.00, 0.19]**			
	collared	**0.80**	**[0.42, 1.17]**			
ros*ermine + species	(Intercept)	-1.19	[-1.50, -1.76]	2.04	5	0.39

	log(ros)	-0.33	[-0.71, 0.06]			
	ermine	0.20	[-0.03, 0.43]			
	collared	**0.65**	**[0.31, 0.98]**			
	log(ros):ermine	0.05	[-0.19, 0.28]			
fr*density + species	(Intercept)	-0.50	[-0.90, -5.76]	2.12	5	0.37
	log(fr)	**-0.31**	**[-0.55, -0.07]**			
	log(density)	0.04	[-0.19, 0.28]			
	collared	**0.82**	**[0.43, 1.21]**			
	log(fr):log(density)	0.04	[-0.12, 0.20]			
ros + species	(Intercept)	-1.00	[-1.21, -0.76]	2.12	3	0.36
	log(ros)	**-0.20**	**[-0.36, -0.04]**			
	collared	**0.60**	**[0.26, 0.94]**			
melt + density + species	(Intercept)	-0.12	[-0.82, -1.76]	2.16	4	0.35
	log(melt)	**-0.24**	**[-0.43, -0.04]**			
	log(density)	0.06	[-0.04, 0.15]			
	collared	**0.73**	**[0.34, 1.12]**			
melt + species	(Intercept)	-0.10	[-0.80, -1.76]	2.18	3	0.34
	log(melt)	**-0.24**	**[-0.44, -0.05]**			
	collared	**0.64**	**[0.29, 1.00]**			
ros*species	(Intercept)	-0.99	[-1.21, -9.76]	2.21	4	0.34
	log(ros)	-0.19	[-0.40, 0.03]			
	collared	**0.59**	**[0.24, 0.95]**			
	log(ros):collared	-0.04	[-0.37, 0.29]			
melt + ermine + species	(Intercept)	-0.12	[-0.88, -1.76]	2.28	4	0.32
	log(melt)	**-0.24**	**[-0.45, -0.04]**			
	ermine	0.02	[-0.21, 0.25]			
	collared	**0.64**	**[0.28, 1.01]**			
melt*density + species	(Intercept)	-0.15	[-0.87, -1.76]	2.25	5	0.32
	log(melt)	**-0.23**	**[-0.43, -0.03]**			
	log(density)	0.14	[-0.35, 0.63]			
	collared	**0.72**	**[0.31, 1.12]**			
	log(melt):log(density)	-0.02	[-0.16, 0.11]			
fr + species	(Intercept)	-0.56	[-0.96, -5.76]	2.30	3	0.31
	log(fr)	**-0.26**	**[-0.50, -0.02]**			
	collared	**0.61**	**[0.26, 0.96]**			
melt*species	(Intercept)	-0.09	[-0.93, -0.76]	2.28	4	0.31
	log(melt)	**-0.25**	**[-0.49, -0.01]**			
	collared	0.63	[-1.05, 2.31]			

log(melt):collared	0.00	[-0.44, 0.45]

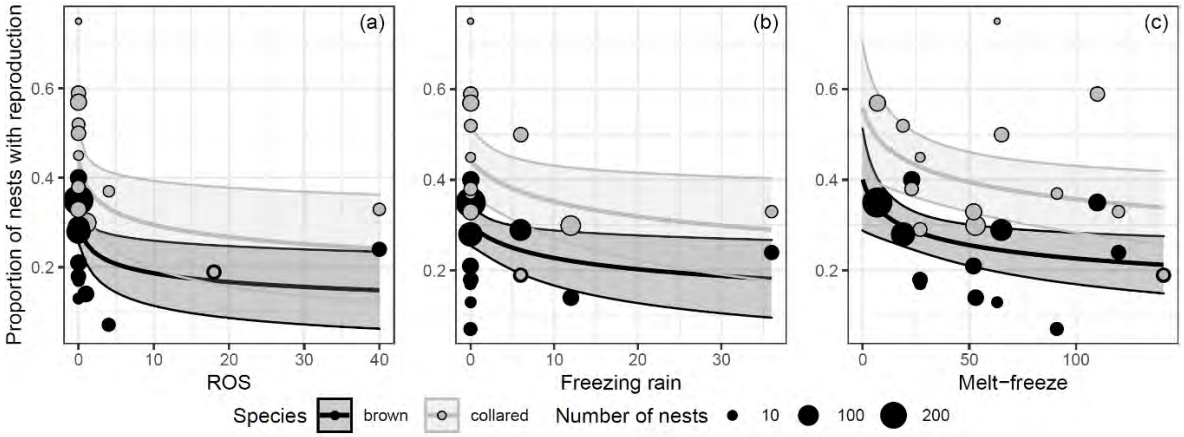

Figure 4.2 Logarithmic relationships between annual proportion of winter nests with reproduction and (a) rain-on-snow (ROS), (b) freezing rain and (c) melt-freeze scores at the beginning of winter in brown and collared lemmings on Bylot Island, 2007-2022. Filled-in areas are 95% CI.

4.5.3 Determinants of winter population growth

Winter population growth of lemmings (*r*) fluctuated from -6.7 to 5.0 between 2004 to 2022 (Supplementary Material S4.2 Fig. S4.26). When examining the influence of snow properties on winter population growth, we found support for negative relationships with rain-on-snow and, to a lesser extent, melt-freeze events, as well as with lemming density (Table 4.2, Fig. 4.3). On average, population growth was reduced from -1.1 to -4.1 by rain-on-snow and from -0.8 to -2.7 by melt-freeze over the range of scores encountered for each of these variables on Bylot Island. We did not find support for a relationship between winter population growth and either snow onset date or snow depth in November (Table 4.2, Supplementary Material S4.2 Table S4.3 and Figs. S4.24-S4.25). We did not find difference in winter population growth between lemming species or evidence of an influence of ermine abundance in the previous summer (Supplementary Material S4.2 Table S4.3, Fig. S4.27). Similarly, we did not find evidence of an interactive effect of lemming species, ermine abundance and lemming density with snow variables.

Table 4.2 Coefficients of the models with the greatest strength of support examining the influence of snow parameters (rain-on-snow (ros), melt-freeze (melt), freezing rain, snow depth in November (depth) and snow onset) on winter population growth of lemmings with additive or multiplicative effects of lemming species, lemming density in August of the previous year (density) and ermine abundance of the previous summer on Bylot Island, 2007 – 2022. The slope estimate (β), its 95% confidence interval (CI), the number of parameters in the model (k) and the adjusted R^2 are presented. Models appear in decreasing order of strength of support based on R^2. Conclusive fixed effects are in bold. See Supplementary Material S4.2 Table S4.3 for the exhaustive model list.

Model	Parameter	β	95% CI	k	R^2
ros + density	(Intercept)	-0.83	[-1.64, -0.01]	3	0.55
	ros	**-0.07**	**[-0.13, -0.02]**		
	log(density)	**-0.80**	**[-1.17, -0.43]**		
ros*density	(Intercept)	-0.75	[-1.59, 0.09]	4	0.55
	ros	**-0.07**	**[-0.14, 0.00]**		
	log(density)	**-0.74**	**[-1.14, -0.34]**		
	ros:log(density)	-0.03	[-0.12, 0.07]		
melt + density	(Intercept)	-0.47	[-1.65, 0.71]	3	0.52
	melt	**-0.01**	**[-0.03, 0.00]**		
	log(density)	**-0.87**	**[-1.19, -0.54]**		
melt*density	(Intercept)	-0.34	[-1.59, 0.92]	4	0.51
	melt	**-0.02**	**[-0.03, 0.00]**		
	log(density)	**-0.70**	**[-1.27, -0.14]**		
	melt:log(density)	0.00	[-0.01, 0.01]		

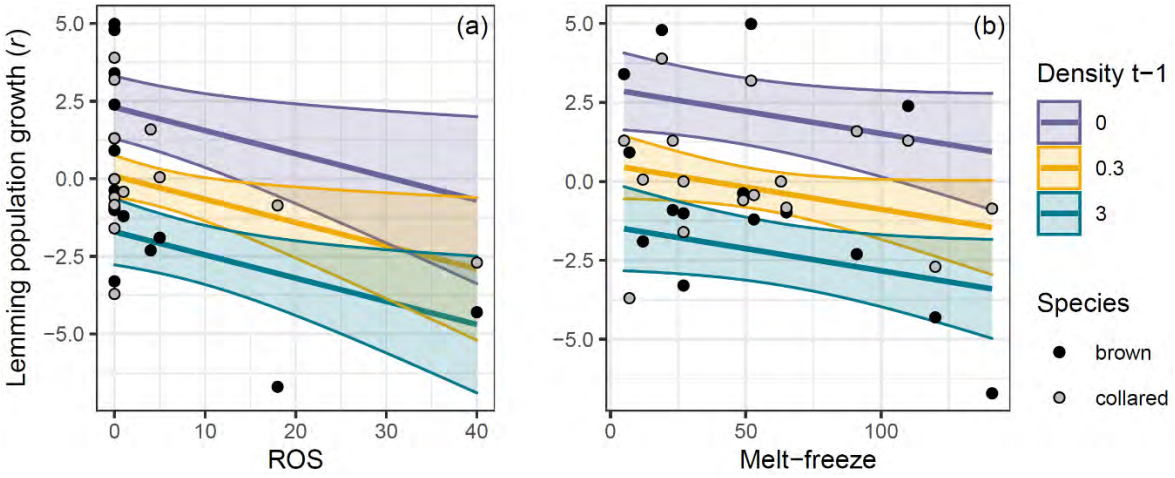

Figure 4.3 Linear relationships between winter population growth (*r*) of brown and collared lemmings and (a) rain-on-snow (ROS) and (b) melt-freeze scores at the beginning of winter with an additive logarithmic effect of lemming density (n/ha) at t-1 on Bylot Island, 2004-2022. Filled-in areas are 95% CI.

4.5.4 Demographic response to snow basal density

During winters 2014 to 2022, snow basal density varied from 200 to 300 kg m^{-3} (Supplementary Material S4.2 Fig. S4.28). We found weak evidence for a negative influence of snow basal density on proportion of winter nests with reproduction (β = -0.01, CI = [-0.01, 0.00]; Fig. 4.4a) and stronger evidence for a negative influence on winter population growth (β = -0.06, CI = [-0.10, -0.02]; Fig. 4.4b).

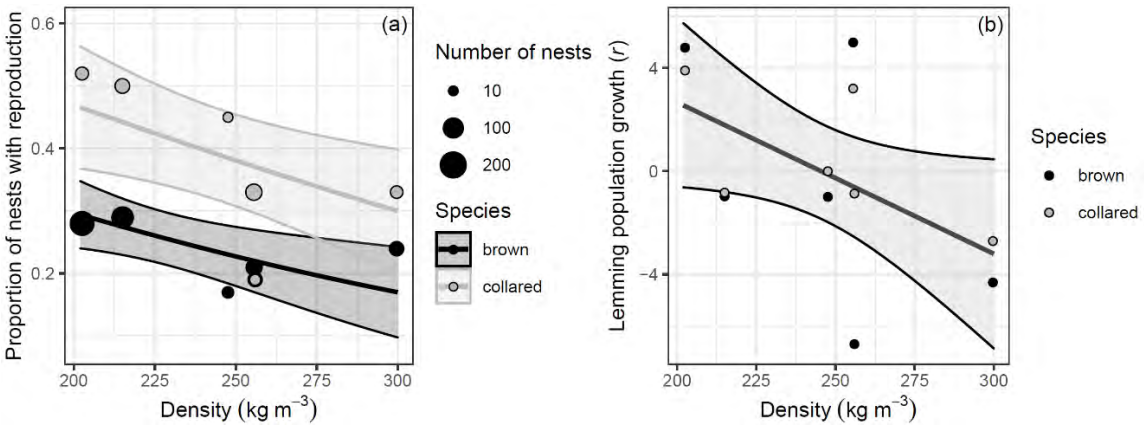

Figure 4.4 Linear relationships between annual proportion of winter nests with reproduction (a) or winter population growth (b) and snow basal density for brown and collared lemmings on Bylot Island, 2014-2022. Filled-in areas are 95% CI.

4.6 Discussion

4.6.1 Linking lemming winter demography to snow conditions

Our results support the hypothesis that snow properties play a significant role in lemming demography during winter. More specifically, we found evidence for detrimental effects of early winter weather events that lead to snow hardening on lemming winter reproduction and population growth. Rain-on-snow events may not be as frequent or intense in the Canadian Arctic compared to regions exposed to oceanic currents (e.g., Northern Europe), but their occurrence still appears to affect lemming population growth and reproduction during winter. Melt-freeze events following onset of the snowpack, which are more frequent than rain-on-snow events, also appear to influence lemming demography in winter. Finally, freezing rain, which leads to the formation of ice layers above the snow, was found to impact lemming winter reproduction. These findings are consistent with those of Domine et al. (2018b), who also observed a decline in lemming populations during winter in presence of a hard basal snow layer inferred through snow physics model. However, whereas Domine et al. (2018b)

identified rain-on-snow as the main source of snow hardening, our study also highlights the importance of melt-freeze and freezing rain events in disturbing the snowpack and lemming demography.

Previous studies have reported collapses of small mammal populations following heavy rain-on-snow events in Arctic regions with milder and wetter climate than the Canadian High Arctic, such as on Svalbard (Stien et al. 2012) and in Norway (Ims et al. 2008). Intense rain-on-snow events are of significant importance because they can encapsulate vegetation in a basal ice layer, depriving small mammals of an access to food and leading to catastrophic winter mortality (Ims et al. 2008, Kausrud et al. 2008). Larger herbivores such as reindeer (*Rangifer tarandus*) and muskoxen (*Ovibos moschatus*) also suffer from the formation of basal ice layers following severe rain-on-snow events (Rennert et al. 2009, Stien et al. 2012). In the Canadian Arctic, where the climate is colder and drier, these weather events are generally less extreme and are more likely to create a hard melt-freeze layer at the base of the snowpack rather than a solid ice layer (Domine et al. 2016b, 2018b). In presence of hard basal snow, lemmings should still be able to access vegetation, but at an increased cost because digging efficiency of lemmings decreases in hard snow despite an increase in their digging effort (Poirier et al. 2021). This could reduce distance traveled within the snowpack, which may decrease the chance of finding adequate food sources or of encountering a mate. In addition, the increased energy spent digging may reduce the energy available for reproduction. These mechanisms could explain the reduction in the intensity of winter reproduction that we observed in presence of specific weather events in early winter. Therefore, our results support the idea that mild to moderate weather events leading to a hardening of the basal snow layer early in the season could lead to reduced population growth or decline of lemmings in winter by reducing the intensity of reproduction.

Other weather events not considered in our study, such as strong wind, can also lead to snow hardening (Domine et al. 2016b). However, hardening of the snow basal layer by wind did not seem to impact lemming population growth (Domine et al. 2018b). Timing of the formation of a hard snow layer can also have varying implications for lemmings. Hardening of upper snow layers after the snowpack is established can occur with strong winds or rain-on-snow events in warmer regions (Liston and Hiemstra 2011, Domine et al. 2016b). These

resulting hard wind slab or melt-freeze layers may actually benefit lemmings by hindering the ability of foxes to hunt them through the snow (Bilodeau et al. 2013b). Further investigation is needed to explore consequences of the timing of weather events leading to hard snow layers on animals, which may differ among Arctic species. For instance, for larger herbivores spending all their time at the surface of the snowpack, we can anticipate negative effects of hard snow layers irrespective of when or where it forms in the snowpack (Rennert et al. 2009).

Contrary to our initial hypothesis, snow onset had no effect on lemming winter demography. Previous studies suggested that an early snow onset would be favorable to lemmings by providing prompt access to a refuge against cold and predators, which are especially numerous in fall (Gilg et al. 2009). The latter study also suggested that a late snow onset would increase the periodicity of lemming cycles and reduce their amplitude. However, several factors could influence the relationship between snow onset date and lemming demography, sometimes in opposite directions. An early snow onset followed by several warm spells and freeze-thaw cycles could be detrimental for lemmings as it would favor the formation of a hard basal snow layer. In contrast, an early snow onset followed by dry and cold temperature would favor the formation of a soft depth hoar by promoting a large thermal gradient within the snowpack (Domine et al. 2018a), which would be advantageous to lemmings. Therefore, we suggest a more complex relationship between snow onset date and lemming winter demography, which could not be elucidated with our current dataset.

The absence of an effect of early winter snow depth on lemming demography was also contrary to our expectations. One limitation regarding the measurement of snow depth is its large variability at a small spatial scale. In presence of wind, snow is rapidly redistributed, and it fills depressions in the ground. Lemmings are known to use snowdrift areas as deep snow accumulation provides a favorable microclimate (Reid et al. 2012, Von Beckerath et al. 2021, Poirier et al. 2023). However, a single snow depth sensor located in relatively flat terrain and exposed to wind may not adequately measure the initial snow accumulation in depressions, and thus may not accurately reflect the snow depth experienced by lemmings in shelters in early winter.

4.6.2 Density dependence and winter predation

Independently of snow conditions, we found that lemming density had a negative impact on winter population growth but not on reproduction, which actually showed a positive trend in relation to density. This suggests that the effect observed on population growth is driven primarily by density-dependent mortality during winter as lemmings can apparently maintain a high reproductive activity at high density. Food resources are not thought to be limiting for lemmings in winter at our study site (Legagneux et al. 2012, Bilodeau et al. 2014). Moreover, we found no interaction between lemming density and weather events in affecting population growth, which suggests that competition, including for resources, is not stronger in years when a hard melt-freeze layer forms in the basal snow. Hence, we suggest that this density-dependent mortality is primarily related to predation, as previously suggested (Fauteux and Gauthier 2022). A diverse community of predators is present at our study site and their abundance usually peaks in fall after the young are weaned or have fledged, especially in years of high lemming abundance when reproductive success of predators is high (Therrien et al. 2014a, Chevallier et al. 2020). Nonetheless, our results suggest that presence of ermines, the only predator that can hunt lemmings under the snow, does not exacerbate the negative effects of early winter weather events on their population growth. We should however specify that our ermine abundance estimates are less accurate than those of lemmings because they are based on indirect indices (Bolduc et al. 2023). Indeed, the use of testimonials to estimate ermine abundance lacks the precision of direct observations recorded *in situ*.

4.6.3 Interspecific differences

The demography of both lemming species responded in a similar way to snow conditions. Nonetheless, we observed a higher reproductive rate in collared lemmings compared to brown lemmings regardless of snow conditions, which is consistent with the known biology of these species and findings from previous work (Poirier et al. 2023). Despite their higher reproductive rate, collared lemmings did not exhibit higher population growth rates than brown lemmings, which is surprising. Moreover, collared lemmings are also known to be less abundant than brown lemmings at our study site despite the presence of suitable habitats (Fauteux et al. 2015). This strongly suggests that collared lemmings experience a higher mortality rate than brown lemmings during winter, likely due to predation. Winter nests with reproductive activity have been associated with a higher predation risk by ermines (MacLean

et al. 1974, Schmidt et al. 2021), which could explain a higher mortality in collared lemmings. Noise or smell owing to the presence of juveniles in a nest can also attract predators, including arctic foxes hunting above the snow due to their acute hearing. Additionally, competition with brown lemmings could be another source of mortality in collared lemmings as the former is known to be more aggressive (Morris et al. 2000). We noticed instances of brown lemmings taking over collared lemming nests and we observed at least one case of infanticide at our study site (M. Poirier, pers. obs).

4.6.4 Limitations

We must acknowledge a limitation of our study concerning the detection of rain-on-snow events. Because reliable precipitation data was not available at our study site, we had to use relative humidity in combination with air temperature to infer the presence of precipitation and its phase, which could be a possible source of error. For freezing rain data, we used a radius of 80 km from the center of our study site to account for limited temporal resolution, but such weather events can be very localized (Roberts and Stewart 2008). Hence, we cannot guarantee that the identified freezing rain events occurred directly at our study site. However, for all three distinct types of weather events used in our study (rain-on-snow, melt-freeze and freezing rain), we can reasonably assume that events occurring at the beginning of winter when the snow cover is thin will lead to a hardening of the basal layer (Colbeck 1982, Domine et al. 2009, Berteaux et al. 2017). This assumption is also supported by the same relationships found between lemming demography and our direct measurements of density of the basal snow layer even if it was based on a small number of years.

Snow models such as CROCUS could in theory have been useful in providing more details on snow properties at the beginning of winter (Vionnet et al. 2012), but these models are still poorly suited to simulate processes occurring in the Arctic snowpack (Domine et al. 2015). This is why we decided to adopt an empirical approach based on a simple characterization of weather events and to keep a focus on processes that could impact lemming winter demography through hardening of the snowpack.

4.6.5 Conclusion

Winter reproduction in lemming is considered a crucial factor influencing their population dynamics and especially their periodic outbreaks (Millar 2001, Ims et al. 2011, Krebs 2011, Fauteux et al. 2015). Our study further supports the importance of winter reproduction in lemming demography and clearly shows that its intensity is impacted by snow condition. More importantly, it highlights the growing concern regarding the influence of climate change on lemming populations (Kausrud et al. 2008, Gilg et al. 2009, Ehrich et al. 2020). Rain-on-snow, melt-freeze and freezing rain events are expected to increase in the Arctic (Hansen et al. 2014, Groisman et al. 2016, Peeters et al. 2019), which should result in an increase frequency of hard snow layers. These conditions should reduce the intensity of winter reproduction in lemmings and could even lead to mortality from starvation if basal ice forms during extreme weather events. Consequently, this could considerably dampen the periodic peaks during cyclic population fluctuations of lemmings (Hörnfeldt et al. 2005, Ims and Fuglei 2005, Kausrud et al. 2008), with strong negative consequences for specialized predators such as snowy owls (*Bubo scandiacus*) that depend upon them for their reproduction (Schmidt et al. 2012, Therrien et al. 2014a). To further enhance our understanding of the role played by these parameters in lemming population fluctuations, we encourage researchers to incorporate snow variables or weather event indices in their modeling (Bergeron et al. 2023).

Due to its reduced adaptation to winter conditions, brown lemmings may be more vulnerable than collared lemmings to an increase in frequency and intensity of winter weather events. In the future, lemmings could evolve traits that may facilitate adaptation to the changing environment. However, the timing and extent of these changes remain uncertain, and it is unclear whether these adaptations could occur rapidly enough for lemmings to effectively cope with the altered conditions (Berteaux et al. 2004).

Snow is a temporary habitat that provides numerous benefits to species inhabiting northern landscapes. However, the quality of this habitat is dependent on weather conditions. Climate change could modify the snowpack in a way that can favor some species, but hinder others. These complex interactions warrant further attention from researchers to improve predictions of how Arctic wildlife will adapt to the ever-changing landscape.

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4.8 Supplementary Material

S4.1 – Yearly estimation of snow onset date

S4.2 – Supplementary material for Chapter 4

4.9 Bibliography

Andreev, A. V. 1991. Winter adaptations in the willow ptarmigan. Arctic 44:106–114.

Audet, B., G. Gauthier, and E. Lévesque. 2007. Feeding ecology of greater snow goose goslings in mesic tundra on Bylot Island, Nunavut, Canada. Condor 109:361–376.

Von Beckerath, X., G. Benadi, O. Gilg, B. Sittler, G. Yannic, A.-M. Klein, and B. Eitzinger. 2021. Long-term monitoring reveals topographical features and vegetation explain winter habitat use of an arctic rodent. Arctic Science 8:349–361.

Bergeron, G., G. Gauthier, F. Lutscher, P. Legagneux, D. Berteaux, C. Hutchison, and D. Gravel. 2023. Simple seasonal switches in food web composition unveil the complexity of an arctic predator-prey system. Biological Conservation [soumis].

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.

Berteaux, D., D. Réale, A. G. McAdam, and S. Boutin. 2004. Keeping pace with fast climate change: can arctic life count on evolution ? Integrative and Comparatie Biology 44:140–151.

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

Bilodeau, F., G. Gauthier, and D. Berteaux. 2013b. The effect of snow cover on lemming population cycles in the Canadian High Arctic. Oecologia 172:1007–1016.

Bilodeau, F., G. Gauthier, D. Fauteux, and D. Berteaux. 2014. Does lemming winter grazing impact vegetation in the Canadian Arctic? Polar Biology 37:845–857.

Bolduc, D., D. Fauteux, C. A. Gagnon, G. Gauthier, J. Bêty, and P. Legagneux. 2023. Testimonials to reconstruct past abundances of wildlife populations. Basic and Applied Ecology 68:23–34.

CEN 2022. Climate station data from Bylot Island in Nunavut, Canada, v. 1.12.0 (1992-2022). Nordicana D2, doi: 10.5885/45039SL-EE76C1BDAADC4890.

Chevallier, C., G. Gauthier, S. Lai, and D. Berteaux. 2020. Pulsed food resources affect reproduction but not adult apparent survival in arctic foxes. Oecologia 193:557–569.

Colbeck, S. C. 1982. An overview of seasonal snow metamorphism. Review of Geophysics and Space Physics 20:45–61.

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.

Domine, F., M. Barrere, and D. Sarrazin. 2016. Seasonal evolution of the effective thermal conductivity of the snow and the soil in high Arctic herb tundra at Bylot Island, Canada. The Cryosphere 10:2573–2588.

Domine, F., M. Belke-Brea, D. Sarrazin, L. Arnaud, M. Poirier, and T. Joint. 2018a. Soil moisture , wind speed and depth hoar formation in the Arctic snowpack. Journal of Glaciology 64:990–1002.

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

Domine, F., G. Lackner, D. Sarrazin, M. Poirier, and M. Belke-Brea. 2021. Meteorological, snow and soil data (2013-2019) from a herb tundra permafrost site at Bylot Island, Canadian high Arctic, for driving and testing snow and land surface models. Earth System Science Data 13:4331–4348.

Domine, F., G. Picard, and S. Morin. 2015. Major issues in simulating some arctic snowpack properties using current detailed snow physics models: consequences for the thermal regime and water budget of permafrost. Journal of Advances in Modeling Earth Systems 11:34–44.

Domine, F., A. S. Taillandier, A. Cabanes, T. A. Douglas, and M. Sturm. 2009. Three examples where the specific surface area of snow increased over time. Cryosphere 3:31–39.

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

Duchesne, D., G. Gauthier, and D. Berteaux. 2011b. Evaluation of a method to determine the breeding activity of lemmings in their winter nests. Journal of Mammalogy 92:511–516.

Efford, M. 2023. secr: Spatially explicit capture-recapture models. R package version 4.6.0.

Ehrich, D., N. M. Schmidt, G. Gauthier, R. Alisauskas, A. Angerbjörn, K. Clark, F. Ecke, N.

E. Eide, E. Framstad, J. Frandsen, A. Franke, O. Gilg, M. A. Giroux, H. Henttonen, B. Hörnfeldt, R. A. Ims, G. D. Kataev, S. P. Kharitonov, S. T. Killengreen, C. J. Krebs, R. B. Lanctot, N. Lecomte, I. E. Menyushina, D. W. Morris, G. Morrisson, L. Oksanen, T. Oksanen, J. Olofsson, I. G. Pokrovsky, I. Y. Popov, D. Reid, J. D. Roth, S. T. Saalfeld, G. Samelius, B. Sittler, S. M. Sleptsov, P. A. Smith, A. A. Sokolov, N. A. Sokolova, M. Y. Soloviev, and D. V. Solovyeva. 2020. Documenting lemming population change in the Arctic: can we detect trends? Ambio 49:786–800.

Fauteux, D., and G. Gauthier. 2022. Density-dependent demography and movements in a cyclic brown lemming population. Ecology and Evolution 12:e9055.

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.

Fauteux, D., G. Gauthier, and D. Berteaux. 2016. Top-down limitation of lemmings revealed by experimental reduction of predators. Ecology 97:3231–3241.

Fauteux, D., G. Gauthier, M. J. Mazerolle, N. Coallier, J. Bêty, and D. Berteaux. 2018. Evaluation of invasive and non-invasive methods to monitor rodent abundance in the Arctic: Ecosphere 9:e02124.

Freedman, D. A. 2006. On the so-called “Huber Sandwich Estimator” and “robust standard errors”. American Statistician 60:299–302.

Gauthier, G., D. Berteaux, J. Bêty, A. Tarroux, J.-F. Therrien, L. McKinnon, P. Legagneux, and M.-C. Cadieux. 2011. The tundra food web of Bylot Island in a changing climate and the role of exchanges between ecosystems. Ecoscience 18:223–235.

Gilg, O., B. Sittler, and I. Hanski. 2009. Climate change and cyclic predator-prey population dynamics in the high Arctic. Global Change Biology 15:2634–2652.

Glass, T. W., G. A. Breed, G. E. Liston, A. K. Reinking, M. D. Robards, and K. Kielland. 2021. Spatiotemporally variable snow properties drive habitat use of an Arctic mesopredator. Oecologia 195:887–899.

Groisman, P. Y., O. N. Bulygina, X. Yin, R. S. Vose, S. K. Gulev, I. Hanssen-Bauer, and E. Førland. 2016. Recent changes in the frequency of freezing precipitation in North America and Northern Eurasia. Environmental Research Letters 11:045007.

Gruyer, N., G. Gauthier, and D. Berteaux. 2008. Cyclic dynamics of sympatric lemming populations on Bylot Island, Nunavut, Canada. Canadian Journal of Zoology 86:910–917.

Hansen, B. B., V. Grøtan, R. Aanes, B. Sæther, E. Fuglei, R. A. Ims, N. G. Yoccoz, Å. Ø. Pedersen, A. Wikner, N. Mait, E. Abbe, J. Jose, L. Chan, A. Phys, S. Jose, and M. Nichols. 2013. Climate events synchronize the dynamics of a resident vertebrate community in the High Arctic. Science 339:313–315.

Hansen, B. B., K. Isaksen, R. E. Benestad, J. Kohler, Å. Pedersen, L. E. Loe, S. J. Coulson, J. O. Larsen, and Ø. Varpe. 2014. Warmer and wetter winters: characteristics and implications of an extreme weather event in the High Arctic. Environmental Research Letters 9:114021.

Hansen, R. M. 1957. Remarks on the bifid claws of the varying lemming. American Society

of Mammalogist 38:127–128.
Hörnfeldt, B., T. Hipkiss, and U. Eklund. 2005. Fading out of vole and predator cycles ? Proceedings of the Royal Society B: Biological Sciences 272:2045–2049.
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.
Ims, R. A., J. A. Henden, and S. T. Killengreen. 2008. Collapsing population cycles. Trends in Ecology and Evolution 23:79–86.
Ims, R. a, N. G. Yoccoz, and S. T. Killengreen. 2011. Determinants of lemming outbreaks. Proceedings of the National Academy of Sciences 108:1970–1974.
Jennings, K. S., T. S. Winchell, B. Livneh, and N. P. Molotch. 2018. Spatial variation of the rain – snow temperature threshold across the Northern Hemisphere. Nature Communications 9:1148.
Kausrud, K. L., A. Mysterud, H. Steen, J. O. Vik, E. Østbye, B. Cazelles, E. Framstad, A. M. Eikeset, I. Mysterud, T. Solhøy, and N. C. Stenseth. 2008. Linking climate change to lemming cycles. Nature 456:93–97.
Krebs, C. J. 2011. Of lemmings and snowshoe hares: the ecology of northern Canada. Proceedings of the Royal Society B 278:481–489.
Langlois, A., C. A. Johnson, B. Montpetit, A. Royer, E. A. Blukacz-Richards, E. Neave, C. Dolant, A. Roy, G. Arhonditsis, D. K. Kim, S. Kaluskar, and L. Brucker. 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.
Legagneux, P., G. Gauthier, D. Berteaux, J. Bêty, M. C. Cadieux, F. Bilodeau, E. Bolduc, L. Mckinnon, A. Tarroux, J. F. Therrien, L. Morissette, and C. J. Krebs. 2012. Disentangling trophic relationships in a High Arctic tundra ecosystem through food web modeling. Ecology 93:1707–1716.
Liston, G. E., and C. A. Hiemstra. 2011. The changing cryosphere: pan-Arctic snow trends (1979-2009). Journal of Climate 24:5691–5712.
MacLean, S. F., B. M. Fitzgerald, and F. A. Pitelka. 1974. Cycles in arctic lemmings: winter reproduction and predation by weasels. Arctic and Alpine Research 6:1–12.
Mazerolle, M. J. 2023. ICcmodavg: Model selection and multimodel inference based on (Q)AIC(c). R package version 2.3.2, https://cran.r-project.org/package=AICcmodavg.
Millar, J. S. 2001. On reproduction in lemmings. Ecoscience 8:145–150.
Morris, D. W., D. L. Davidson, and C. J. Krebs. 2000. Measuring the ghost of competition: Insights from density-dependent habitat selection on the co-existence and dynamics of lemmings. Evolutionary Ecology Research 2:41–67.
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.
Poirier, M., D. Fauteux, G. Gauthier, F. Domine, and J. F. Lamarre. 2021. Snow hardness impacts intranivean locomotion of arctic small mammals. Ecosphere 12:e03835.

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

Poirier, M., G. Gauthier, F. Domine, and D. Fauteux. 2023. Lemming winter habitat: the quest for warm and soft snow. Oecologia 202:211–225.

R Core Team. 2021. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Rantanen, M., A. Y. Karpechko, A. Lipponen, K. Nordling, O. Hyvärinen, K. Ruosteenoja, T. Vihma, and A. Laaksonen. 2022. The Arctic has warmed nearly four times faster than the globe since 1979. Communications Earth and Environment 3:1–10.

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.

Rennert, K. J., G. Roe, J. Putkonen, and C. M. Bitz. 2009. Soil thermal and ecological impacts of rain on snow events in the circumpolar arctic. Journal of Climate 22:2302–2315.

Riggs, G., and D. Hall. 2015. MODIS Snow Products Collection 6 User Guide. https://nsidc.org/sites/nsidc.org/files/files/MODIS-snow-user-guide-C6.pdf.

Roberts, E., and R. E. Stewart. 2008. On the occurrence of freezing rain and ice pellets over the eastern Canadian Arctic. Atmospheric Research 89:93–109.

Saunders, P. A., and F. Veyrunes. 2021. Unusual mammalian sex determination systems: a cabinet of curiosities. Genes 12:1770.

Schmidt, N. M., F. M. Van Beest, A. Dupuch, L. H. Hansen, J. Pierre, and D. W. Morris. 2021. Long-term patterns in winter habitat selection, breeding and predation in a density-fluctuating, high Arctic lemming population. Oecologia 195:927–935.

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.

Soininen, E. M., G. Gauthier, F. Bilodeau, D. Berteaux, L. Gielly, P. Taberlet, G. Gussarova, E. Bellemain, K. Hassel, H. K. Stenøien, L. Epp, A. Schrøder-Nielsen, C. Brochmann, and N. G. Yoccoz. 2015. Highly overlapping winter diet in two sympatric lemming species revealed by DNA metabarcoding. PLOS ONE 10:e0115335.

Sokolov, A. A., N. A. Sokolova, R. A. Ims, L. Brucker, and D. Ehrich. 2016. Emergent rainy winter spells may promote boreal predator expansion into the Arctic. Arctic 69:121–129.

Sorum, M. S., K. Joly, A. G. Wells, M. D. Cameron, G. V. Hilderbrand, and D. D. Gustine. 2019. Den-site characteristics and selection by brown bears (*Ursus arctos*) in the central Brooks Range of Alaska. Ecosphere 10:e02822.

Stien, A., R. A. Ims, S. D. Albon, E. Fuglei, R. J. Irvine, E. Ropstad, O. Halvorsen, R. Langvatn, L. E. Loe, V. Veiberg, and N. G. Yoccoz. 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.
Therrien, J. F., G. Gauthier, E. Korpimäki, and J. Bêty. 2014. Predation pressure by avian predators suggests summer limitation of small-mammal populations in the Canadian Arctic. Ecology 95:56–67.
Vionnet, V., E. Brun, S. Morin, A. Boone, S. Faroux, P. Le Moigne, E. Martin, and J. M. Willemet. 2012. The detailed snowpack scheme Crocus and its implementation in SURFEX v7.2. Geoscientific Model Development 5:773–791.
Zedler, P. H. 2003. Vernal pools and the concept of "Isolated wetlands." Wetlands 23:597–607.
Zimova, M., K. Hackl, J. M. Good, C. Paulo, 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.

Conclusion

Les lemmings occupent un rôle central dans l'écosystème arctique, étant la proie principale de nombreux prédateurs retrouvés dans ces régions. Ces petits rongeurs passent la majeure partie de leur vie sous la neige, mais les études sur leur écologie hivernale demeuraient jusqu'à ce jour très rares. Avec cette thèse, je suis parvenue à contribuer significativement à l'avancement des connaissances sur cette période critique du cycle de vie des lemmings. Afin de mieux comprendre l'impact des propriétés physiques de la neige sur les populations de lemmings en Arctique, j'ai opté pour une approche multidisciplinaire mêlant des concepts propres à l'écologie et à la nivologie (c.-à-d. l'étude de la neige). Plus concrètement, j'ai pu mettre en commun des mesures empiriques de l'écologie hivernale d'un petit mammifère avec celles de propriétés physiques du manteau neigeux arctique. Les méthodes utilisées pour obtenir ces mesures étaient variées, allant de données écologiques à long terme récoltées sur le terrain, aux données obtenues par des suivis automatisés ou provenant d'expériences en milieu contrôlé. Les études déjà réalisées sur les lemmings et leur habitat à mon site d'étude à long terme m'ont également aidé à formuler des hypothèses de recherche plus solides et mes nombreuses observations sur le terrain n'ont permis de les valider et d'approfondir l'interprétation de mes résultats.

En somme, ma thèse amène une meilleure compréhension de l'écologie hivernale des espèces nordiques, pour qui cette phase de leur cycle de vie demeure assez peu documentée. Ces espèces entretiennent des liens étroits avec le manteau neigeux, en particulier dans les régions où celui-ci recouvre le sol pendant plus des trois-quarts de l'année. Les changements climatiques ont le potentiel de perturber ces liens de façon significative, en altérant les propriétés physiques du manteau neigeux arctique. Mes travaux soulignent ainsi l'importance de s'intéresser au manteau neigeux dans toute sa complexité, en tenant compte de son hétérogénéité temporelle et spatiale, afin de mieux comprendre son rôle crucial pour les espèces qui en dépendent.

L'espace sous-nival : un habitat complexe

Jusqu'à maintenant, il était connu que le lemming s'abritait dans les couches profondes de neige pour se protéger du froid en hiver et qu'il devait se déplacer dans cet espace sous-nival

afin d'accéder aux plantes pour se nourrir (MacLean et al. 1974, Jarrel and Fredga 1993, Duchesne et al. 2011a). Cependant, le comportement fouisseur du lemming dans ce micro-habitat hivernal avait surtout fait l'objet d'observations anecdotiques sans avoir été étudié plus rigoureusement (Sutton and Hamilton 1932). Les travaux de mon Chapitre 1 ont confirmé que les lemmings utilisent la couche de neige la plus friable, le givre de profondeur, pour creuser leurs tunnels dans le manteau neigeux, puis mon Chapitre 2 a permis de mieux comprendre les motifs de cette utilisation préférentielle. En effet, la diminution de la vitesse de creusage ainsi que de la longueur des tunnels en fonction de la dureté et de la densité de la neige illustre bien l'avantage des lemmings à creuser dans le givre de profondeur friable (Chapitre 2). Bien que la densité et la dureté de la neige soient fortement corrélées, ces deux paramètres semblent influencer le creusage via différents mécanismes. En effet, lorsqu'ils tentent de déchirer la neige avec leurs pattes avant, la résistance au cisaillement imposée par une neige plus dure semble fortement limiter leur progression. Puis, en creusant dans une neige plus dense, le lemming doit détacher une plus grande quantité de grains de neige, augmentant la masse de cristaux qu'ils doivent ensuite pousser avec leurs pattes arrière. En présence d'une neige affectée par une pluie-sur-neige (très fortes dureté et densité), les lemmings utilisent davantage leurs incisives pour progresser dans la neige (Chapitre 2). Ce changement de stratégie ainsi que l'augmentation du temps passé à creuser dans cette neige plus dure démontrent une augmentation de l'effort de creusage. Bien que notre étude n'ait pas été conçue pour mesurer directement les dépenses énergétiques des lemmings, ces résultats laissent supposer un coût énergétique beaucoup plus élevé à creuser dans une neige plus dure.

L'habitat sous-nival est défini par plusieurs écologistes comme étant un refuge à l'interface entre le sol et la neige, utilisé par les animaux pour se protéger principalement des froides températures (Marchand 2013, Pauli et al. 2013). Les résultats de ma thèse appuient toutefois une définition plus générale de ce terme proposée par Halfpenny and Ozanne (1989) qui inclut également l'habitat intra-nival, c'est-à-dire à l'intérieur du manteau neigeux. Cette définition me semble davantage appropriée lorsque reliée à l'écologie hivernale des animaux puisqu'il est sans doute faux d'assumer une utilisation stricte de l'interface sol-neige. L'utilisation de l'habitat sous-nival par les petits mammifères serait en fait beaucoup plus complexe que ce qui était depuis longtemps assumé. En effet, il m'a été possible d'observer

que les lemmings creusent rarement au niveau du sol, contrairement à la croyance générale (Chapitre 1). Les lemmings évitent parfois les couches de regel lorsque présentes au niveau du sol, mais ils maintiennent toujours une certaine hauteur par rapport au sol dans le manteau neigeux lors de leurs déplacements, même en l'absence de ces couches dures. En effet, les lemmings creusent presque toujours tout juste sous une couche de neige ventée, plus dure, probablement pour éviter l'effondrement de leurs tunnels et ainsi les réutiliser (Chapitre 2). Bien entendu, mes travaux concernent les populations lemmings de l'île Bylot et les résultats pourraient différer en fonction de l'espèce ou encore du site d'étude. Par exemple, des observations de Knaust (2014) en Norvège faisaient état de tunnels de lemmings norvégiens (*Lemmus lemmus*) creusés à l'interface sol-neige. Néanmoins, en remettant en question une croyance depuis longtemps établie quant à l'utilisation de l'espace sous-nival par les petits mammifères, mes travaux appuient l'idée qu'il s'agit d'un concept encore mal compris à ce jour et qui mérite davantage d'attention de la part des écologistes.

Mes travaux ont également permis d'améliorer la compréhension de ce que représente l'espace sous-nival d'un point de vue de la physique de la neige, ce qui aide à comprendre son impact sur les petits mammifères. Le givre de profondeur qui se développe dans ce micro-habitat est d'une importance capitale pour les lemmings qui l'utilisent pour se déplacer en limitant les efforts déployés (Chapitres 1-2). Les propriétés physiques de ce givre de profondeur varient toutefois énormément d'année en année, en fonction des conditions météorologiques, ainsi qu'à travers les différents habitats (Chapitres 3-4). En effet, le givre n'est pas toujours uniquement une couche de neige peu dense et friable, car s'il se développe à partir d'une couche de neige durcie, il peut être induré et nuire au déplacement des lemmings (Chapitres 2-3).

Les températures dans l'espace sous-nival sont plus clémentes que les températures de l'air, mais il est important de souligner que cette température varie en fonction de nombreux facteurs. Par exemple, dans mon Chapitre 3, j'ai documenté des fluctuations quotidiennes de températures de 3 à 4 °C sous environ 40 cm de neige. Cependant, ces fluctuations quotidiennes dépendaient fortement des propriétés isolantes du manteau neigeux, qui varient selon le type de milieu, ainsi que des températures de l'air. C'est sans doute pour cette raison que les lemmings utilisent davantage les habitats avec un épais couvert de neige (plus de 60

cm; Duchesne et al. 2011) ainsi qu'une plus grande fraction de givre de profondeur aux propriétés isolantes, ce qui limite les variations quotidiennes de température (moins de 0.5 °C; Chapitre 3).

Certains ouvrages tendent à simplifier la notion d'espace sous-nival en suggérant l'idée d'un refuge idéal exempt de variations de température où les déplacements des petits mammifères sont facilités (Casey 1981, Marchand 2013, Pauli et al. 2013, Thompson et al. 2021). À la lumière de ma recherche, je soutiens qu'il faut plutôt accepter qu'une grande variabilité existe dans les propriétés de ce micro-habitat et mieux documenter les conditions propices aux espèces qui l'utilisent.

Variations spatiales de l'habitat hivernal des lemmings

Pour les lemmings, s'abriter sous la neige en hiver représente un avantage thermique notable (Chappell 1980a), mais cette isolation favorable varie grandement à l'échelle du paysage. Les résultats de mon Chapitre 3 vont dans la même veine que les études antérieures, appuyant une utilisation préférentielle des habitats riverains par les lemmings, là où la neige s'accumule abondamment (Batzli et al. 1983, Duchesne et al. 2011a, Schmidt et al. 2021, Von Beckerath et al. 2021). Cependant, cet habitat imposerait un compromis aux lemmings puisque la neige retrouvée dans l'espace sous-nival est plus dense que dans les autres habitats accumulant moins de neige (Chapitre 3). En plus de nuire au déplacement des lemmings dans la neige (Chapitre 2), une neige plus dense nuit également à la reproduction hivernale (Chapitre 3). Cette augmentation de la densité dans l'habitat riverain pourrait en partie s'expliquer par une réduction du gradient de température due à une plus grande épaisseur de la neige, menant à un givre moins développé (Marbouty 1980). L'isolation offerte par le manteau neigeux semble ainsi être la caractéristique principale recherchée par les lemmings lorsqu'ils établissent leur nid d'hiver, au détriment d'une couche basale de neige potentiellement plus dense. Cela appuie l'idée d'un coût de thermorégulation élevé chez ces petits mammifères et de l'importance de limiter les dépenses énergétiques qui y sont associées durant cette période critique (Chappell 1980a).

En comparaison avec les habitats mésique et humide, les arbustaies étaient davantage utilisées par les lemmings à l'hiver et la reproduction hivernale y était également plus élevée

(Chapitre 3). En effet, les branches de saules permettent de piéger la neige balayée par le vent, favorisant une plus grande accumulation et une compaction réduite des grains de neige (Domine et al. 2016a). Les arbustaies représentent donc un habitat d'une certaine qualité pour les lemmings en hiver. Les résultats de mon Chapitre 3 soutiennent également l'absence d'un effet de la densité de la population de lemmings sur l'utilisation de l'habitat, suggérant que les refuges ne sont pas limitants pour les lemmings de l'île Bylot en hiver.

Comment l'utilisation de l'habitat hivernal des lemmings évoluera-t-elle avec les changements climatiques? D'abord, on peut anticiper un durcissement de la couche basale par l'augmentation d'épisodes de pluie-sur-neige ou fonte-regel (Liston and Hiemstra 2011). Ce durcissement pourrait avoir lieu préférentiellement dans l'habitat riverain, étant donné l'accumulation plus précoce de la neige dans cet habitat par rapport aux habitats humide et mésique (15 jours plus tôt en moyenne), impliquant un plus grand risque d'exposition aux épisodes de redoux. Un durcissement excessif de l'espace sous-nival pourrait contraindre les lemmings à devoir quitter cet habitat. Par contre, à long terme, l'augmentation des températures en Arctique devrait également favoriser l'expansion des arbustes (Tape et al. 2006), ce qui pourrait créer plus de refuges pour les lemmings en hiver. Cependant, les épisodes de pluie-sur-neige pourraient compromettre les avantages offerts par cet habitat en durcissant la surface du manteau neigeux, empêchant le transport de la neige par le vent et ainsi sa captation par les branches des arbustes (Barrere et al. 2018). Il est ainsi difficile de prévoir comment les changements climatiques influenceront l'utilisation de l'habitat par les lemmings à l'hiver et si les retombées seront majoritairement positives ou négatives. Toutefois, compte tenu de l'impact direct des conditions météorologiques sur ces habitats saisonniers, on peut s'attendre à d'importants changements au cours des prochaines années.

Rôle de la neige dans la dynamique des populations de lemmings

Réalisant que la prédation et la nourriture ne pouvaient expliquer entièrement les cycles de population de petits mammifères, de plus en plus d'études se sont intéressées au rôle des conditions de neige sur ces cycles en milieu nordique. Certaines études suggèrent qu'une diminution de la durée d'enneigement au sol pourrait augmenter la longueur de la période des cycles de lemmings en plus de diminuer leur amplitude (Ims et al. 2008, Gilg et al. 2009). D'autres études soutiennent qu'un durcissement de la couche basale du manteau neigeux

entraîne une baisse des populations de rongeurs en hiver (Aars and Ims 2002, Stien et al. 2012, Bilodeau et al. 2013a, Domine et al. 2018b) et même un effondrement des cycles chez certaines populations (Ims et al. 2008, Kausrud et al. 2008). Toutefois, les mécanismes sous-jacents à ces relations demeurent peu compris.

Le Haut-Arctique canadien est réputé pour son climat très froid et ses faibles précipitations, ce qui rend les épisodes de pluie-sur-neige et de fonte-regel relativement rares et de faible intensité en comparaison à d'autres régions nordiques (Sturm et al. 1995, Royer et al. 2021). Toutefois, même dans ces conditions, de tels événements météorologiques peuvent survenir et entraîner des variations dans les propriétés physiques de la neige, ce qui peut avoir des effets non négligeables sur les lemmings. En effet, mon Chapitre 4 appuie l'hypothèse que les déclins hivernaux des lemmings sont influencés par les événements météorologiques menant au durcissement de la couche basale comme la pluie-sur-neige ou la fonte-regel dans l'Arctique canadien. De plus, les résultats de mes Chapitres 3 et 4 montrent qu'un durcissement de la couche basale de neige a un impact négatif sur la reproduction hivernale des lemmings. Il est depuis longtemps suggéré que la reproduction hivernale joue un rôle clé dans les cycles de population de lemmings (Millar 2001, Ims et al. 2011, Fauteux et al. 2015). En démontrant un tel lien entre la dureté de la couche basale de neige et la reproduction hivernale, les résultats de ma thèse amènent un nouvel éclairage sur la façon dont la neige influence les cycles de lemmings.

Dans les régions où le climat est influencé par les courants océaniques (p. ex. Svalbard et Norvège; Ims et al. 2008, Stien et al. 2012), les redoux et épisodes de pluie-sur-neige sont beaucoup plus fréquents et il arrive qu'une couche de glace recouvre presque entièrement la végétation au niveau du sol (Serreze et al. 2015, Peeters et al. 2019). Dans de telles conditions, la prise alimentaire des petits rongeurs s'en trouve gravement entravée, entraînant un déclin des populations par une hausse de la mortalité (Stien et al. 2012, Fauteux et al. 2021). À l'inverse, le mécanisme avancé par les résultats de ma thèse concerne plutôt les régions de l'Arctique où le climat est beaucoup plus froid et où de tels épisodes météorologiques demeurent pour le moment de plus faible intensité. Des épisodes modérés de pluie-sur-neige ou de fonte-regel mènent plutôt à la formation de couches de regel qui ne bloquent pas nécessairement l'accès à la nourriture, mais forcent les lemmings à augmenter

leur effort pour creuser leurs tunnels (Chapitre 2). Il est raisonnable de supposer qu'une telle augmentation de l'effort entraînera une augmentation des dépenses énergétiques, entraînant ainsi une baisse de l'énergie disponible pour la reproduction et donc une réduction de la capacité des lemmings à se reproduire. De plus, une couche basale de neige durcie diminue la performance des lemmings à creuser (Chapitre 2), ce qui pourrait réduire les chances de rencontrer un partenaire de reproduction en creusant dans la neige.

À notre site d'étude et à plusieurs autres sites en Arctique, les cycles de lemmings semblent être principalement contrôlés par la forte pression de prédation (Gilg et al. 2003, Legagneux et al. 2012, Fauteux et al. 2016). Il est supposé que la période hivernale est une période de récupération pour les populations de lemmings pendant laquelle la pression de prédation y est moindre et où ils peuvent remonter leurs effectifs en se reproduisant sous la neige (Fauteux et al. 2016, Bergeron et al. 2023). Cependant, à la lumière de mes résultats, je tiens à souligner l'importance de tenir compte des propriétés physiques de la neige dans l'estimation de la croissance hivernale des populations de lemmings étant donné l'important rôle que semble jouer la neige dans leur reproduction hivernale.

Variations interspécifiques de l'impact des conditions de neige

Avec leur pelage qui devient blanc et les coussinets de leurs pattes avant qui s'élargissent à l'hiver, les lemmings variables semblent mieux adaptés à la vie arctique que leurs confrères les lemmings bruns (Hansen 1957, Fuller et al. 1975, Zimova et al. 2018). Les résultats de mon Chapitre 2 soutiennent également cette idée, puisque les lemmings variables se sont montrés plus performants à creuser dans la neige que les lemmings bruns. En effet, les lemmings variables étaient plus rapides à creuser, leurs tunnels étaient plus longs et ils mettaient moins de temps à rejoindre la couche basale de neige comparativement aux lemmings bruns. En présence d'une neige durcie, les lemmings variables utilisaient leurs incisives pour creuser seulement 30 % du temps comparativement à 70 % du temps pour les lemmings bruns. Cela suggère que l'élargissement de leurs pattes avant à l'hiver leur permet d'être plus efficace à creuser dans une neige dure. Ce creusage plus efficace des lemmings variables leur permet sans doute d'économiser de l'énergie, ce qui pourrait expliquer leur meilleur taux de reproduction à l'hiver comparativement aux lemmings bruns (Chapitres 3-4).

Si les lemmings variables se reproduisent davantage que les lemmings bruns à l'hiver, comment alors expliquer que ceux-ci se trouvent en plus faible abondance à notre site d'étude (Gauthier et al. 2013)? D'abord, il semblerait que les lemmings variables soient davantage vulnérables à la prédation, puisqu'ils sont retrouvés en plus grande proportion dans le régime alimentaire de plusieurs prédateurs aviaires (Therrien et al. 2014a, Seyer et al. 2020). Les lemmings variables seraient peut-être aussi davantage vulnérables aux renards et hermines à l'hiver, soit en raison de leur comportement ou de leur propension à se reproduire, ce qui attirerait les prédateurs à leur nid (Duchesne et al. 2011a, Schmidt et al. 2021). Une compétition entre les deux espèces, en faveur du lemming brun, pourrait également expliquer une partie de ces différences (Morris et al. 2000). En effet, le lemming brun semble être plus agressif et nous avons également des preuves d'un infanticide effectué par ce dernier dans un nid de lemming variable (M. Poirier, obs. pers.). On pourrait également assister à un phénomène de compétition apparente où l'augmentation en nombre des lemmings bruns ferait augmenter le nombre de prédateurs, ce qui défavoriserait le lemming variable, plus vulnérable à cette prédation (Holt 1977, Therrien et al. 2014a). Les résultats de ma thèse renforcent ainsi l'idée que la prédation ou la compétition, particulièrement en hiver, expliqueraient la présence de lemming variable à une plus faible densité que celle des lemmings bruns à notre site d'étude.

Limites de l'étude

Les résultats présentés par ma thèse avancent grandement les connaissances de l'écologie hivernale des lemmings, mais il est toutefois important de reconnaître les limites associées au contexte de l'étude.

D'abord, même si j'ai caractérisé pour la toute première fois les tunnels de lemmings à même le manteau neigeux (Chapitre 1), il est important de reconnaître que ceux-ci ont été trouvés aux sites où des renards arctiques ont creusé à travers la neige afin de tenter une prédation sur les lemmings. Cette méthode a pu influencer les caractéristiques associées aux tunnels, certains de ceux-ci, par exemple, ayant pu avoir été creusés rapidement au moment de l'attaque afin d'échapper au prédateur. Cela nous semble néanmoins peu probable étant donné que la plupart des tunnels semblaient appartenir à un réseau complexe qui avait probablement été creusé depuis un certain temps. Ensuite, le réseau de tunnels semble être

influencé par la microtopographie du terrain, en particulier la présence de hummocks au niveau du sol, et ainsi ces résultats ne sont peut-être pas généralisables aux régions où la microtopographie est différente, voire dépourvue d'un tel relief. En effet, les lemmings à notre site d'étude creusaient presque toujours plus haut que le niveau du sol puisque leurs tunnels croisaient à l'occasion des hummocks sur lesquels il leur était possible de s'alimenter sans nécessairement retourner au niveau du sol. Il serait donc très intéressant d'effectuer une caractérisation des tunnels de petits mammifères à d'autres sites d'études présentant des caractéristiques géomorphologiques différentes.

En ce qui concerne l'expérience de creusage des lemmings dans différentes duretés de neige (Chapitre 2), le nombre d'individus à l'étude était plutôt faible ($n_{brun} = 4$, $n_{variable} = 3$), mais cela ne nous a tout de même pas empêchés d'obtenir des résultats plutôt convaincants. Nos lemmings présentaient des différences interindividuelles dans leurs comportements, mais nous avons tâché d'en tenir compte dans nos analyses statistiques. Néanmoins, des effectifs plus élevés auraient peut-être pu nous permettre de mettre en évidence davantage de différences entre les deux espèces. Il faut également garder en tête qu'il s'agissait d'une expérience en conditions contrôlées et que le creusage des lemmings dans le manteau neigeux en conditions naturelles pourrait différer.

En ce qui concerne l'utilisation de l'habitat hivernal par les lemmings (Chapitre 3), les sites où les mesures des propriétés physiques de la neige ont été réalisées ne correspondaient pas exactement aux mêmes sites où les nids d'hiver ont été recensés (c.-à-d. le long des transects). Cependant, notre connaissance du terrain nous a permis de sélectionner des sites dans chacun des habitats où les propriétés de la neige étaient vraisemblablement similaires à celles des sites où les nids ont été trouvés le long de nos transects. De plus, le fait que les nids d'hiver aient été échantillonnés pendant seulement 3 ans dans les arbustaies comparativement à 13 ans dans les autres habitats limite la capacité à bien évaluer la qualité de cet habitat pour les lemmings. Aussi, il est important de noter que nous avons uniquement considéré les variables de neige dans notre analyse. Le type de végétation dans chaque habitat n'a pas été pris en compte directement bien qu'il s'agit d'une variable qui aurait pu contribuer à l'utilisation de l'habitat par les lemmings en hiver. Il faut aussi préciser que ce chapitre se concentre sur l'habitat utilisé comme refuge ou pour se reproduire par les lemmings en hiver puisque la

présence de nids de lemmings était utilisée comme indice d'utilisation de l'habitat. Il est possible que l'habitat utilisé pour creuser la majorité des tunnels destinés à s'alimenter ou pour chercher un partenaire pour se reproduire diffère de celui utilisé comme refuge.

Au Chapitre 4, nous avons créé des indices d'événements météorologiques comme la pluie-sur-neige ou la fonte-regel à partir de données de températures et d'humidité en raison d'une absence de données de précipitations fiables à utiliser. La principale force de cette méthode réside dans sa simplicité, la rendant potentiellement applicable à d'autres sites d'étude qui seraient aussi limités par une absence de données de précipitation. Cependant, il convient de noter que ceci demeure un indicateur des conditions propices à de tels événements météorologiques, sans pour autant garantir que ces événements se soient effectivement produits à chaque fois. De plus, le rayon utilisé pour déterminer les épisodes de pluie verglaçante à partir des données de réanalyses (80 km) a peut-être pu engendrer une surestimation de ces épisodes comme certains d'entre eux ont pu être très localisés. Néanmoins, ces indices semblent être plutôt fiables pour estimer le durcissement de la couche basale de neige.

Lorsque présente, l'hermine est considérée comme étant le plus vorace des prédateurs de lemmings à l'hiver, étant donné qu'elle peut pénétrer directement dans leurs tunnels (Gilg et al. 2003). Nous étions donc surpris de constater que la présence de ce prédateur en interaction avec les épisodes météorologiques menant au durcissement de la couche basale n'a pas eu d'effet sur les paramètres démographiques des lemmings (Chapitre 4). Il faut préciser que nous avons utilisé un indice d'abondance estival d'hermine dans nos analyses, basé sur des estimations indirectes (Bolduc et al. 2023). Il s'agit, pour le moment, de la meilleure variable de suivi à long terme que nous avions à notre disposition pour cette espèce. Cependant, cet indice d'abondance est sans doute moins fiable que celui utilisé pour les lemmings, d'autant plus qu'il est estimé pour la période estivale et non hivernale. De plus, comme la présence d'hermines à notre site d'étude est intermittente, de longues séries temporelles sont nécessaires afin de tester les effets de différentes combinaisons d'épisodes météorologiques et d'abondances d'hermine sur les paramètres démographiques des lemmings. Dans ce chapitre, la longueur des séries temporelles (14 et 17 ans) a donc pu être un élément limitant dans la détection de ces effets et de leurs interactions.

Finalement, les mesures de propriétés physiques de la neige ont presque toutes été prises manuellement à la fin de l'hiver en raison de contraintes logistiques. Cependant, il est important de noter que le manteau neigeux arctique évolue pendant l'hiver, ce qui signifie que les mesures effectuées à la fin de l'hiver pourraient ne pas refléter les conditions exactes auxquelles les lemmings étaient exposés pendant une partie de leur vie sous-nivale. La prise de mesures en continu d'un plus grand nombre de paramètres à plusieurs sites tout au long de l'hiver serait hautement bénéfique pour suivre l'évolution des propriétés physiques du manteau neigeux et comprendre comment le lemming s'adapte à ces changements. Il serait par exemple très intéressant de documenter le déplacement des lemmings dans le manteau neigeux en tout début d'hiver, lorsque le givre de profondeur commence tout juste à se développer.

Perspectives

Étudier les petits mammifères sous la neige en hiver pose un défi logistique important, car il est très difficile, voire impossible, de les capturer ou de les observer directement durant cette période. C'est pourquoi je considère que l'utilisation de caméras sous-nivale sera un outil puissant pour documenter l'écologie hivernale des lemmings. En parallèle de ma thèse, j'ai contribué à l'élaboration et au déploiement de caméras automatisées permettant de filmer le comportement des lemmings en continu dans des boîtes placées sous le manteau neigeux arctique (Figs. 5.1, 5.2; Kalhor et al. 2019, 2021, Pusenkova et al. 2022). Parmi les différentes observations que nous souhaitons obtenir avec ces caméras, la reproduction hivernale est particulièrement ciblée. En effet, nous souhaitons obtenir des informations sur le moment et l'intensité de la reproduction hivernale ainsi que sur le taux de survie des jeunes. Dans de futurs développements, il serait en effet possible d'intégrer des caméras infrarouges aux dispositifs, permettant de suivre l'activité se déroulant à l'intérieur d'un nid d'hiver qui serait construit dans la boîte. Les caméras pourraient également détecter des événements de compétition entre espèces de lemmings ou encore de prédation par l'hermine. De plus, un algorithme est en cours de développement afin de permettre l'identification automatique des espèces de lemmings utilisant la boîte et ainsi simplifier le traitement des vidéos. En déployant davantage de systèmes sur le terrain, il serait ultimement possible d'effectuer des analyses d'occupation de sites afin d'estimer les variations dans la présence des lemmings,

et indirectement dans leur abondance, à travers le temps et l'espace (Mos and Hofmeester 2020, Mölle et al. 2021). Ce type d'analyse pourrait également être effectué pour les hermines pour lesquelles nous détenons très peu d'informations concernant leur activité à l'hiver.

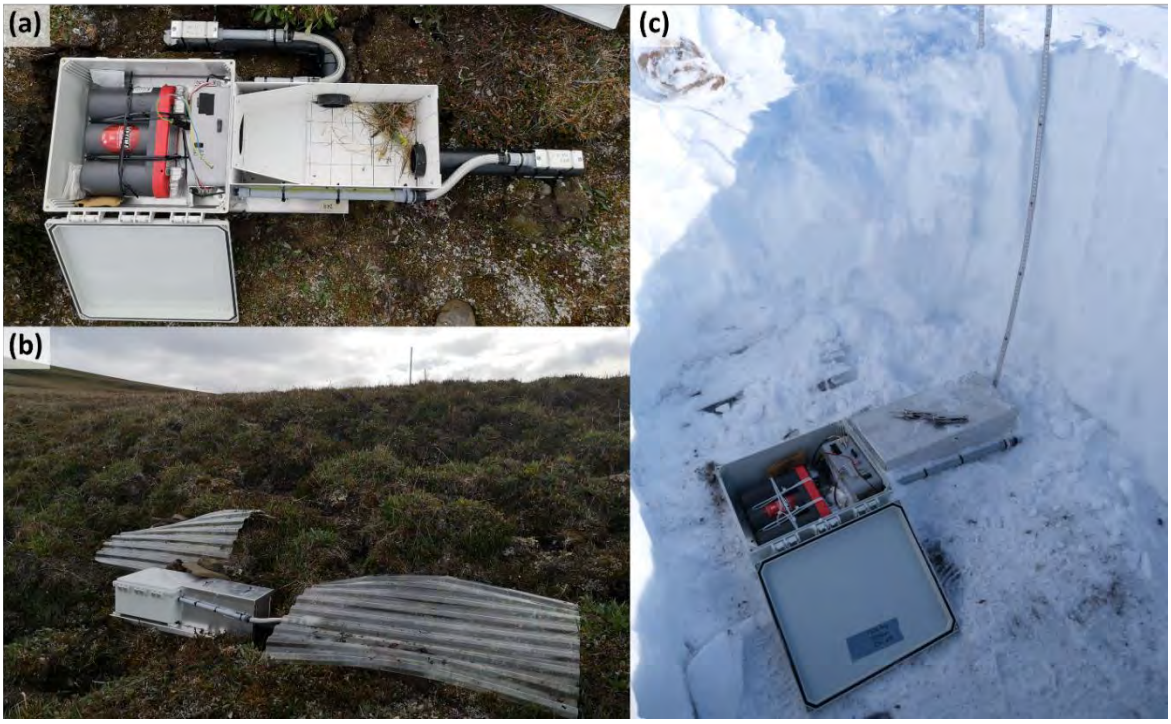


Figure 5.1 Caméras sous-nivales déployées à l'île Bylot depuis l'été 2017. (a) Présentation du dispositif avec son boîtier électronique (gauche) et la boîte par laquelle les lemmings peuvent pénétrer (droite) via les 2 entrées indépendantes (tuyaux noirs). (b) Caméra sous-nivale déployée sur le terrain avec des panneaux de plastiques limitant l'entrée de la neige par les tunnels. (c) Caméra sous-nivale en mai lors de la récolte des données.

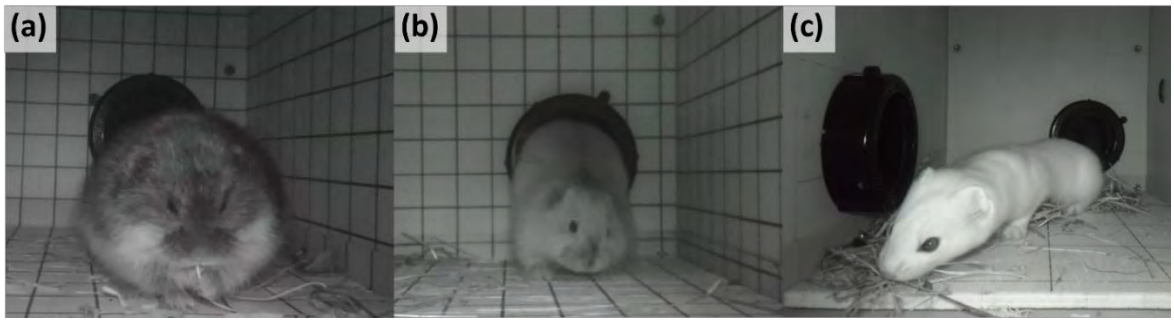


Figure 5.2 Exemples d'images enregistrées par les caméras déployées à l'île Bylot entre 2017 et 2022. (a) Un lemming brun s'alimentant de brindilles de végétation. (b) Un lemming variable entrant dans la boîte par le tunnel principal. (c) Une hermine dans son pelage d'hiver.

En termes d'utilisation de l'habitat, ma thèse s'est surtout concentrée à étudier le refuge hivernal des lemmings, soit où les lemmings construisent leur nid, mais l'habitat utilisé pour

creuser la majorité des tunnels pourrait différer de celui-ci. Il serait donc intéressant de cartographier à plus grande échelle spatiale l'ensemble des réseaux de tunnels de lemmings afin d'approfondir l'impact des propriétés physiques du manteau neigeux et du type de végétation sur ceux-ci. Par la présence de signes de broutement, nous pourrions confirmer quels tunnels sont utilisés spécifiquement pour s'alimenter. Il serait également possible de déterminer la taille totale du réseau de tunnels d'un individu, qui demeure pour le moment inconnue, ainsi que la présence de double utilisation de ces tunnels par les lemmings bruns et variables.

L'étude des conditions favorisant ou non la reproduction hivernale me semble cruciale pour mieux comprendre les cycles de populations de lemmings et, à la lumière de ma thèse, les propriétés physiques de la neige pourraient jouer un rôle crucial. Il serait intéressant d'approfondir ce lien en déterminant comment les propriétés physiques de la neige affectent les dépenses énergétiques des lemmings. À ma connaissance, seul Chappell (1980a, 1980b) a documenté leurs dépenses énergétiques en chauffant un modèle taxidermique constitué d'une bobine de résistance à l'intérieur d'une peau de lemmings avec son pelage sous différentes conditions ambiantes arctiques. Avec cette approche, l'auteur a estimé que les coûts énergétiques pour les lemmings de demeurer à la surface de la neige serait de 15 à 25 % plus élevées que de demeurer dans l'espace sous-nival. Il serait pertinent de répéter une telle étude sous des manteaux neigeux de différents types et dans des nids d'hiver afin mesurer l'effet des variations de température induites par le manteau neigeux sur les dépenses énergétiques liées à la thermorégulation chez les lemmings. Afin d'intégrer les coûts reliés à la locomotion sous-nivale, il serait également possible de travailler avec des animaux vivants afin de mesurer leur consommation d'oxygène au repos et lorsqu'ils creusent dans de la neige de différentes duretés. De telles mesures effectuées sur des lemmings au repos en captivité ont permis de déterminer leurs taux métaboliques de base (Klaassen et al. 2002). Des expériences similaires ont également été réalisées sur des taupes (*Georychus capensis*) et des géomyidés (*Thomomys bottae*) afin de quantifier leurs dépenses énergétiques à creuser dans des sols de différentes duretés (Vleck 1979, Du Toit et al. 1985). De telles expériences pourraient également s'appliquer aux lemmings afin d'améliorer notre compréhension de leurs dépenses énergétiques sous différentes conditions du manteau neigeux et mieux comprendre les conditions favorables ou au contraire néfastes à la reproduction hivernale.

Ma thèse a permis de mieux comprendre l'influence de la neige sur les composantes démographiques des lemmings. Dans un deuxième temps, il serait intéressant de vérifier l'influence des propriétés physiques de la neige sur les cycles de population de lemmings. Bergeron et al. (2023) ont récemment développé un modèle à dynamique hybride permettant de modéliser l'effet des prédateurs sur la dynamique de populations des lemmings en tenant compte des changements d'état du système. Dans notre système d'étude, les principaux changements d'état sont les saisons (été/hiver) et l'abondance de lemmings à l'été (pic/creux) (Hutchison et al. 2020, Bergeron et al. 2023). Tenir compte de ces changements d'état permet de prendre en considération les variations dans la pression de prédation exercée par chacun des prédateurs sur les lemmings. Ce type de modèle performe plutôt bien pour prédire les cycles de lemmings à notre site d'étude, mais semble moins bien prédire les phases prolongées de faible abondance (Bergeron et al. 2023). L'occurrence de périodes prolongées de faible abondance pourrait être partiellement causée par un durcissement de la couche basale de neige qui influencerait négativement la reproduction hivernale des lemmings. Ainsi, je crois qu'une prochaine étape à l'application de modèles hybrides à la dynamique des populations de petits mammifères en milieu saisonnier serait d'y incorporer l'état de la neige. Actuellement, la paramétrisation du modèle de Bergeron et al. (2023) utilise un taux constant de reproduction des lemmings. Une façon de raffiner le modèle serait de modifier le taux de reproduction hivernal en lien avec la dureté de la couche basale de neige, ce qui améliorerait peut-être la capacité du modèle à prédire la durée de la phase de faible abondance. La paramétrisation du taux d'attaque des renards arctiques en hiver pourrait également être améliorée en tenant compte de l'impact des propriétés physiques de la neige. En effet, il semble que l'épaisseur de neige interfère avec le taux d'attaque des renards (Duchesne et al. 2011a, Bilodeau et al. 2013b), mais cette relation mériterait d'être explorée davantage en tenant compte également de la dureté du manteau neigeux. Bref, les modèles hybrides constituent une approche prometteuse pour améliorer notre compréhension de la dynamique des populations de lemmings et de leurs cycles en tenant compte de la forte saisonnalité.

Les espèces arctiques au cœur d'un Nord en plein changement

L'Arctique se réchauffe plus rapidement que n'importe quelle autre région de la planète, une situation qui devient préoccupante pour les espèces adaptées à ce climat polaire. Qu'il s'agisse de la perte de l'habitat de l'ours polaire par la fonte accélérée de la banquise (Burek et al. 2008), ou de la destruction des sites de nidification de la buse pattue par des épisodes de fortes pluies entraînant l'éboulement de terrains escarpés (Beardsell et al. 2017), les conséquences sur les espèces seront variées. L'augmentation des précipitations liquides à l'hiver et des épisodes de fonte-regel est particulièrement préoccupante puisque cela devrait entraîner un fort durcissement du manteau neigeux arctique. En plus de nuire à la prise alimentaire de nombreux herbivores, grands ou petits, ce durcissement dégrade la qualité de l'espace sous-nival où les petits mammifères creusent leurs tunnels à l'hiver.

Pour certaines régions du cercle arctique, la situation est déjà critique en ce qui a trait au durcissement du manteau neigeux. En raison de sa configuration régionale bien particulière, le Svalbard est souvent aux prises avec d'importants épisodes de pluie-sur-neige, responsables de la formation de couches de glace au sol (Serreze et al. 2015). Ces conditions anormales entraînent une augmentation de la mortalité de petits et grands herbivores, campagnols et rennes, qui n'arrivent plus à s'alimenter convenablement (Rennert et al. 2009, Hansen et al. 2011, Stien et al. 2012). Cependant, tel que discuté dans ma thèse, le mécanisme par lequel le durcissement du manteau neigeux impacterait les animaux dépendrait de l'intensité de ces épisodes météorologiques. Dans les régions de l'Arctique où le climat est plutôt continental, comme dans l'Arctique canadien, les épisodes de pluie-sur-neige sont pour le moment modérés et entraînent la formation de couches de neige durcie au niveau du sol. Pour les lemmings, l'accès à la nourriture à travers de telles couches durcies demeure possible, mais exigerait un plus grand effort de creusage, ce qui pourrait mettre en péril leur reproduction hivernale.

Les résultats de ma thèse soutiennent l'existence de variations interspécifiques dans la réponse au durcissement de la neige, en fonction des adaptations propres à chaque espèce. Pour les petits mammifères, par exemple, la taille de leurs pattes avant semble jouer un rôle dans leur capacité à creuser, particulièrement dans des conditions de neige dure. Ainsi, les seuils de dureté de la neige au-delà desquels le creusage devient inefficace pour l'animal

devraient différer d'une espèce à l'autre en fonction de leur morphologie respective. Un autre exemple nous est fourni chez les ongulés avec la différence entre les rennes et les bœufs musqués. Les rennes, avec leurs sabots creux aux bords tranchants, semblent avoir plus de facilité à creuser dans la neige dure en comparaison aux bœufs musqués (Skogland 1978, Larter and Nagy 2001). Certaines espèces pourraient donc être plus avantagées que d'autres pour faire face aux perturbations du manteau neigeux causées par les changements climatiques.

La thermorégulation en hiver est un processus énergétique coûteux pour les homéothermes de petite taille, et mes travaux supportent l'idée qu'il est important pour ces espèces de privilégier les conditions qui minimisent les pertes de chaleur. Pour les petits mammifères, l'utilisation d'un manteau neigeux isolant semble être d'une grande importance, même si cela implique de composer parfois avec des couches basales plus denses pouvant nuire au creusage. De tels compromis en faveur de la thermorégulation ont également été observés chez le carcajou, qui quitte à l'occasion un habitat intra-nival lui offrant une protection contre la prédation afin de s'exposer à des conditions thermiques avantageuses à la surface de la neige (Glass et al. 2021b). En effet, s'exposer à la surface de la neige peut être avantageux pour la thermorégulation lorsque la température de l'air et la radiation solaire sont élevées. Il apparaît donc difficile pour les animaux de trouver un habitat hivernal qui soit idéal en tous points. Cependant, les conditions favorisant une réduction des coûts de thermorégulation semblent être parmi les critères les plus importants pour affronter l'hiver.

Mes travaux soulignent le rôle crucial que joue le manteau neigeux pour les espèces nordiques et l'importance de mieux comprendre l'impact qu'auront les changements climatiques sur ces interactions. Dans les régions nordiques où les risques de périodes de redoux sont fréquents en hiver (p. ex. forêt boréale, régions arctiques influencées par les courants océaniques), des épisodes de pluie-sur-neige pourraient survenir à tout moment, y compris en plein cœur de l'hiver. La formation de couches de regel plus denses entraînerait une réduction de l'isolation offerte par le manteau neigeux, ce qui pourrait avoir d'importantes conséquences chez ces espèces qui dépendent de cet abri pour mieux conserver leur énergie. À l'inverse, de telles couches durcies pourraient favoriser le déplacement et la prise alimentaire chez certains carnivores chassant à la surface de la neige (Stenseth et al.

2004). Une meilleure compréhension de la complexité qui existe dans la façon dont le manteau neigeux influence les espèces nordiques est essentielle afin de mieux prédire les répercussions des changements climatiques sur ces interactions.

Ma thèse brosse un portrait inédit du rôle des propriétés physiques de la neige sur les populations de lemmings en Arctique. Les lemmings auront-ils le temps de s'adapter à cet environnement en pleine mutation? Bien que les outils de modélisation actuels puissent nous guider dans la quête de cette réponse (Bergeron et al. 2023, Martin et al. 2023), seul le temps permettra de correctement mesurer l'impact de ces changements sur les populations de lemmings. Et si les effectifs de leurs populations venaient à diminuer, de profondes perturbations des populations des prédateurs qui dépendent directement des lemmings pour leur survie et leur reproduction seraient à prévoir. Le lien étroit qu'entretiennent les lemmings avec le manteau neigeux et la dégradation anticipée de ce refuge éphémère soulignent l'importance d'approfondir nos connaissances sur ce phénomène écologique, dont les implications pourraient s'étendre bien au-delà de la simple existence d'un petit rongeur arctique.

Bibliographie

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

Aitchison, C. W. 2001. The effect of snow cover on small animals. Pages 229–265 *in* H. G. Jones, J. W. Pomeroy, D. A. Walker, and R. W. Hoham, editors. Snow ecology: an interdisciplinary examination of snow-covered ecosystems. Cambridge University Press, Cambridge.

AMAP. 2017. Snow, water, ice and permafrost in the Arctic (SWIPA). Arctic Monitoring and Assessment Programme (AMAP). Oslo, Norway.

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, MA.

Andreev, A. V. 1991. Winter adaptations in the willow ptarmigan. Arctic 44:106–114.

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 Proceedings of the International Symposium on Physics of Ice Core Records, Shikotsukohan, Hokkaido, Japan, September 14–17, 1998. Hokkaido University Press, Sapporo, Japan.

Atkinson, D. E., R. Brown, B. Alt, T. Agnew, J. Bourgeois, M. Burgess, C. Duguay, G. Henry, S. Jeffers, R. Koerner, A. G. Lewkowicz, S. McCourt, H. Melling, M. Sharp, S. Smith, A. Walker, K. Wilson, S. Wolfe, M. Woo, and K. L. Young. 2006. Canadian cryospheric response to an anomalous warm summer: a synthesis of the climate change action fund project "the state of the arctic cryosphere during the extreme warm summer of 1998." Atmosphere-Ocean 44:347–375.

Audet, B., G. Gauthier, and E. Lévesque. 2007. Feeding ecology of greater snow goose goslings in mesic tundra on Bylot Island, Nunavut, Canada. Condor 109:361–376.

Banks, E. M., R. J. Brooks, and J. Schnell. 1975. A radiotracking study of home range and activity of the brown lemming (*Lemmus trimucronatus*). Journal of Mammalogy 56:888–901.

Barnes, E. A., and L. M. Polvani. 2015. CMIP5 projections of arctic amplification, of the North American/North Atlantic circulation, and of their relationship. Journal of Climate 28:5254–5271.

Barrere, M., F. Domine, M. Belke-Brea, and D. Sarrazin. 2018. Snowmelt events in autumn can reduce or cancel the soil warming effect of snow-vegetation interactions in the Arctic. Journal of Climate 31:9507–9518.

Barton, K. 2022. Package MuMIn: Multi-model inference.

Bates, D., M. Mächler, B. M. Bolker, and S. C. Walker. 2020. lme4: linear mixed-effects models. R package version 1.1-26.

Batzli, G. O., F. A. Pitelka, and G. N. Cameron. 1983. Habitat use by lemming near Barrow, Alaska. Holarctic Ecology 6:255–262.

Beardsell, A., G. Gauthier, D. Fortier, J. Therrien, and J. Bêty. 2017. Vulnerability to geomorphological hazards of an Arctic cliff-nesting raptor, the rough-legged hawk. Arctic Science 3:203–219.

Beardsell, A., G. Gauthier, J.-F. Therrien, and J. Bêty. 2016. Nest site characteristics, patterns of nest reuse, and reproductive output in an Arctic-nesting raptor, the rough-legged hawk. The Auk 133:718–732.

Beardsell, A., D. Gravel, D. Berteaux, G. Gauthier, J. Clermont, V. Careau, N. Lecomte, C. C. Juhasz, P. Royer-Boutin, and J. Bêty. 2021. Derivation of predator functional responses using a mechanistic approach in a natural system. Frontiers in Ecology and Evolution 9:1–12.

Beardsell, A., D. Gravel, J. Clermont, D. Berteaux, G. Gauthier, and J. Bêty. 2022. A mechanistic model of functional response provides new insights into indirect interactions among arctic tundra prey. Ecology 103:e3734.

Von Beckerath, X., G. Benadi, O. Gilg, B. Sittler, G. Yannic, A.-M. Klein, and B. Eitzinger. 2021. Long-term monitoring reveals topographical features and vegetation explain winter habitat use of an arctic rodent. Arctic Science 8:349–361.

Bergeron, G., G. Gauthier, F. Lutscher, P. Legagneux, D. Berteaux, C. Hutchison, and D. Gravel. 2023. Simple seasonal switches in food web composition unveil the complexity of an arctic predator-prey system. Biological Conservation [soumis].

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.

Berteaux, D., D. Réale, A. G. McAdam, and S. Boutin. 2004. Keeping pace with fast climate change: can arctic life count on evolution ? Integrative and Comparatie Biology 44:140–151.

Bêty, J., G. Gauthier, J. F. Giroux, and E. Korpimäki. 2001. Are goose nesting success and lemming cycles linked? Interplay between nest density and predators. Oikos 93:388–400.

Bêty, J., G. Gauthier, E. Korpimäki, and J. F. Giroux. 2002. Shared predators and indirect trophic interactions: lemming cycles and arctic-nesting geese. Journal of Animal Ecology 71:88–98.

Bilodeau, F., G. Gauthier, and D. Berteaux. 2013a. The effect of snow cover on lemming population cycles in the Canadian High Arctic. Oecologia 172:1007–1016.

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

Bilodeau, F., G. Gauthier, D. Fauteux, and D. Berteaux. 2014. Does lemming winter grazing impact vegetation in the Canadian Arctic? Polar Biology 37:845–857.

Bilodeau, F., D. G. Reid, G. Gauthier, C. J. Krebs, D. Berteaux, and A. J. Kenney. 2013c. Demographic response of tundra small mammals to a snow fencing experiment. Oikos 122:1167–1176.

Bolduc, D., D. Fauteux, C. A. Gagnon, G. Gauthier, J. Bêty, and P. Legagneux. 2023. Testimonials to reconstruct past abundances of wildlife populations. Basic and Applied Ecology 68:23–34.

Boonstra, R., H. P. Andreassen, S. Boutin, J. Hušek, R. A. Ims, C. J. Krebs, C. Skarpe, and P. Wabakken. 2016. Why do the boreal forest ecosystems of Northwestern Europe differ from those of Western North America? BioScience 66:722–734.

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

Buckland, S. T., D. R. Anderson, K. P. Burnham, J. L. Laake, D. L. Borchers, and L. Thomas. 2004. Advanced distance sampling: estimating abundance of biological populations. Oxford University Press, London.

Brooks, R.K. 1993. Dynamics of home range in collared lemmings. Pages 355–386 *in*

Stenseth N.C., Ims R.A., editors. The biology of lemmings. Linnean Society of London, Academic Press, London, United Kingdom.
Burek, K. A., F. M. D. Gulland, and T. M. O'Hara. 2008. Effects of climate change on arctic marine mammal health. Ecological Applications 18:126–134.
Callaghan, T. V, M. Johansson, R. D. Brown, P. Y. Groisman, N. Labba, V. Radionov, R. S. Bradley, S. Blangy, O. N. Bulygina, T. R. Christensen, J. E. Colman, R. L. H. Essery, B. C. Forbes, C. Forchhammer, V. N. Golubev, R. E. Honrath, G. P. Juday, V. Anna, G. K. Phoenix, J. Pomeroy, A. Rautio, D. A. Robinson, M. Schmidt, T. V Callaghan, M. Johansson, R. D. Brown, P. Y. Groisman, N. Labba, V. Radionov, R. S. Bradley, S. Blangy, B. C. Forbes, M. C. Forchhammer, V. N. Golubev, R. E. Honrath, G. P. Juday, A. V Meshcherskaya, G. K. Phoenix, J. Pomeroy, A. Rautio, D. A. Robinson, N. M. Schmidt, M. C. Serreze, V. P. Shevchenko, A. I. Shiklomanov, A. B. Shmakin, P. Sköld, M. Sturm, M. Woo, and E. F. Wood. 2011. Multiple effects of changes in Arctic snow cover. Ambio 40:32–45.
Casey, T. M. 1981. Nest insulation: energy savings to brown lemmings using a winter nest. Oecologia 50:199–204.
CEN. 2022. Données des stations climatiques de l'île Bylot au Nunavut, Canada, v. 1.12.0 (1992-2022). Nordicana D2, doi: 10.5885/45039SL-EE76C1BDAADC4890.
Chami, P., R. Antoine, and A. Sahai. 2007. On efficient confidence intervals for the log-normal mean. Journal of Applied Sciences 7:1790–1794.
Chappell, M. A. 1980a. Thermal energetics and thermoregulatory costs of small arctic mammals. Journal of Mammalogy 61:278–291.
Chappell, M. A. 1980b. Insulation, radiation, and convection in small arctic mammals. Journal of Mammalogy 61:268–277.
Chevallier, C., G. Gauthier, S. Lai, and D. Berteaux. 2020. Pulsed food resources affect reproduction but not adult apparent survival in arctic foxes. Oecologia 193:557–569.
Coe, P. K., D. A. Clark, R. M. Nielson, S. C. Gregory, J. B. Cupples, M. J. Hedrick, B. K. Johnson, and D. H. Jackson. 2018. Multiscale models of habitat use by mule deer in winter. Journal of Wildlife Management 82:1285–1299.
Colbeck, S. C. 1982. An overview of seasonal snow metamorphism. Review of Geophysics and Space Physics 20:45–61.
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.
Cornulier, T., N. G. Yoccoz, V. Bretagnolle, J. E. Brommer, A. Butet, F. Ecke, D. A. Elston, E. Framstad, H. Henttonen, B. Hornfeldt, O. Huitu, C. Imholt, R. A. Ims, J. Jacob, J. BogumiłaJe, A. Millon, S. J. Petty, H. Pietiainen, E. Tkadlec, K. Zub, and X. Lambin. 2013. Herbivores Europe-wide dampening of population cycles in keystone. Science 340:63–66.
Derksen, C., and R. Brown. 2012. Spring snow cover extent reductions in the 2008-2012 period exceeding climate model projections. Geophysical Research Letters 39:L19504.
Derksen, C., J. Lemmetyinen, P. Toose, A. Silis, J. Pulliainen, and M. Sturm. 2014. Physical properties of Arctic versus subarctic snow: implications for high latitude passive microwave snow water equivalent retrievals. Journal of Geophysical Research: Atmospheres 119:7254–7270.
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.
Dolant, C., B. Montpetit, A. Langlois, L. Brucker, O. Zolina, C. A. Johnson, A. Royer, and P. Smith. 2018. Assessment of the Barren Ground caribou die-off during winter 2015–2016 using passive microwave observations. Geophysical Research Letters 45:4908–4916.
Domine, F., M. Barrere, and S. Morin. 2016a. The growth of shrubs on high Arctic tundra at Bylot Island: impact on snow physical properties and permafrost thermal regime. Biogeosciences 13:6471–6486.
Domine, F., M. Barrere, and D. Sarrazin. 2016b. Seasonal evolution of the effective thermal conductivity of the snow and the soil in high Arctic herb tundra at Bylot Island, Canada. The Cryosphere 10:2573–2588.
Domine, F., M. Belke-Brea, D. Sarrazin, L. Arnaud, M. Poirier, and T. Joint. 2018a. Soil moisture, wind speed and depth hoar formation in the Arctic snowpack. Journal of Glaciology 64:990–1002.
Domine, F., J. Bock, S. Morin, and G. Giraud. 2011. Linking the effective thermal conductivity of snow to its shear strength and density. Journal of Geophysical Research: Earth Surface 116:1–10.
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., K. Fourteau, G. Picard, G. Lackner, D. Sarrazin, and M. Poirier. 2022. Permafrost cooled in winter by thermal bridging through snow-covered shrub branches. Nature geoscience 15:554–560.
Domine, F., J. C. Gallet, J. Bock, and S. Morin. 2012. Structure, specific surface area and thermal conductivity of the snowpack around Barrow, Alaska. Journal of Geophysical Research Atmospheres 117:D00R14.
Domine, F., G. Gauthier, V. Vionnet, D. Fauteux, M. Dumont, and M. Barrere. 2018b. Snow physical properties may be a significant determinant of lemming population dynamics in the high Arctic. Arctic Science 4:813–826.
Domine, F., G. Lackner, D. Sarrazin, M. Poirier, and M. Belke-Brea. 2021a. Meteorological, snow and soil data (2013-2019) from a herb tundra permafrost site at Bylot Island, Canadian high Arctic, for driving and testing snow and land surface models. Earth System Science Data 13:4331–4348.
Domine, F., G. Lackner, D. Sarrazin, M. Poirier, and M. Belke-Brea. 2021b. Données météorologiques, de neige et de sol de l'Île Bylot, haut Arctique canadien, pour forcer et tester des modèles de neige et de surfaces continentales, v. 1.100000 (2013-2019). Nordicana D86, doi: 10.5885/45693CE-02685A5200DD4C38.
Domine, F., G. Picard, and S. Morin. 2015. Major issues in simulating some arctic snowpack properties using current detailed snow physics models: consequences for the thermal regime and water budget of permafrost. Journal of Advances in Modeling Earth Systems 11:34–44.
Domine, F., A. S. Taillandier, A. Cabanes, T. A. Douglas, and M. Sturm. 2009. Three examples where the specific surface area of snow increased over time. Cryosphere 3:31–39.
Dozier, J. 1989. Spectral signature of alpine snow cover from the landsat thematic mapper. Remote Sensing of Environment 28:9–22.
Duchesne, D., G. Gauthier, and D. Berteaux. 2011a. Habitat selection, reproduction and

predation of wintering lemmings in the Arctic. Oecologia 167:967–980.
Duchesne, D., G. Gauthier, and D. Berteaux. 2011b. Evaluation of a method to determine the breeding activity of lemmings in their winter nests. Journal of Mammalogy 92:511–516.
Durner, G. M., S. C. Amstrup, and A. S. Fischbach. 2003. Habitat characteristics of polar bear terrestrial maternal den sites in Northern Alaska. Arctic 56:55–62.
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.
Efford, M. 2023. secr: Spatially explicit capture-recapture models. R package version 4.6.0.
Ehrich, D., N. M. Schmidt, G. Gauthier, R. Alisauskas, A. Angerbjörn, K. Clark, F. Ecke, N. E. Eide, E. Framstad, J. Frandsen, A. Franke, O. Gilg, M. A. Giroux, H. Henttonen, B. Hörnfeldt, R. A. Ims, G. D. Kataev, S. P. Kharitonov, S. T. Killengreen, C. J. Krebs, R. B. Lanctot, N. Lecomte, I. E. Menyushina, D. W. Morris, G. Morrisson, L. Oksanen, T. Oksanen, J. Olofsson, I. G. Pokrovsky, I. Y. Popov, D. Reid, J. D. Roth, S. T. Saalfeld, G. Samelius, B. Sittler, S. M. Sleptsov, P. A. Smith, A. A. Sokolov, N. A. Sokolova, M. Y. Soloviev, and D. V. Solovyeva. 2020. Documenting lemming population change in the Arctic: can we detect trends? Ambio 49:786–800.
Elton, C. S. 1924. Periodic fluctuations in the numbers of animals: their causes and effects. British Journal of Experimental Biology 2:119–163.
Fauteux, D., and G. Gauthier. 2022. Density-dependent demography and movements in a cyclic brown lemming population. Ecology and Evolution 12:e9055.
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.
Fauteux, D., G. Gauthier, and D. Berteaux. 2016. Top-down limitation of lemmings revealed by experimental reduction of predators. Ecology 97:3231–3241.
Fauteux, D., G. Gauthier, M. J. Mazerolle, N. Coallier, J. Bêty, and D. Berteaux. 2018. Evaluation of invasive and non-invasive methods to monitor rodent abundance in the Arctic. Ecosphere 9:e02124.
Fauteux, D., G. Slevan-Tremblay, G. Gauthier, and D. Berteaux. 2017. Feeding preference of brown lemmings (*Lemmus trimucronatus*) for plant parts of Arctic willow (*Salix arctica*). Polar Biology 40:2329–2334.
Fauteux, D., A. Stien, N. G. Yoccoz, E. Fuglei, and R. A. Ims. 2021. Climate variability and density-dependent population dynamics: lessons from a simple High Arctic ecosystem. Proceedings of the National Academy of Sciences 118:e2106635118.
Feng, C., H. Wang, N. Lu, T. Chen, H. He, Y. Lu, and X. M. Tu. 2014. Log-transformation and its implications for data analysis. Shanghai Archives of Psychiatry 26:105–109.
Formozov, A. 1946. Snow cover as an integral factor of the environment and its importance in the ecology of mammals and birds (Translated from Russian). Boreal Institute, University of Alberta, Occasionnal publication no 1.
Fourteau, K., P. Hagenmuller, J. Roulle, and F. Domine. 2022. On the use of heated needle probes for measuring snow thermal conductivity. Journal of Glaciology 68:705–719.
Freedman, D. A. 2006. On the so-called "Huber Sandwich Estimator" and "robust standard errors". American Statistician 60:299–302.
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.
Gallet, J.-C. C., F. Domine, C. S. Zender, and G. Picard. 2009. Measurement of the specific surface area of snow using infrared reflectance in an integrating sphere at 1310 and 1550

nm. The Cryosphere 3:167–182.
Gardner, A. S., and M. J. Sharp. 2010. A review of snow and ice albedo and the development of a new physically based broadband albedo parameterization. Journal of Geophysical Research: Earth Surface 115:1–15.
Gauthier, G. 2020. Lemming monitoring on Bylot Island, Nunavut, Canada, v. 1.3 (1994-2019). Nordicana D22, doi: 10.5885/45400AW-9891BD76704C4CE2.
Gauthier, G., D. Berteaux, J. Bêty, A. Tarroux, J.-F. Therrien, L. McKinnon, P. Legagneux, and M.-C. Cadieux. 2011. The tundra food web of Bylot Island in a changing climate and the role of exchanges between ecosystems. Ecoscience 18:223–235.
Gauthier, G., J. Bêty, M.-C. Cadieux, P. Legagneux, M. Doiron, C. Chevallier, S. Lai, A. Tarroux, and D. Berteaux. 2013. Long-term monitoring at multiple trophic levels suggests heterogeneity in responses to climate change in the Canadian Arctic tundra. Philosophical transactions of the Royal Society of London. Series B, Biological sciences 368:20120482.
Gauthier, G., J. Bêty, J.-F. Giroux, and L. Rochefort. 2004. Trophic interactions in a high Arctic snow goose colony. Integrative and Comparatie Biology 44:119–129.
Gauthier, G., M. Cadieux, D. Berteaux, J. Bêty, P. Legagneux, E. Lévesque, and C. Gagnon. 2023. Long-term study of the tundra food web at a hotspot of Arctic biodiversity, the Bylot Island field station. Arctic Science (in press).
Gilg, O. 2002. The summer decline of the collared lemming, *Dicrostonyx groenlandicus*, in high arctic Greenland. Oikos 99:499–510.
Gilg, O., I. Hanski, and B. Sittler. 2003. Cyclic dynamics in a simple vertebrate predator-prey community. Science (New York, N.Y.) 302:866–868.
Gilg, O., K. M. Kovacs, J. Aars, J. Fort, G. Gauthier, D. Grémillet, R. A. Ims, H. Meltofte, J. Moreau, E. Post, N. M. Schmidt, G. Yannic, and L. Bollache. 2012. Climate change and the ecology and evolution of Arctic vertebrates. Annals of the New York Academy of Sciences 1249:166–190.
Gilg, O., B. Sittler, and I. Hanski. 2009. Climate change and cyclic predator-prey population dynamics in the high Arctic. Global Change Biology 15:2634–2652.
Gilg, O., B. Sittler, B. Sabard, A. Hurstel, R. Sané, P. Delattre, and I. Hanski. 2006. Functional and numerical responses of four lemming predators in high arctic Greenland. Oikos 113:193–216.
Glass, T. W., G. A. Breed, G. E. Liston, A. K. Reinking, M. D. Robards, and K. Kielland. 2021a. Spatiotemporally variable snow properties drive habitat use of an Arctic mesopredator. Oecologia 195:887–899.
Glass, T. W., G. A. Breed, M. D. Robards, C. T. Williams, and K. Kielland. 2021b. Trade-off between predation risk and behavioural thermoregulation drives resting behaviour in a cold-adapted mesocarnivore. Animal Behaviour 175:163–174.
Groisman, P. Y., O. N. Bulygina, X. Yin, R. S. Vose, S. K. Gulev, I. Hanssen-Bauer, and E. Førland. 2016. Recent changes in the frequency of freezing precipitation in North America and Northern Eurasia. Environmental Research Letters 11:045007.
Gruyer, N., G. Gauthier, and D. Berteaux. 2008. Cyclic dynamics of sympatric lemming populations on Bylot Island, Nunavut, Canada. Canadian Journal of Zoology 86:910–917.
Halfpenny, J. C., and R. D. Ozanne. 1989. Winter: an ecological Handbook. Johnson Books: Boulder, Colorado.
Halpin, M. A., and J. A. Bissonette. 1988. Influence of snow depth on prey availability and

habitat use by red fox. Canadian Journal of Zoology 66:587–592.
Hansen, B. B., R. Aanes, I. Herfindal, J. Kohler, and B.-E. Seather. 2011. Climate, icing, and wild arctic reindeer: past relationships and future prospects. Ecology 92:1917–1923.
Hansen, B. B., V. Grøtan, R. Aanes, B. Sæther, E. Fuglei, R. A. Ims, N. G. Yoccoz, Å. Ø. Pedersen, A. Wikner, N. Mait, E. Abbe, J. Jose, L. Chan, A. Phys, S. Jose, and M. Nichols. 2013. Climate events synchronize the dynamics of a resident vertebrate community in the High Arctic. Science 339:313–315.
Hansen, B. B., K. Isaksen, R. E. Benestad, J. Kohler, Å. Pedersen, L. E. Loe, S. J. Coulson, J. O. Larsen, and Ø. Varpe. 2014. Warmer and wetter winters: characteristics and implications of an extreme weather event in the High Arctic. Environmental Research Letters 9:114021.
Hansen, R. M. 1957. Remarks on the bifid claws of the varying lemming. American Society of Mammalogist 38:127–128.
Hansson, L., and H. Henttonen. 1985. Gradients in density variations of small rodents: the importance of latitude and snow cover. Oecologia 67:394–402.
Holt, D. 1977. Predation, apparent competition, and the structure of prey communities. Theoretical Population Biology 12:197–229.
Hörnfeldt, B., T. Hipkiss, and U. Eklund. 2005. Fading out of vole and predator cycles? Proceedings of the Royal Society B: Biological Sciences 272:2045–2049.
Hutchison, C., F. Guichard, P. Legagneux, G. Gauthier, J. Bêty, D. Berteaux, D. Fauteux, and D. Gravel. 2020. Seasonal food webs with migrations: multi-season models reveal indirect species interactions in the Canadian Arctic tundra. Philosophical Transactions of the Royal Society A 378:20190354.
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.
Ims, R. A., J. A. Henden, and S. T. Killengreen. 2008. Collapsing population cycles. Trends in Ecology and Evolution 23:79–86.
Ims, R. a, N. G. Yoccoz, and S. T. Killengreen. 2011. Determinants of lemming outbreaks. Proceedings of the National Academy of Sciences 108:1970–1974.
IPCC. 2022. Climate Change 2022: Impacts, Adaptation and Vulnerability. Contribution of Working Group II to the Sixth Assessment Report of the Intergovernmental Panel on Climate Change. H.-O. Pörtner, D. C. Roberts, M. Tignor, E. S. Poloczanska, K. Mintenbeck, A. Alegría, M. Craig, S. Langsdorf, S. Löschke, V. Möller, A. Okem, and B. Rama, editors. Cambridge University Press, Cambridge, UK and New York, NY, USA.
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, editor. The biology of lemmings. Linnean Society of London, Academic Press, London, United Kingdom.
Jennings, K. S., T. S. Winchell, B. Livneh, and N. P. Molotch. 2018. Spatial variation of the rain – snow temperature threshold across the Northern Hemisphere. Nature Communications 9:1148.
Johnsen, K., R. Boonstra, S. Boutin, O. Devineau, C. J. Krebs, and H. P. Andreassen. 2017. Surviving winter: Food, but not habitat structure, prevents crashes in cyclic vole populations. Ecology and Evolution 7:115–124.
Kalhor, D., M. Poirier, A. Pusenkova, X. Maldague, G. Gauthier, and T. Galstian. 2021. A camera trap to reveal the obscure world of the Arctic subnivean ecology. IEEE Sensors Journal 21:28025–28036.

Kalhor, D., A. Pusenkova, M. Poirier, G. Gauthier, T. Galstian, and X. Maldague. 2019. Using near infrared for studying lemming subnival behavior in the High Arctic. Proceedings 27:11.

Kausrud, K. L., A. Mysterud, H. Steen, J. O. Vik, E. Østbye, B. Cazelles, E. Framstad, A. M. Eikeset, I. Mysterud, T. Solhøy, and N. C. Stenseth. 2008. Linking climate change to lemming cycles. Nature 456:93–97.

Klaassen, M., J. Agrell, and Å. Lindström. 2002. Metabolic rate and thermal conductance of lemmings from high-arctic Canada and Siberia. Journal of Comparative Physiology B: Biochemical, Systemic, and Environmental Physiology 172:371–378.

Knaust, D. 2014. Burrows and related traces in snow and vegetation produced by the Norwegian lemming (*Lemmus lemmus*). Pages 395–404 Experimental Approaches to Understanding Fossil Organisms: Lessons from the Living.

Korpimäki, E., and C. J. Krebs. 1996. Predation and population cycles of small mammals. BioScience 46:754–764.

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. 1996. Population cycles revisited. Journal of Mammalogy 77:8–24.

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.

Krebs, C. J. 2013. Population fluctuations in rodents. The University of Chicago Press, Chicago, Illinois.

Lamare, M., F. Domine, J. Revuelto, M. Pelletier, L. Arnaud, and G. Picard. 2023. Investigating the role of shrub height and topography in snow accumulation on low-arctic tundra using UAV-Borne lidar. Journal of Hydrometeorology 24:853–871.

Lamarre, J. F., P. Legagneux, G. Gauthier, E. T. Reed, and J. Bêty. 2017. Predator-mediated negative effects of overabundant snow geese on arctic-nesting shorebirds. Ecosphere 8:e01788.

Langlois, A., C. A. Johnson, B. Montpetit, A. Royer, E. A. Blukacz-Richards, E. Neave, C. Dolant, A. Roy, G. Arhonditsis, D. K. Kim, S. Kaluskar, and L. Brucker. 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.

Larter, N. C., and J. A. Nagy. 2001. Variation between snow conditions at peary caribou and muskox feeding sites and elsewhere in foraging habitats on Banks Island in the Canadian High Arctic. Arctic, Antarctic, and Alpine Research 33:123–130.

Lawrence, D. M., and S. C. Swenson. 2011. Permafrost response to increasing Arctic shrub abundance depends on the relative influence of shrubs on local soil cooling versus large-scale climate warming. Environmental Research Letters 6:045504.

Legagneux, P., G. Gauthier, D. Berteaux, J. Bêty, M. C. Cadieux, F. Bilodeau, E. Bolduc, L. Mckinnon, A. Tarroux, J. F. Therrien, L. Morissette, and C. J. Krebs. 2012. Disentangling trophic relationships in a High Arctic tundra ecosystem through food web modeling. Ecology 93:1707–1716.

Legagneux, P., G. Gauthier, N. Lecomte, N. M. Schmidt, D. Reid, M. C. Cadieux, D. Berteaux, J. Bêty, C. J. Krebs, R. a Ims, N. G. Yoccoz, R. I. G. Morrison, S. J. Leroux, M. Loreau, and D. Gravel. 2014. Arctic ecosystem structure and functioning shaped by climate and herbivore body size. Nature Climate Change 4:379–383.

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.
Lindström, E. R., and B. Hörnfeldt. 1994. Vole cycles, snow depth and fox predation. Oikos 70:156–160.
Liston, G. E., and C. A. Hiemstra. 2011. The changing cryosphere: pan-Arctic snow trends (1979-2009). Journal of Climate 24:5691–5712.
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.
MacLean, S. F., B. M. Fitzgerald, and F. A. Pitelka. 1974. Cycles in arctic lemmings: winter reproduction and predation by weasels. Arctic and Alpine Research 6:1–12.
Magoun, A. J., and J. P. Copeland. 1998. Characteristics of wolverine reproductive den sites. The Journal of Wildlife Management 62:1313–1320.
Marbouty, D. 1980. An experimental study of temperature-gradient metamorphism. Journal of Glaciology 26:303–312.
Marchand, P. J. 2013. Life in the cold : an introduction to winter ecology. University Press of New England.
Marjakangas, A., H. Rintamäki, and R. Hissa. 1984. Thermal responses in the Capercaillie *Tetrao urogallus* and the Black Grouse *Lyrurus tetrix* roosting in the snow. Physiological Zoology 57:99–104.
Martin, M. E., K. M. Moriarty, and J. N. Pauli. 2020. Forest structure and snow depth alter the movement patterns and subsequent expenditures of a forest carnivore, the Pacific marten. Oikos 129:356–366.
Martin, R. A., C.R. da Silva, M. P. Moore and S.E. Diamond. 2023. When will a changing climate outpace adaptive evolution? Wiley Interdisciplinary Reviews: Climate Change e852.
Mazerolle, M. J. 2023. ICcmodavg: Model selection and multimodel inference based on (Q)AIC(c). R package version 2.3.2.
Millar, J. S. 2001. On reproduction in lemmings. Ecoscience 8:145–150.
Miller, D. L., E. Rexstad, L. Thomas, J. L. Laake, and L. Marshall. 2019. Distance sampling in R. Journal of Statistical Software 89:1–28.
Mölle, J. P., E. F. Kleiven, R. A. Ims, and E. M. Soininen. 2021. Using subnivean camera traps to study Arctic small mammal community dynamics during winter. Arctic Science 8:183–199.
Morris, D. W., D. L. Davidson, and C. J. Krebs. 2000. Measuring the ghost of competition: insights from density-dependent habitat selection on the co-existence and dynamics of lemmings. Evolutionary Ecology Research 2:41–67.
Mos, J., and T. R. Hofmeester. 2020. The Mostela: an adjusted camera trapping device as a promising non-invasive tool to study and monitor small mustelids. Mammal Research 65:843–853.
Murray, D. L., S. Boutin, and M. O'Donoghue. 1994. Winter habitat selection by lynx and coyotes in relation to snowshoe hare abundance. Canadian Journal of Zoology 72:1444–1451.

Myers, J. H. 2018. Population cycles: generalities, exceptions and remaining mysteries. Proceedings of the Royal Society B: Biological Sciences 285:20172841.
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.
Oksanen, L., S. D. Fretwell, J. Arruda, and P. Niemela. 1981. Exploitation ecosystems in gradients of primary productivity. The American Naturalist 118:240–261.
Pauli, J. N., B. Zuckerberg, J. P. Whiteman, and W. Porter. 2013. The subnivium: a deteriorating seasonal refugium. Frontiers in Ecology and the Environment 11:260–267.
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.
Pithan, F., and T. Mauritsen. 2014. Arctic amplification dominated by temperature feedbacks in contemporary climate models. Nature geoscience 7:181–184.
Poirier, M., D. Fauteux, G. Gauthier, F. Domine, and J. F. Lamarre. 2021. Snow hardness impacts intranivean locomotion of arctic small mammals. Ecosphere 12:e03835.
Poirier, M., G. Gauthier, and F. Domine. 2019. What guides lemmings movements through the snowpack? Journal of Mammalogy 100:1416–1426.
Poirier, M., G. Gauthier, F. Domine, and D. Fauteux. 2023. Lemming winter habitat: the quest for warm and soft snow. Oecologia 202:211–225.
Pomeroy, J. W. W., and E. Brun. 1990. Physical properties of snow. Pages 45-118 *in* H.G. Jones, editor. Snow ecology: An interdisciplinary examination of snow-covered ecosystems. Cambridge University Press.
Predavec, M., and C. J. Krebs. 2000. Microhabitat utilisation, home ranges, and movement patterns of the collared lemming (*Dicrostonyx groenlandicus*) in the central Canadian Arctic. Canadian Journal of Zoology 78:1885–1890.
Pruitt, W. O. 1984. Snow and small mammals. Pages 1–8 *in* J.F. Merritt, editor. Winter ecology of small mammals. Special Publication No.10 Carnegie Museum of Natural History.
Pusenkova, A., M. Poirier, D. Kalhor, T. Galstian, G. Gauthier, and X. Maldague. 2022. Optical design challenges of subnivean camera trapping under extreme Arctic conditions. Arctic Science 8:313–328.
Quéno, L., V. Vionnet, F. Cabot, D. Vrécourt, and I. Dombrowski-Etchevers. 2018. Forecasting and modelling ice layer formation on the snowpack due to freezing precipitation in the Pyrenees. Cold Regions Science and Technology 146:19–31.
R Core Team. 2021. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.
Rantanen, M., A. Y. Karpechko, A. Lipponen, K. Nordling, O. Hyvärinen, K. Ruosteenoja, T. Vihma, and A. Laaksonen. 2022. The Arctic has warmed nearly four times faster than the globe since 1979. Communications Earth and Environment 3:1–10.
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 and London.
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.
Reid, D. G., and C. J. Krebs. 1996. Limitations to collared lemming population growth in winter. Canadian Journal of Zoology 74:1284–1291.
Rennert, K. J., G. Roe, J. Putkonen, and C. M. Bitz. 2009. Soil thermal and ecological impacts of rain on snow events in the circumpolar arctic. Journal of Climate 22:2302–2315.
Riggs, G., and D. Hall. 2015. MODIS Snow Products Collection 6 User Guide. https://nsidc.org/sites/nsidc.org/files/files/MODIS-snow-user-guide-C6.pdf.
Ripley, B., B. Venables, D. M. Bates, K. Hornik, A. Gebhardt, and D. Firth. 2022. Package ‘ MASS ’ version 7.3-58.
Roberts, E., and R. E. Stewart. 2008. On the occurrence of freezing rain and ice pellets over the eastern Canadian Arctic. Atmospheric Research 89:93–109.
Royer, A., F. Domine, A. Roy, A. Langlois, N. Marchand, and G. Davesne. 2021. New northern snowpack classification linked to vegetation cover on a latitudinal mega-transect across northeastern Canada. Écoscience 28:225–242.
Sanecki, G. M., K. Green, H. Wood, and D. Lindenmayer. 2006. The characteristics and classification of australian snow cover: an ecological perspective. Arctic, Antarctic and Alpine Research 38:429–435.
Saunders, P. A., and F. Veyrunes. 2021. Unusual mammalian sex determination systems: a cabinet of curiosities. Genes 12:1770.
Schmidt, N. M., F. M. Van Beest, A. Dupuch, L. H. Hansen, J. Pierre, and D. W. Morris. 2021. Long-term patterns in winter habitat selection, breeding and predation in a density-fluctuating, high Arctic lemming population. Oecologia 195:927–935.
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.
Seldal, T., K. Andersen, and G. Hogstedt. 1994. Grazing-induced proteinase inhibitors: a possible cause for lemming population cycles. Oikos 70:3–11.
Serreze, M. C., A. D. Crawford, and A. P. Barrett. 2015. Extreme daily precipitation events at Spitsbergen, an Arctic Island. International Journal of Climatology 35:4574–4588.
Seyer, Y., G. Gauthier, D. Fauteux, and J. F. Therrien. 2020. Resource partitioning among avian predators of the Arctic tundra. Journal of Animal Ecology 89:2934–2945.
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.
Skogland, T. 1978. Characteristics of the snow cover and its relationship to wild mountain reindeer (*Rangifer tarandus tarandus L.*) feeding strategies. Arctic and Alpine Research 10:569–579.
Soininen, E. M., G. Gauthier, F. Bilodeau, D. Berteaux, L. Gielly, P. Taberlet, G. Gussarova, E. Bellemain, K. Hassel, H. K. Stenøien, L. Epp, A. Schrøder-Nielsen, C. Brochmann, and N. G. Yoccoz. 2015. Highly overlapping winter diet in two sympatric lemming species revealed by DNA metabarcoding. PLOS ONE 10:e0115335.
Sokolov, A. A., N. A. Sokolova, R. A. Ims, L. Brucker, and D. Ehrich. 2016. Emergent rainy winter spells may promote boreal predator expansion into the Arctic. Arctic 69:121–

129.
Sorum, M. S., K. Joly, A. G. Wells, M. D. Cameron, G. V. Hilderbrand, and D. D. Gustine. 2019. Den-site characteristics and selection by brown bears (*Ursus arctos*) in the central Brooks Range of Alaska. Ecosphere 10:e02822.
Spencer, A. W. 1984. Food habits, grazing activities and reproductive development of long-tailed voles, *Microtus longicaudus* (Merriam) in relation to snow cover in the mountains of Colorado. Pages 67-90 *in* J.F. Merritt, editor. Winter ecology of small mammals. Special Publication No.10 Carnegie Museum of Natural History.
St-Georges, M., S. Nadeau, and D. Lambert. 1995. Winter habitat use by ptarmigan, snowshoe hares, red foxes, and river otters in the boreal forest - tundra transition zone of western Quebec. Canadian Journal of Zoology 73:755–764.
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.
Stenseth N.C., Ims R.A. 1993. Population dynamics of lemmings: temporal and spatial variation – an introduction. Pages 61–96 *in* Stenseth N.C., Ims R.A., editors. The biology of lemmings. Linnean Society of London, Academic Press, London, United Kingdom.
Stenseth, N. C., A. Shabbar, K. S. Chan, S. Boutin, E. K. Rueness, D. Ehrich, J. W. Hurrell, O. C. Lingjærde, and K. S. Jakobsen. 2004. Snow conditions may create an invisible barrier for lynx. Proceedings of the National Academy of Sciences of the United States of America 101:10632–10634.
Stern, P., and L. Stevenson. 2006. Critical Inuit studies: an anthology of contemporary arctic ethnography. P. Stern and L. Stevenson, editors. University of Nebraska Press.
Stien, A., R. A. Ims, S. D. Albon, E. Fuglei, R. J. Irvine, E. Ropstad, O. Halvorsen, R. Langvatn, L. E. Loe, V. Veiberg, and N. G. Yoccoz. 2012. Congruent responses to weather variability in high arctic herbivores. Biology Letters 8:1002–1005.
Sturm, M., and C. Benson. 2004. Scales of spatial heterogeneity for perennial and seasonal snow layers. Annals of Glaciology 38:253–260.
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.
Sturm, M., J. Holmgren, M. König, and K. Morris. 1997. Thermal conductivity of seasonal snow. Journal of Glaciology 43:26–41.
Sturm, M., J. Holmgren, and G. E. Liston. 1995. A seasonal snow cover classification system for local to global applications. Journal of Climate 8:1261–1283.
Sturm, M., J. P. McFadden, G. E. Liston, S. Chapin III, C. H. Racine, and J. Holmgren. 2001. Snow – shrub interactions in arctic tundra: a hypothesis with climatic implications. Journal of Climate 14:336–344.
Sutton, G. M., and J. Hamilton. 1932. The mammals of Southampton Island. Pages 1–109 Memoirs of the Carnegie Museum, Pittsburgh.
Tape, K., M. Sturm, and C. Racine. 2006. The evidence for shrub expansion in Northern Alaska and the Pan-Arctic. Global Change Biology 12:686–702.
Therrien, J. F., G. Gauthier, E. Korpimäki, and J. Bêty. 2014a. Predation pressure by avian predators suggests summer limitation of small-mammal populations in the Canadian Arctic. Ecology 95:56–67.
Therrien, J. F., G. Gauthier, D. Pinaud, and J. Bêty. 2014b. Irruptive movements and breeding dispersal of snowy owls: a specialized predator exploiting a pulsed resource. Journal of

Avian Biology 45:536–544.
Thompson, K. L., B. Zuckerberg, W. P. Porter, and J. N. Pauli. 2021. The decline of a hidden and expansive microhabitat: the subnivium. Frontiers in Ecology and the Environment 19:268–273.
Du Toit, J. T., J. U. M. Jarvis, and G. N. Louw. 1985. Nutrition and burrowing energetics of the Cape mole-rat *Georychus capensis*. Oecologia 66:81–87.
Turchin, P., L. Oksanen, P. Ekerholm, T. Oksanen, and H. Henttonen. 2000. Are lemmings prey or predators? Nature 405:562–565.
Le Vaillant, M., R. Erlandsson, B. Elmhagen, B. Hörnfeldt, N. E. Eide, and A. Angerbjörn. 2018. Spatial distribution in Norwegian lemming Lemmus lemmus in relation to the phase of the cycle. Polar Biology 41:1391–1403.
Venables, W. N., and B. D. Ripley. 2002. Modern applied statistics with S. Fourth Edi. Springer-Verlag.
Vionnet, V., E. Brun, S. Morin, A. Boone, S. Faroux, P. Le Moigne, E. Martin, and J. M. Willemet. 2012. The detailed snowpack scheme Crocus and its implementation in SURFEX v7.2. Geoscientific Model Development 5:773–791.
Vleck, D. 1979. The energy cost of burrowing by the pocket gopher Thomomys bottae. Physiological Zoology 52:122–136.
Zedler, P. H. 2003. Vernal pools and the concept of "Isolated wetlands." Wetlands 23:597–607.
Zhang, T. 2005. Influence of the seasonal snow cover on the ground thermal regime: an overview. Reviews of Geophysics 43:RG4002.
Zimova, M., K. Hackl, J. M. Good, C. Paulo, 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.

Annexe S1 – Documentation supplémentaire pour le Chapitre 1

S1.1 Supplementary material for Chapter 1

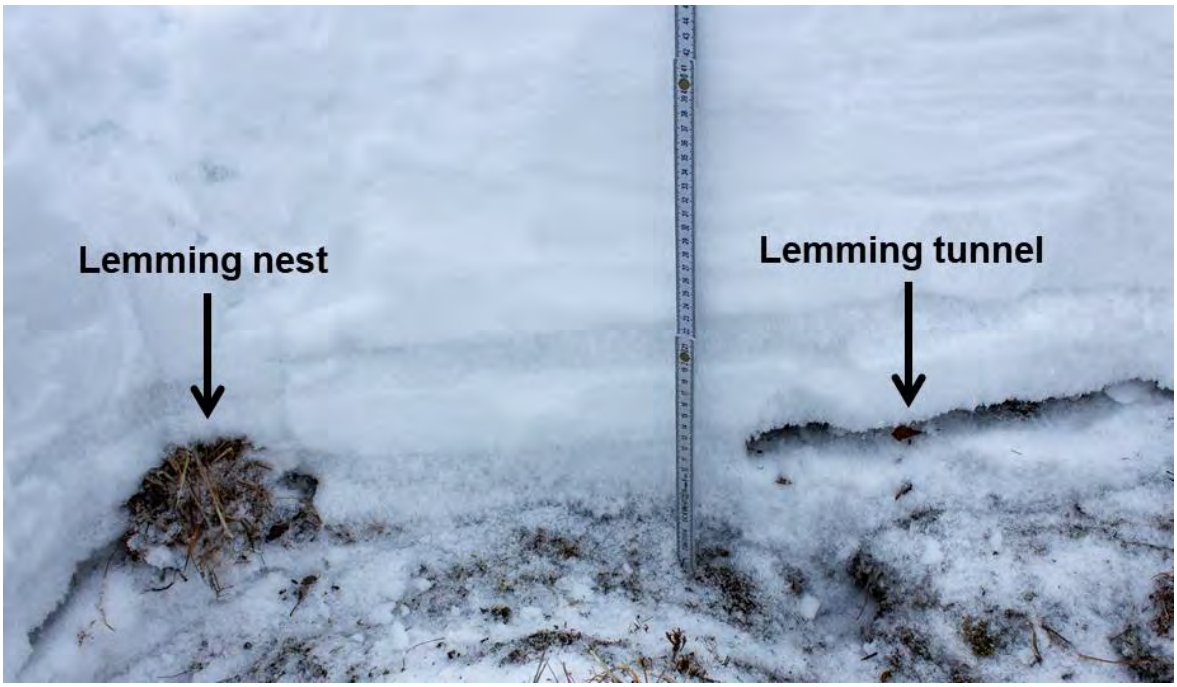


Figure S1.1 Example of a lemming nest (left) found in a snow pit with lemming tunnel (right) reaching this nest through the snow.

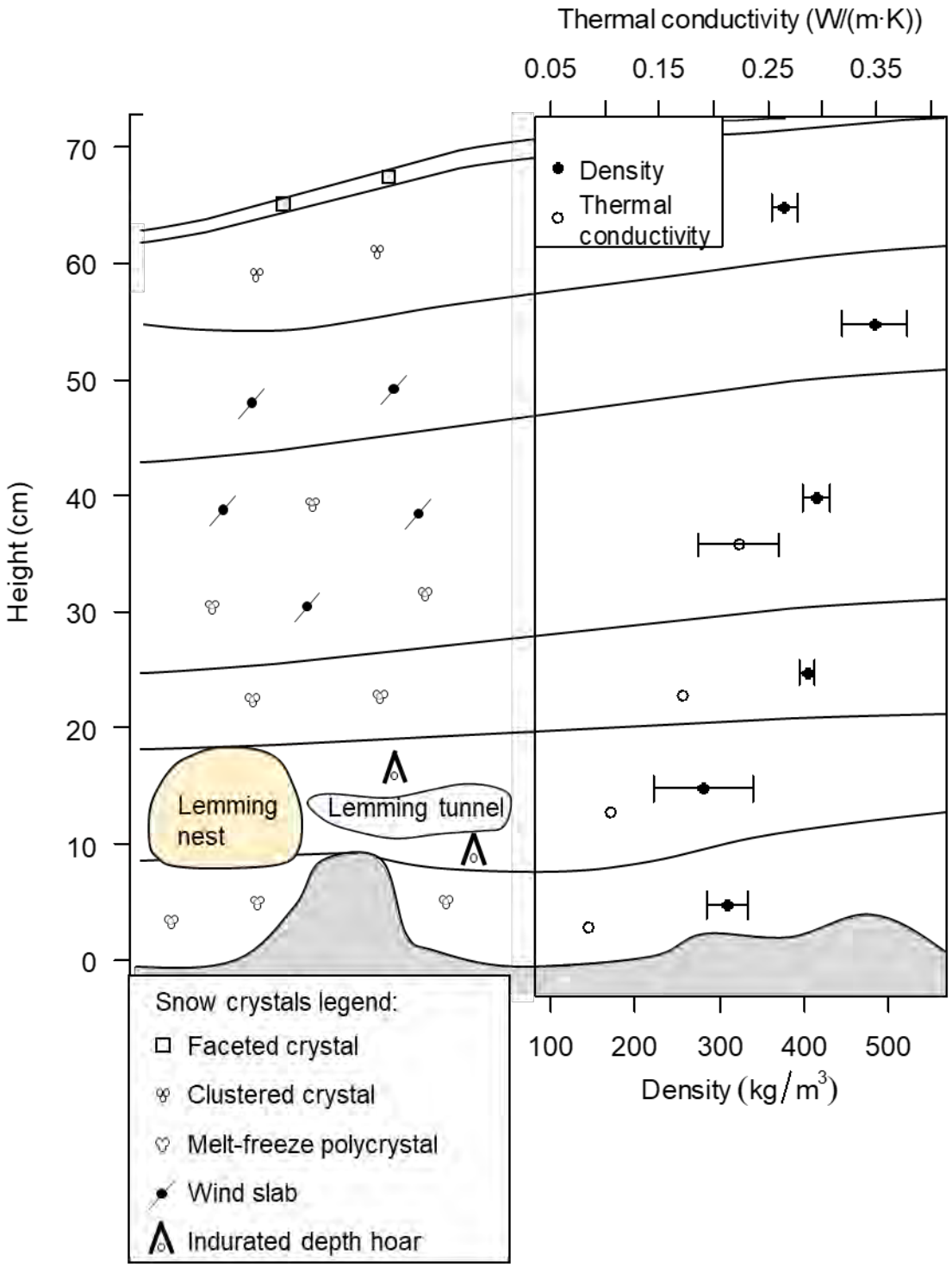


Figure S1.2 Left stratigraphy of the different layers measured in a snow pit dug in 2017 and typical of conditions encountered that year with melt-freeze layer at the ground level (gray shading represents the ground). Right: snow physical properties (density and thermal conductivity) measured in the different layers (mean ± *SE*).

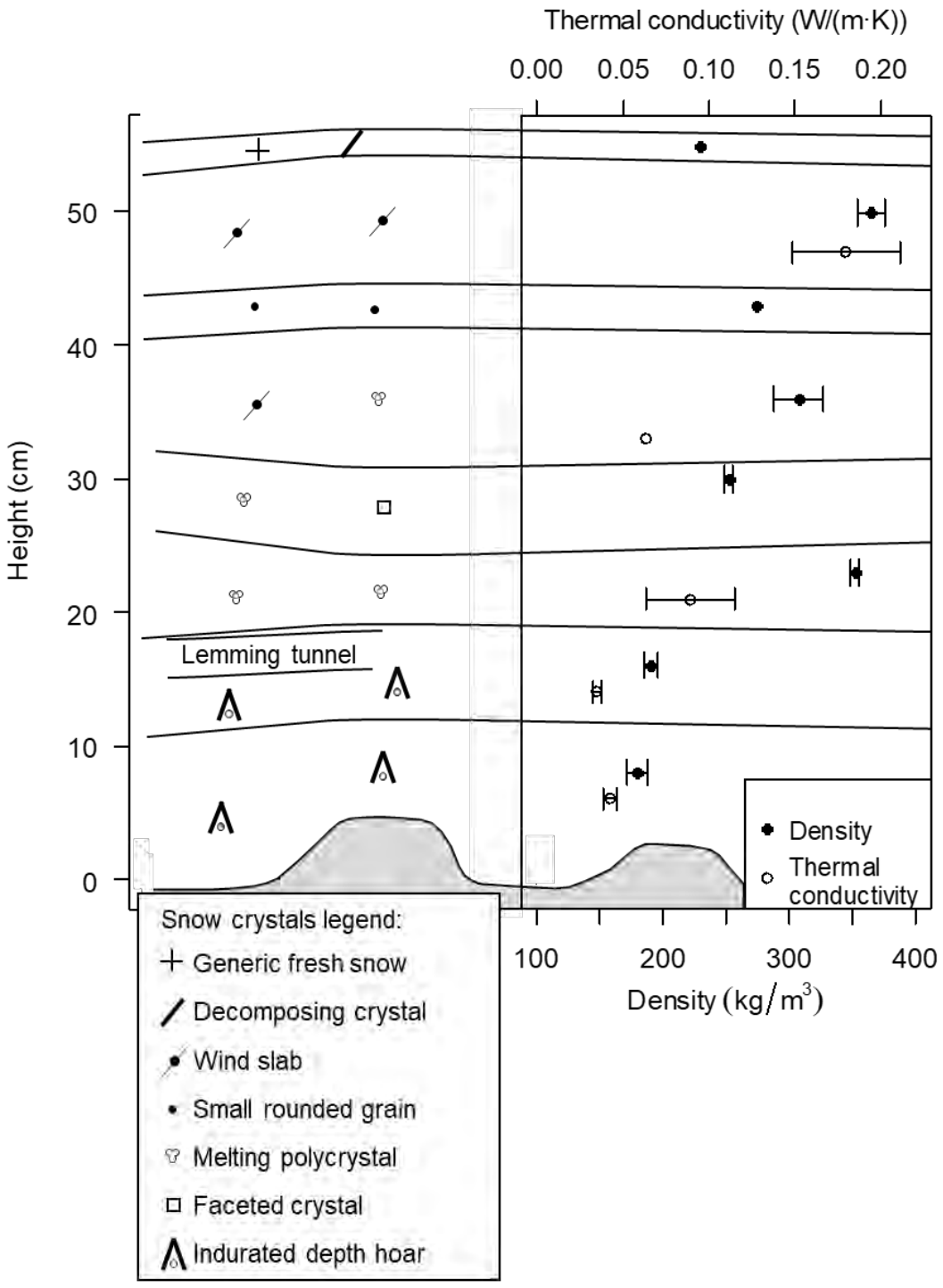


Figure S1.3 Left: stratigraphy of the different layers measured in a snow pit dug in 2018 and typical of conditions encountered that year with no melt-freeze layer at the ground level (gray shading represents the ground). Right: snow physical properties (density and thermal conductivity) measured in the different layers (mean ± *SE*).

Annexe S2 – Documentation supplémentaire pour le Chapitre 2

S2.1 Supplementary material for Chapter 2

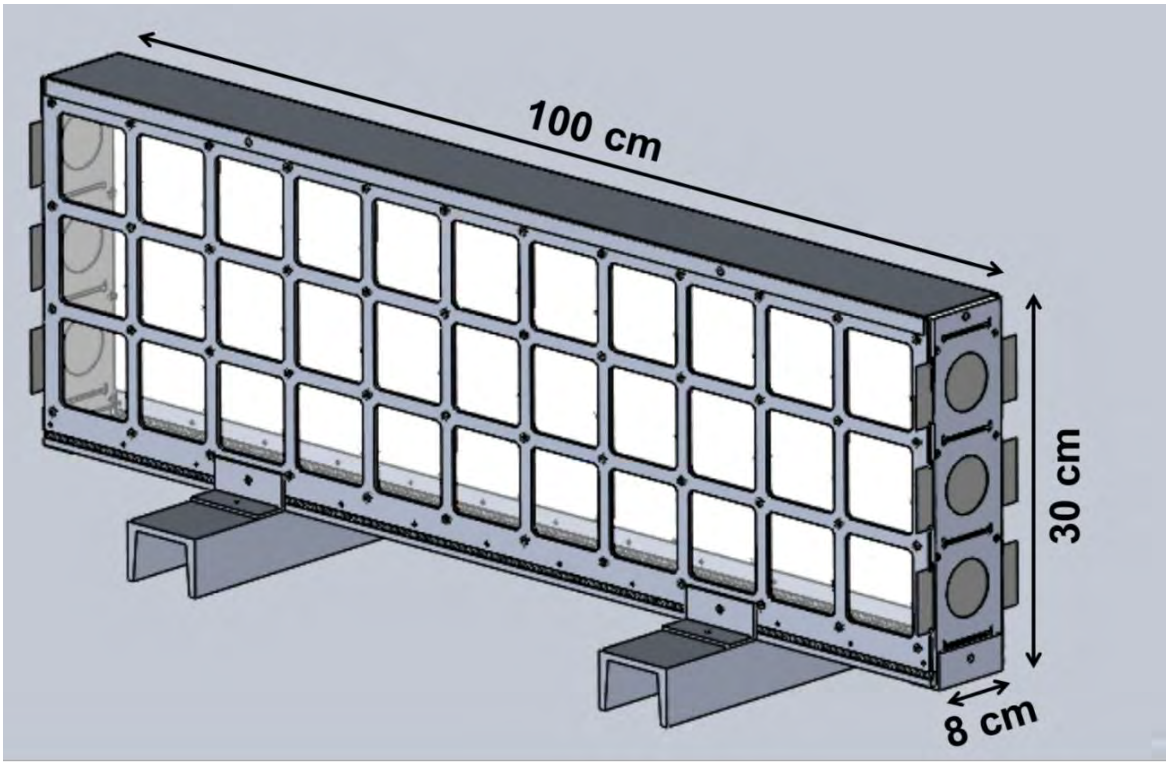
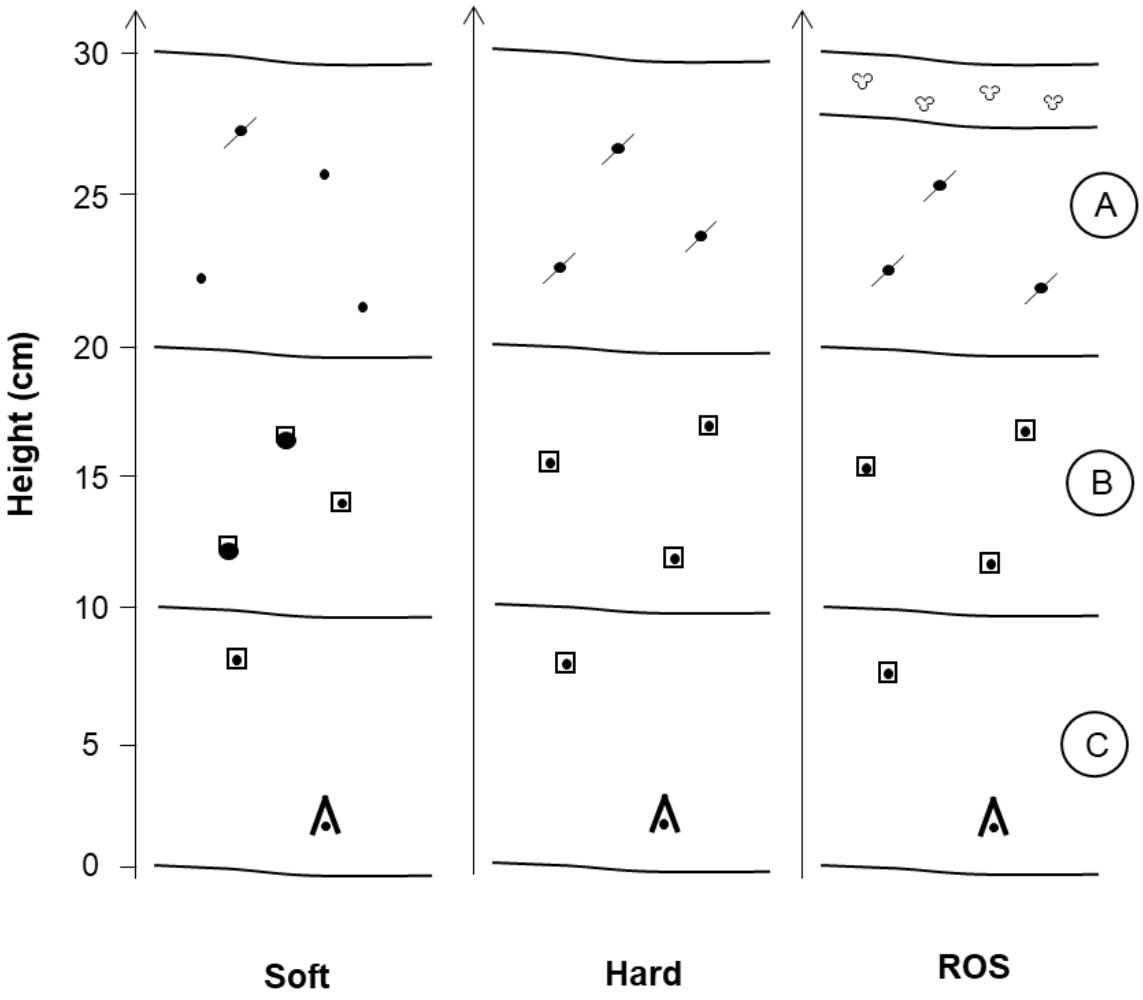


Figure S2.1 Representation of the experimental box used to collect snow samples and conduct observations of lemmings digging into the snow. The frame of the box was in aluminum with 33 8x8 cm open squares on each side, as a compromise between allowing us to see inside the box and ensuring enough rigidity. Two clear polycarbonate sheets through which we could see were attached to the inner sides of the aluminium frame with screws and silicon. The bottom part was open to allow collection of snow samples by inserting the box vertically in the snowpack. Two long blades fixed at the bottom edge of the lateral sides of the frame helped cut through the snowpack while inserting the box. The snowpack was cut with a handsaw, following the shape and size of the base of the box, before inserting the box for facilitation. After inserting the box in the snowpack, one side of the box was cleared of snow in order to be able to pull it horizontally. Before the box was pulled out, we slid and secured an aluminium floor to keep the snow inside the box. Two aluminium stands could be added at the bottom of the box to keep it stable during the experiments. Finally, a removable lid fixed with screws had two handles to allow transportation of the box from the field to the laboratory.



Snow grain legend
Melt-freeze polycrystals from ROS event (✾); wind slab (🖌); small rounded grains (•); indurated faceted crystals from wind slab (▣); faceting rounded crystals (◒); faceted crystals (□); indurated depth hoar from wind slab (🜂) (Domine et al. 2016b).

Figure S2.2 Typical stratigraphic profiles of the different types of snowpack used for our experiments (left: soft; middle: hard; right: rain-on-snow (ROS)) and the typical snow grains composition of their main snow layers (A, B, C).

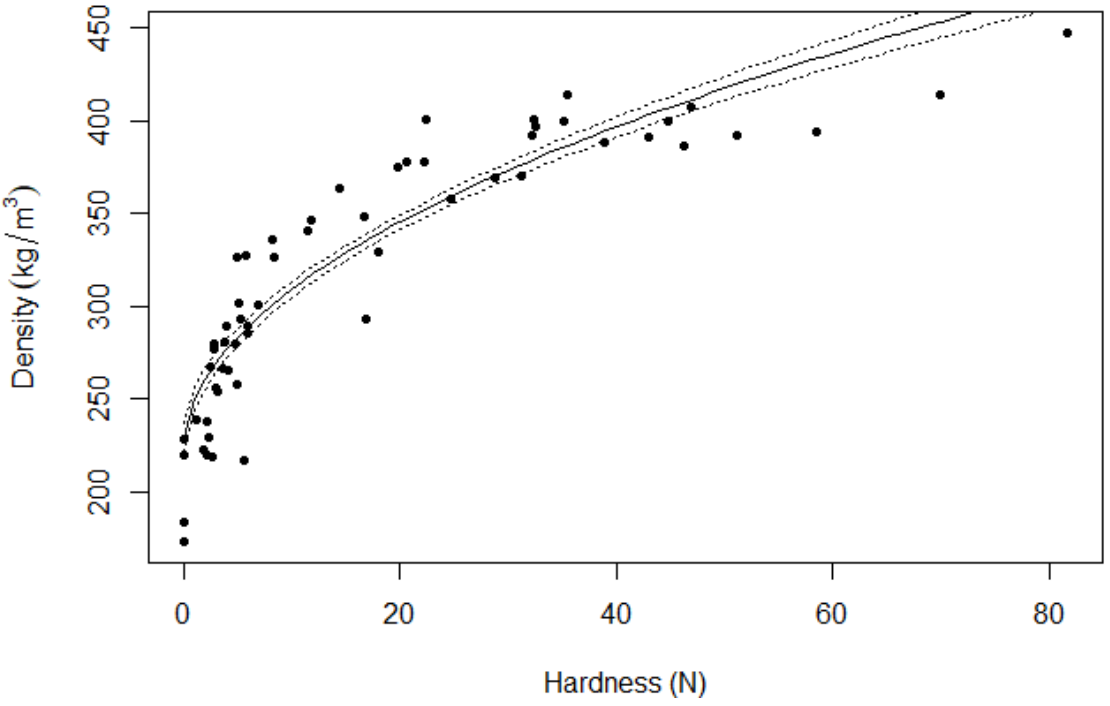


Figure S2.3 Relationship between measured snow density and snow hardness (β = 21.81, 95% CI = [20.07, 23.55] (dotted lines), R^2 = 0.84) from a linear model excluding data from the AA (i.e., top) layer of ROS snow. Solid line represents the square root fit.

Table S2.1 Coefficients of the linear models examining the differences in hardness (A) or density (B) between the different layers shown on Fig. 2.2 for every type of snow. Estimates in bold indicate that the 95% confidence interval did not include 0.

A) Hardness

Snow type	Layers	β	95% CI
Soft snow	**B-A**	**3.73**	**[1.30, 6.16]**
	C-A	**3.54**	**[1.10, 5.96]**
	C-B	-0.19	[-2.62, 2.24]
Hard snow	**B-A**	**-24.4**	**[-31.9, -16.9]**
	C-A	**-41.0**	**[-48.6, -33.5]**
	C-B	**-16.7**	**[-24.2, -9.2]**
ROS snow	**A-AA**	**-49.0**	**[-59.4, -38.6]**
	B-AA	**-67.2**	**[-77.6, -56.8]**
	C-AA	**-85.3**	**[-95.7, -74.9]**
	B-A	**-18.2**	**[-7.8, -28.6]**
	C-A	**-36.3**	**[-25.9, -46.7]**
	C-B	**-18.1**	**[-7.7, -28.5]**

B) Density

Snow type	Layers	β	95% CI
Soft snow	**B-A**	**43.2**	**[19.2, 67.1]**
	C-A	**46.9**	**[22.9, 70.9]**
	C-B	3.7	[-20.2, 27.7]
Hard snow	**B-A**	**-27.0**	**[-43.9, -10.2]**
	C-A	**-94.6**	**[-111.5, -77.8]**
	C-B	**-67.6**	**[-84.5, -50.8]**

Table S2.2 Model selection of the relationship between lemmings digging speed and snow physical properties (either density or hardness), lemming species and their interaction. The number of parameters (k), the Delta AICc (ΔAICc), the Akaike weight (Wt), the log-likelihood (LL) and the marginal R^2 (R^2_m) considering only the fixed effects are presented. Animal ID was used as a random effect. The preferred model is shown in bold.

Model (density)	k	ΔAICc	Wt	LL	R^2_m
species + density^2	**5**	**0.00**	**0.29**	**20.94**	**0.50**
species + (density < 255) + (density >= 255)	6	0.76	0.20	21.77	0.52
density^2	4	1.76	0.12	18.88	0.47
species + density + density^2	6	1.79	0.12	21.25	0.51
species + density	5	1.83	0.12	20.02	0.49
species + density^2 + species:density^2	6	2.42	0.09	20.94	0.50
species + density$^{1/2}$	5	3.46	0.05	19.21	0.48
species + log(density)	5	5.55	0.02	18.16	0.46

Model (hardness)					
species + hardness + hardness^2	6	0.00	0.32	19.54	0.48
species + hardness$^{1/2}$	**5**	**0.56**	**0.24**	**18.05**	**0.46**
species + log(hardness)	5	1.74	0.14	17.46	0.45
hardness$^{1/2}$	4	1.86	0.13	16.23	0.43
species + hardness$^{1/2}$ + species:hardness$^{1/2}$	6	2.88	0.08	18.10	0.51
species + hardness$^{1/3}$	5	3.40	0.06	16.63	0.43
species + hardness	5	5.74	0.02	15.46	0.41
species + (hardness < 23) + (hardness >= 23)	6	6.07	0.02	16.51	0.43

References

Domine, F., Barrere, M., & Sarrazin, D. (2016). Seasonal evolution of the effective thermal conductivity of the snow and the soil in high Arctic herb tundra at Bylot Island, Canada. The Cryosphere, 10, 2573–2588. https://doi.org/10.5194/tc-2016-107

S2.2 Videos of the experiment

Video S2.1 – Two examples in accelerate of 30 minutes lemming trials in different snow types (first: soft, second: hard). Video accessible online.

Video S2.2 – Compilation of the 7 main behaviors (efficient digging, inefficient digging, scratching, exploring, travelling, resting, grooming) performed by lemmings during the trials. Video accessible online.

Video S2.3 – Example of the 2 types of digging technique used by lemmings: the scratch-digging being the most common and the chisel-tooth being used mostly in rain-on-snow (ROS) type of snow. Video accessible online.

Annexe S3 – Documentation supplémentaire pour le Chapitre 3

S3.1 Supplementary material for Chapter 3

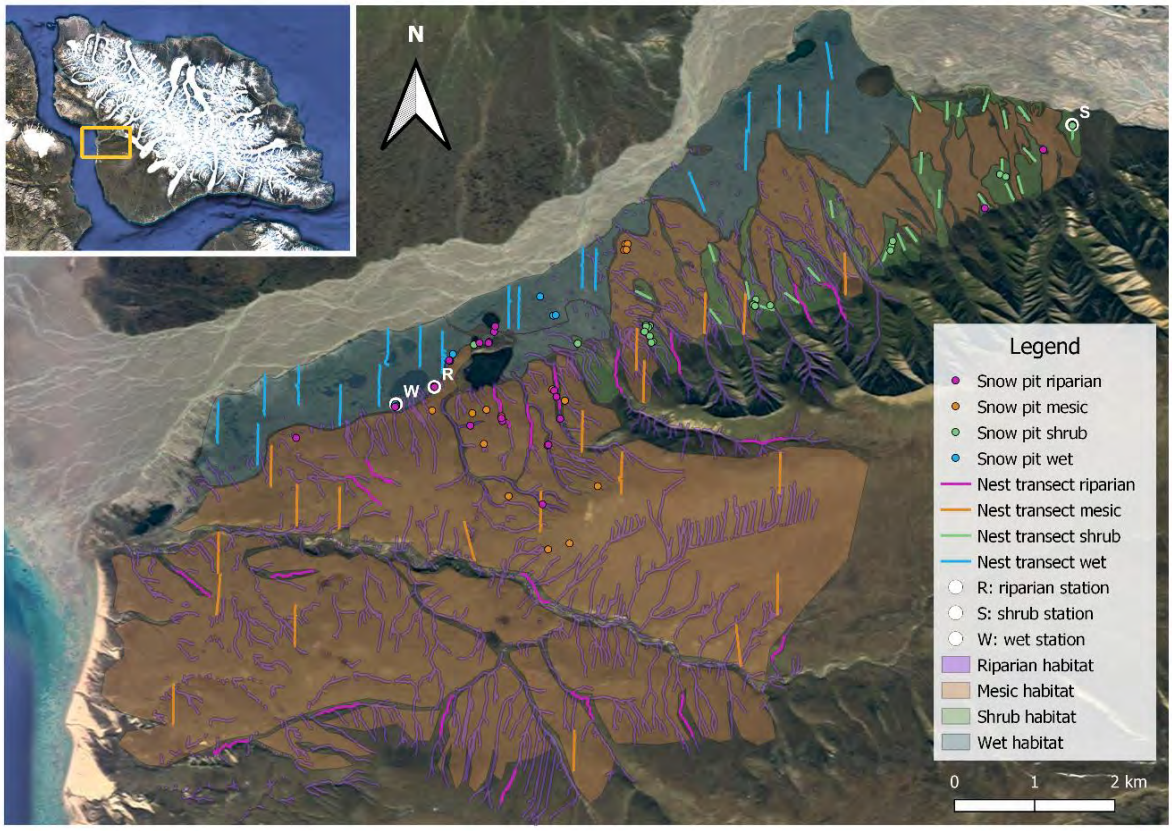


Figure S3.1 Location of snow pits and lemming winter nest transects in each habitat and the three automated stations recording snow temperature in the study area. Delimitation of habitats is based on a satellite image. The riparian habitat corresponds to the hydrological network (15 m on either side of rivers, streams or gullies). Note that riparian habitat might be slightly underestimated because some areas with topographic features conducive to deep snow accumulation may have been missed.

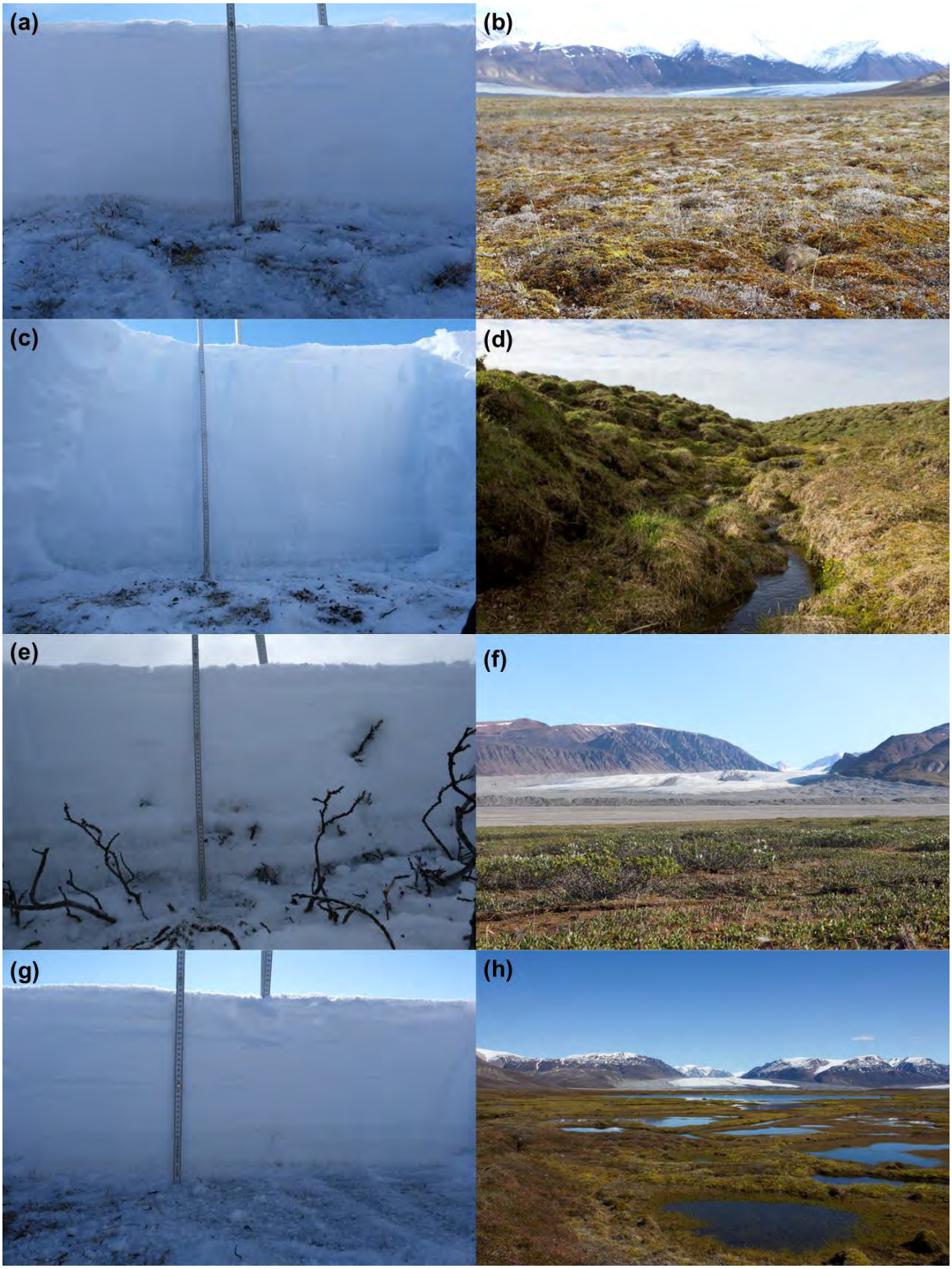


Figure S3.2 Main habitat types and snow profiles found in the 51 km^2 study area at Bylot Island; (a-b) mesic, (c-d) riparian, (e-f) shrubland and (g-h) wetland. Typical cross-sections of the snowpack (left) and views of the landscape during the summer (right) are shown.

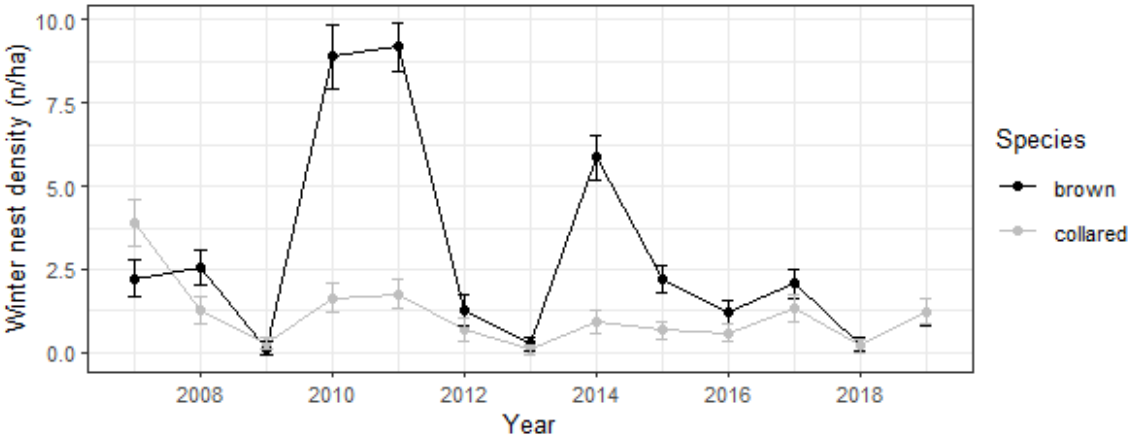


Figure S3.3 Time series of mean annual winter nest density in three habitats (mesic, riparian, wet) for brown lemmings (black) and collared lemmings (gray) at Bylot Island (2007-2019). Error bars represent SE, calculated with the delta method (Powell et al., 2007). For time series of summer lemming densities, see Fauteux and Gauthier (2022).

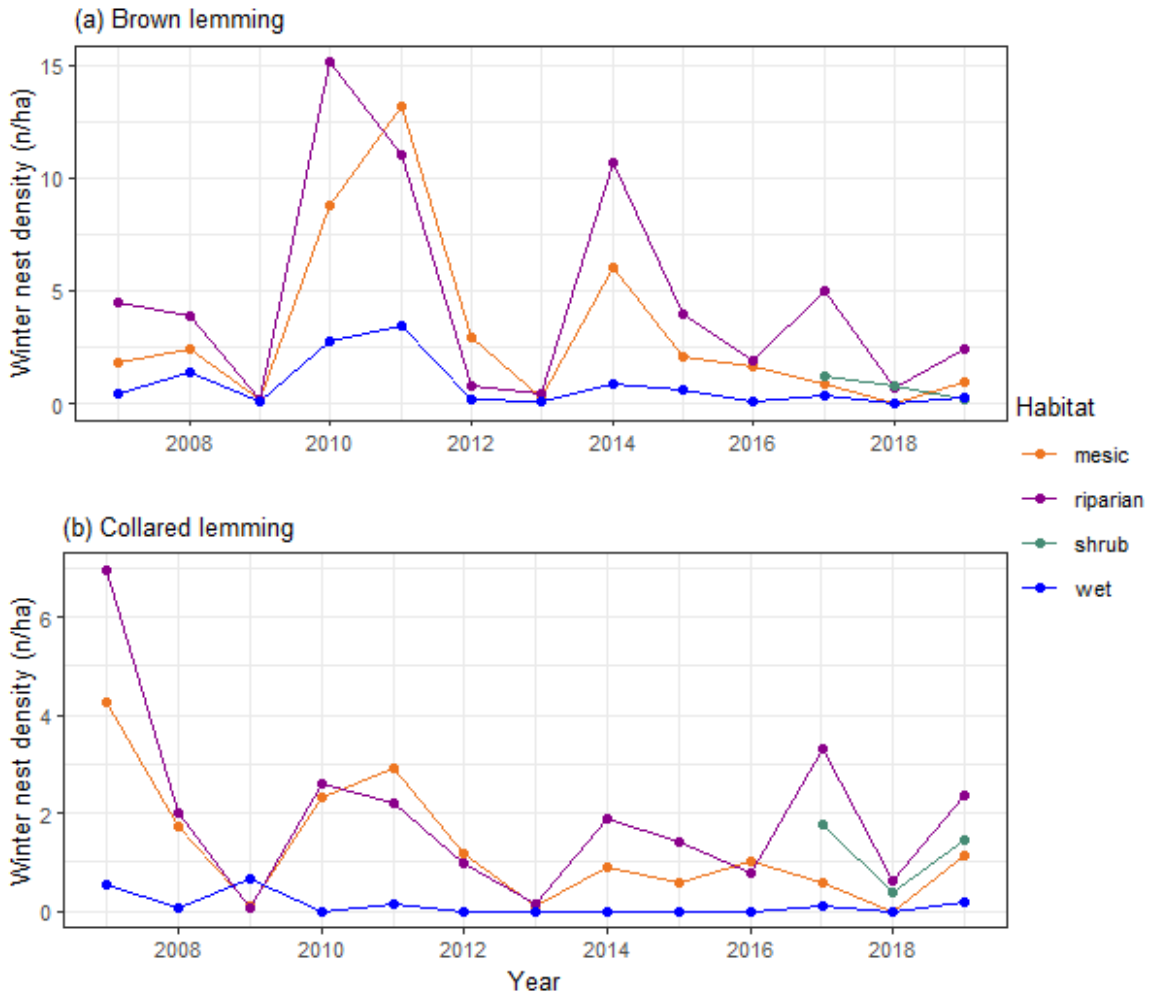


Figure S3.4 Time series of annual winter nest density in four different habitats for (a) brown lemmings and (b) collared lemmings at Bylot Island.

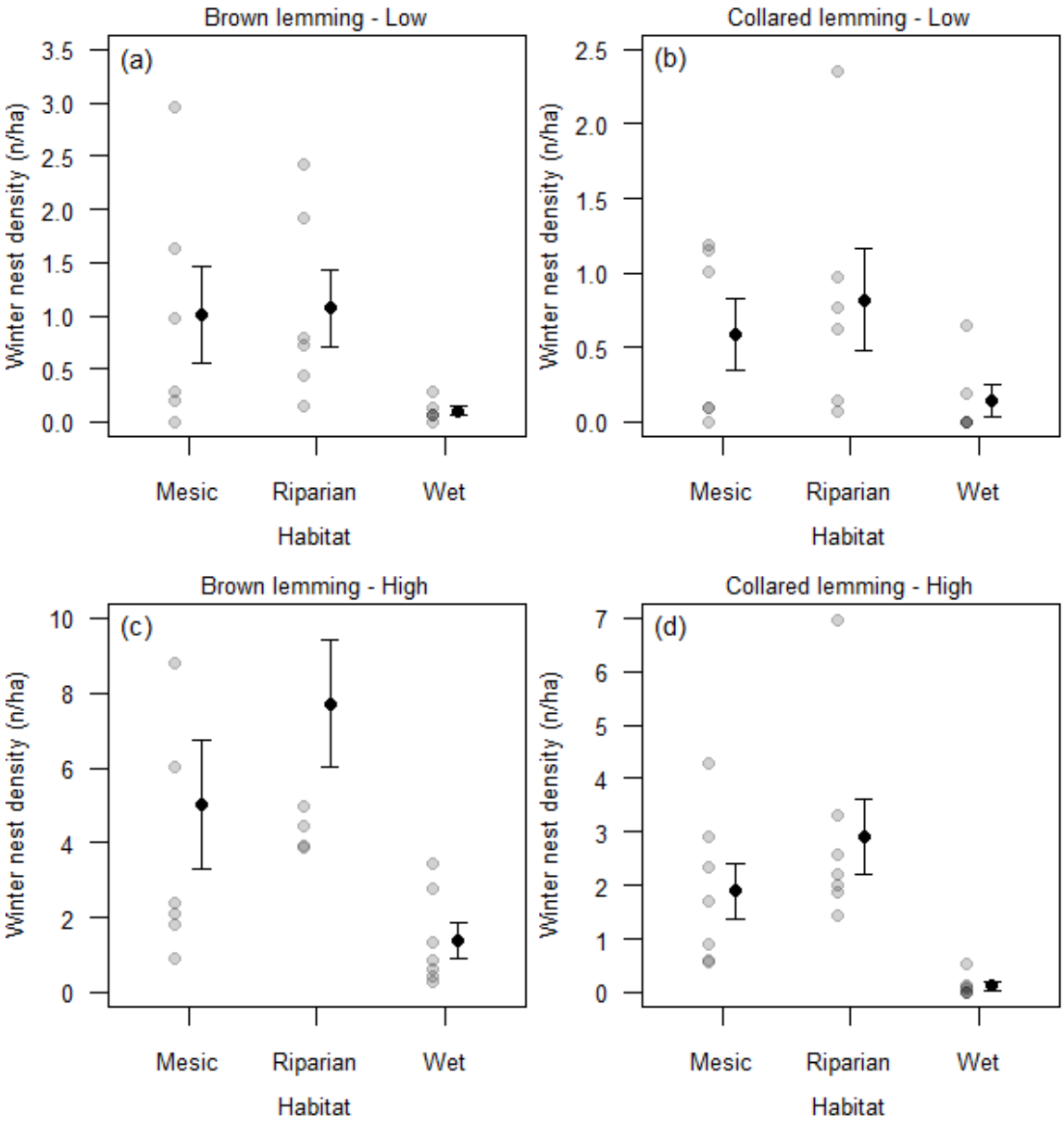


Figure S3.5 Lemming winter nest density in three different habitats in years of low abundance for (a) brown lemming (n_{mesic} = 63, $n_{riparian}$ = 89, n_{wet} = 10; total number of nests found) and (b) collared lemming (n_{mesic} = 50, $n_{riparian}$ = 65, n_{wet} = 4) and in years of high abundance for (c) brown lemming (n_{mesic} = 329, $n_{riparian}$ = 587, n_{wet} = 123) and (d) collared lemming (n_{mesic} = 129, $n_{riparian}$ = 197, n_{wet} = 16) at Bylot Island, 2007 – 2019. Gray circles are individual years, black circles are the mean and error bars represent SE.

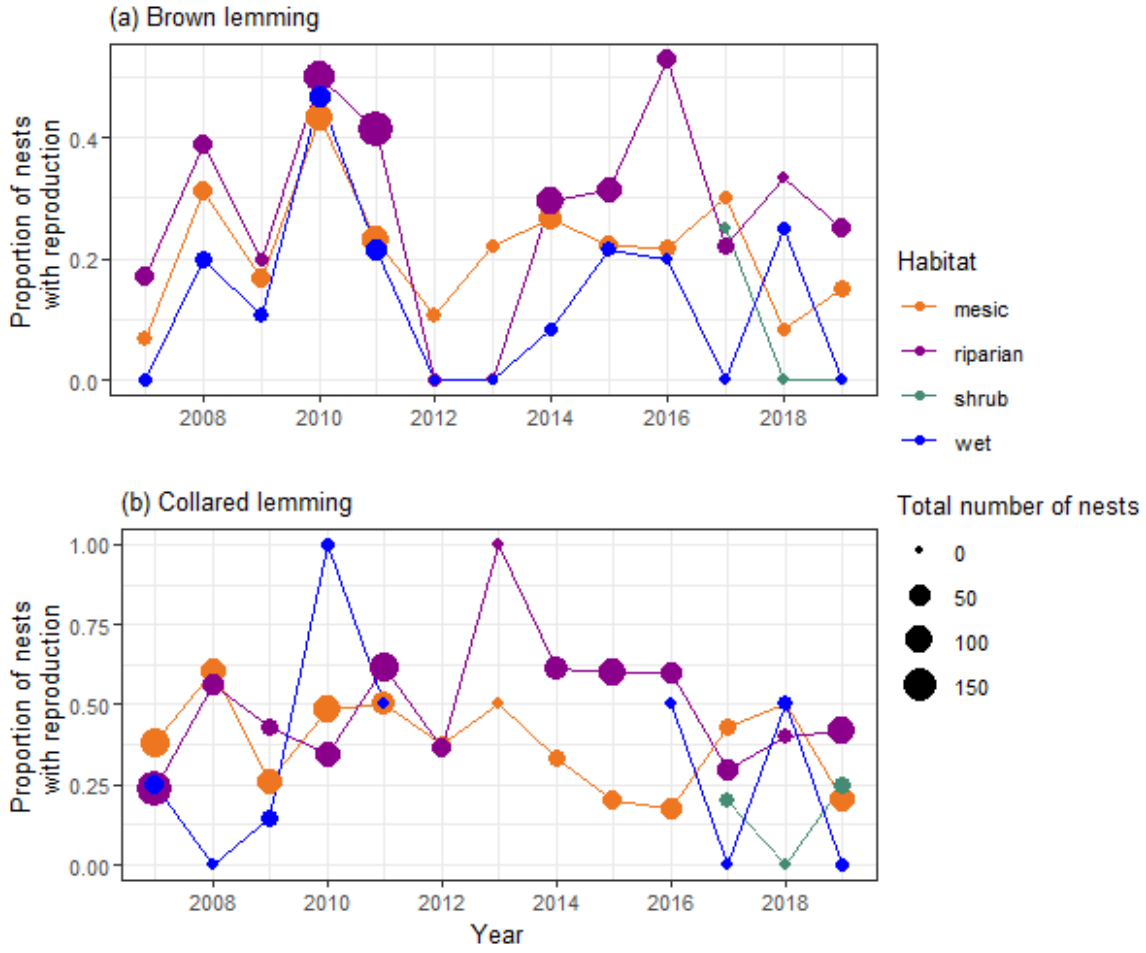


Figure S3.6 Time series of proportion of winter nests with reproduction in four different habitats for (a) brown lemmings and (b) collared lemmings at Bylot Island. The absence of data points for some habitats and years means that no winter nest was found.

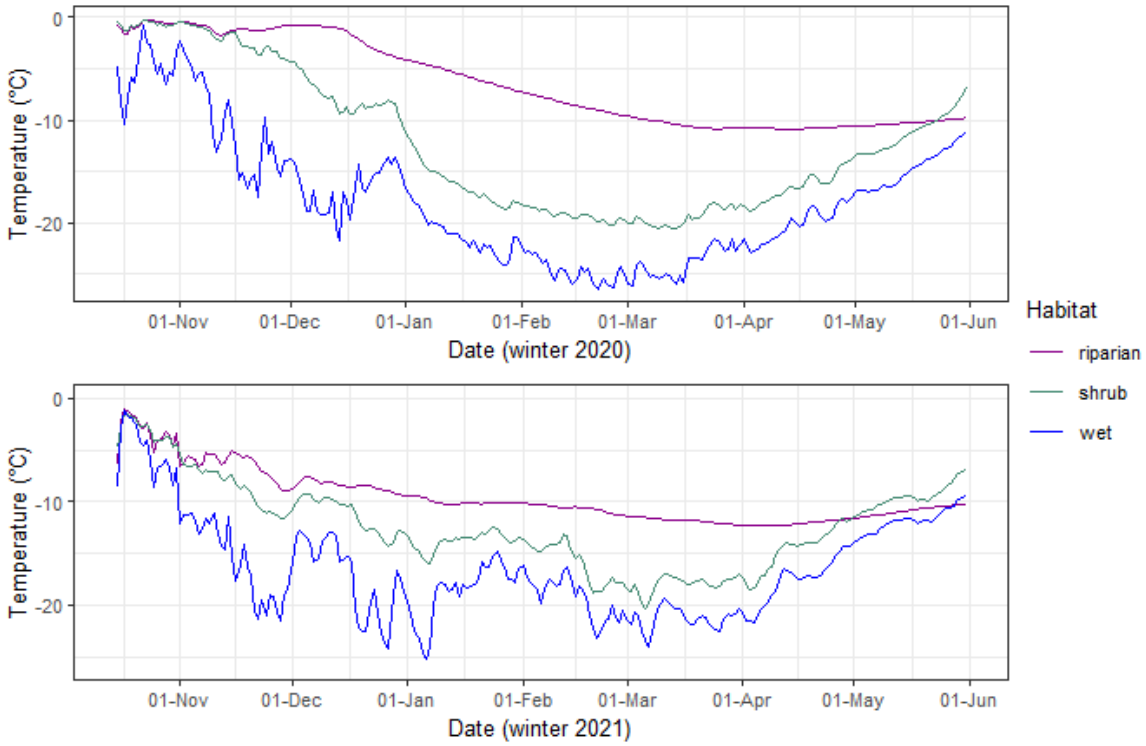


Figure S3.7 Daily temperature in the basal snow layer over winters 2020 and 2021 in three winter habitats used by lemmings at Bylot Island.

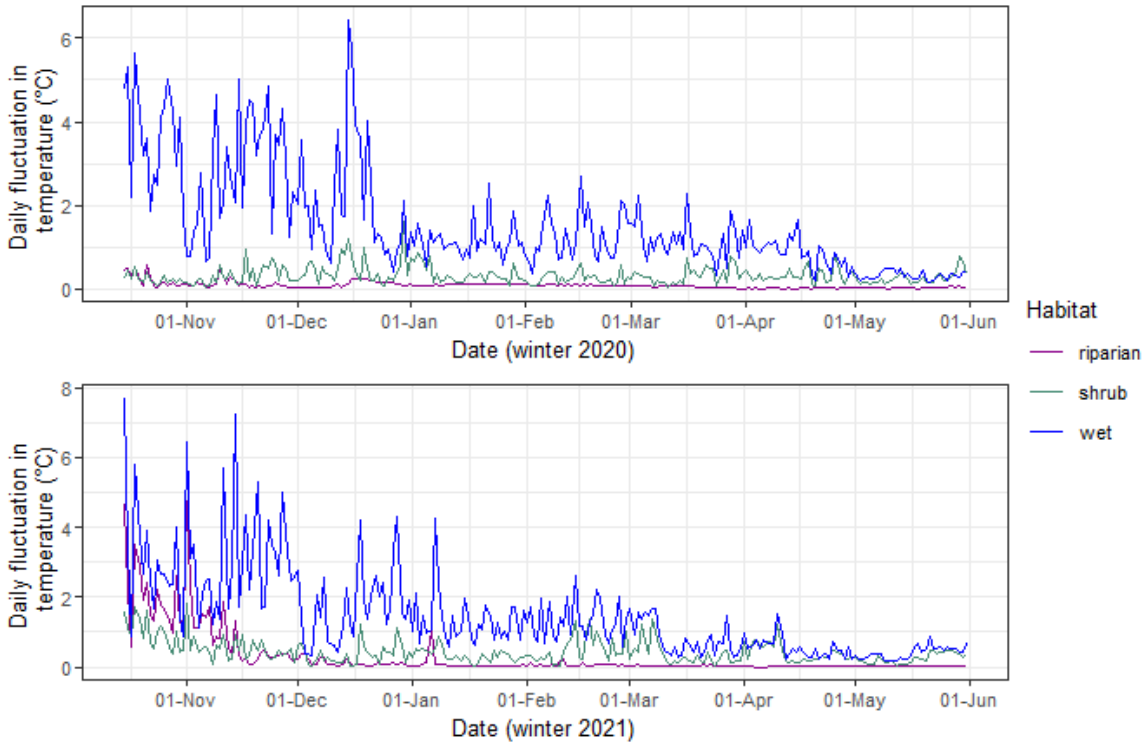


Figure S3.8 Daily temperature fluctuation in the basal snow layer over the winters 2020 and 2021 in three winter habitats used by lemmings at Bylot Island.

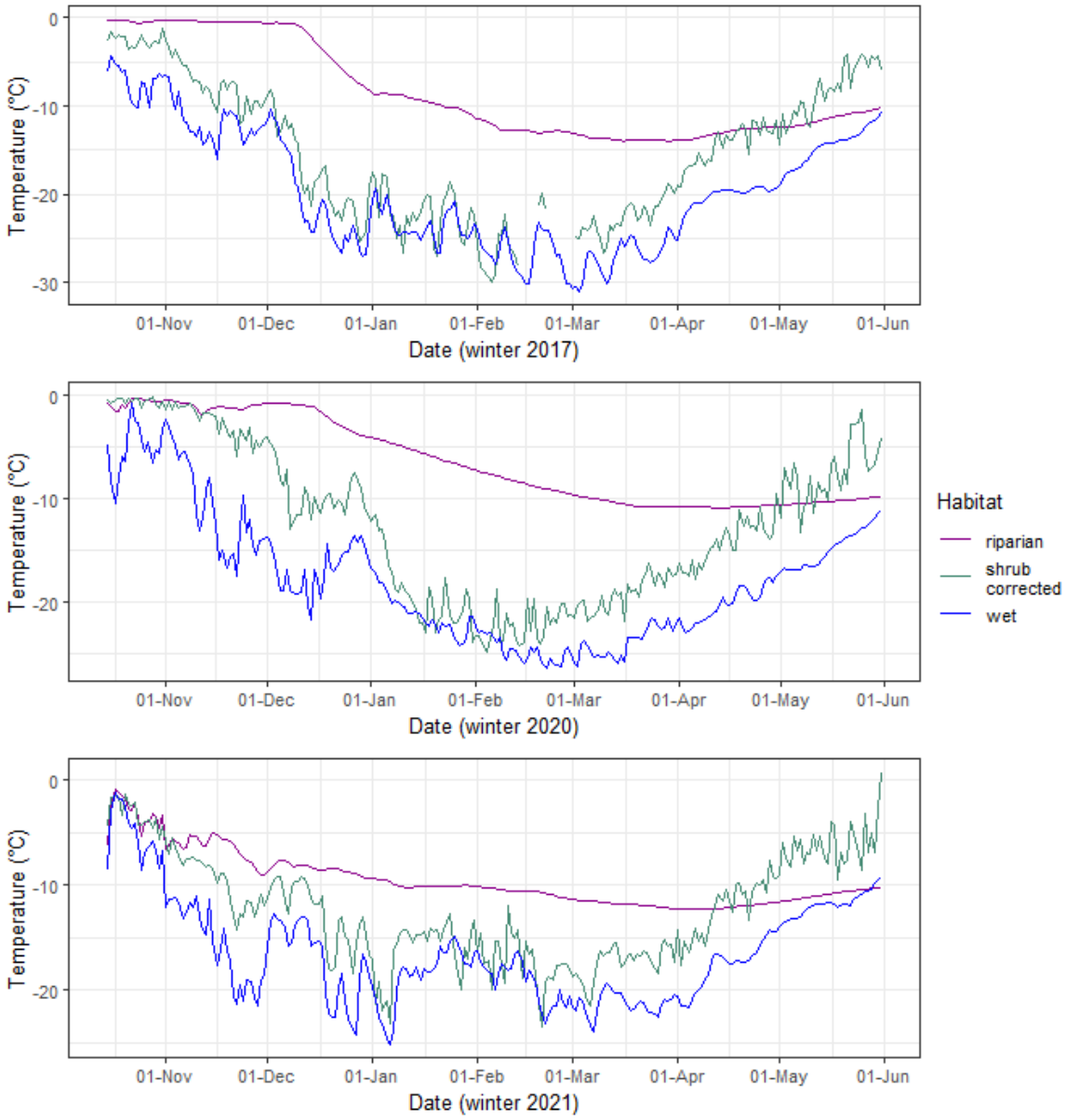


Figure S3.9 Daily temperature in the basal snow layer over winters 2017, 2020 and 2021 in three winter habitats used by lemmings at Bylot Island with a correction for shrub ($T_{shrub\ corrected} = T_{shrub} - \Delta T_{air\ wet\ -\ shrub}$) ($\beta_{riparian\text{-}shrub\ corrected} = 5.15$, CI = [3.45, 6.83]; $\beta_{shrub\ corrected\text{-}wet} = 4.4$, CI = [2.71, 6.09]).

Table S3.1 Coefficients of the models examining the influence of three habitats on lemming nest density (ln-transformed) between in all years (2007 – 2019) and in years of low and high density. Estimates in bold indicate that the 95% confidence interval did not include 0.

Years	Habitat comparisons	β	95% CI	R^2_m	R^2_c
All	**riparian - mesic**	**0.57**	**[0.07, 1.07]**	0.41	0.72
	wet - mesic	**-1.78**	**[-2.29, -1.28]**		
	wet - riparian	**-2.35**	**[-2.86, -1.85]**		
Low	riparian - mesic	0.54	[-0.21, 1.29]	0.36	0.59
	wet - mesic	**-1.47**	**[-2.22, -0.72]**		
	wet - riparian	**-2.01**	**[-2.77, -1.26]**		
High	**riparian - mesic**	**0.59**	**[0.01, 1.19]**	0.72	0.76
	wet - mesic	**-2.05**	**[-2.64, -1.46]**		
	wet - riparian	**-2.65**	**[-3.24, -2.06]**		

Table S3.2 Ranking of candidate models examining the influence of snow parameters and lemming species on (a) nest density or (b) proportion of nest with reproduction (2014 – 2019). The number of parameters (*k*), the difference in AICc between the current model and the most parsimonious model (ΔAICc), the log-likelihood (LL) and the marginal R^2 (R^2_m) and conditional R^2 (R^2_c) are presented. Year was used as random effect. Models in bold have been used to perform the model-averaging (ΔAICc < 4, Table 2).

a) Nest density

ID	Model	k	ΔAICc	LL	R^2_m	R^2_c
D2	**species + snow depth**	**5**	**0**	**-56.55**	**0.3**	**0.55**
D9	**species + snow depth + max height depth hoar**	**6**	**0.21**	**-55.21**	**0.34**	**0.81**
D3	**species + snow depth^{-1}**	**5**	**0.63**	**-56.87**	**0.29**	**0.6**
D6	**species + max height depth hoar**	**5**	**2.79**	**-57.94**	**0.34**	**0.85**
D8	**species + snow depth + basal k_{eff}**	**6**	**2.85**	**-56.53**	**0.29**	**0.55**
D7	**species + snow depth + basal density**	**6**	**2.89**	**-56.55**	**0.29**	**0.55**
D11	species + max height depth hoar + basal k_{eff}	6	4.66	-57.43	0.35	0.87
D10	species + max height depth hoar + basal density	6	5.29	-57.74	0.34	0.86
D1	species	4	10.71	-63.26	0.05	0.17
D4	species + snow density	5	12.67	-62.88	0.08	0.23
D5	species + k_{eff}	5	13.11	-63.1	0.06	0.18

b) Proportions of nests with reproduction

ID	Model	*k*	ΔAICc	LL	R^2
R9	**species + snow depth^{-1} + max height depth hoar**	**4**	**0**	**-52.03**	**0.55**
R7	**species + snow depth^{-1} + basal density**	**4**	**1.31**	**-52.69**	**0.55**
R8	**species + snow depth^{-1} + basal k_{eff}**	**4**	**2.14**	**-53.1**	**0.59**
R5	species + basal k_{eff}	3	4.61	-55.63	0.59
R4	species + basal density	3	5.15	-55.9	0.53
R3	species + snow depth^{-1}	3	6.06	-56.35	0.45
R11	species + max height depth hoar + basal k_{eff}	4	6.99	-55.53	0.58
R2	species + snow depth	3	7.23	-56.94	0.44
R10	species + max height depth hoar + basal density	4	7.71	-55.89	0.53
R6	species + max height depth hoar	3	8.05	-57.35	0.5
R1	species	2	9.6	-59.33	0.37

Table S3.3 Coefficients of the models examining the influence of four habitats on six snow property variables (2014 – 2019). Estimates in bold indicate that the 95% confidence interval did not include 0.

Response variable	Habitat comparisons	β	95% CI	R^2_m	R^2_c
Snow basal density[1]	mesic - shrub	0.06	[-0.05, 0.17]	0.03	0.22
	riparian - shrub	**0.11**	**[0.002, 0.21]**		
	wet - shrub	0.03	[-0.08, 0.15]		
	riparian - mesic	0.04	[-0.07, 0.16]		
	wet - mesic	-0.03	[-0.16, 0.10]		
	wet - riparian	-0.07	[-0.19, 0.05]		
Snow basal thermal conductivity (k_{eff})[2]	mesic - shrub	-0.17	[-5.17, 4.83]	0.02	0.05
	riparian - shrub	-2.07	[-6.55, 2.41]		
	wet - shrub	1.76	[-2.95, 6.46]		
	riparian - mesic	-1.90	[-7.16, 3.35]		
	wet - mesic	1.92	[-3.53, 7.38]		
	wet - riparian	3.83	[-1.17, 8.82]		
Snow basal specific surface area (SSA)[1]	mesic - shrub	0.02	[-0.09, 0.12]	0.12	0.50
	riparian - shrub	**-0.14**	**[-0.24, -0.04]**		
	wet - shrub	0.05	[-0.04, 0.14]		
	riparian - mesic	**-0.16**	**[0.28, -0.04]**		
	wet - mesic	0.03	[-0.08, 0.14]		
	wet - riparian	**0.19**	**[0.08, 0.30]**		
Snow depth[3]	**mesic - shrub**	**-0.45**	**[-0.58, -0.32]**	0.21	0.42
	riparian - shrub	**4.55**	**[4.03, 5.07]**		
	wet - shrub	**-0.66**	**[-0.79, -0.53]**		
	riparian - mesic	**5.00**	**[4.47, 5.53]**		
	wet - mesic	**-0.21**	**[-0.34, -0.08]**		
	wet - riparian	**-5.21**	**[-5.74, -4.69]**		
Maximal height of depth hoar[1]	mesic - shrub	-0.18	[-0.41, 0.04]	0.09	0.52
	riparian - shrub	0.09	[-0.13, 0.30]		
	wet - shrub	**-0.38**	**[-0.62, -0.15]**		
	riparian - mesic	0.27	[0.03, 0.51]		
	wet - mesic	-0.20	[-0.46, 0.05]		
	wet - riparian	**-0.47**	**[-0.72, -0.22]**		
Montly basal temperature[4]	**riparian - shrub**	**5.01**	**[1.69, 8.33]**	0.31	0.31
	wet - shrub	**-4.53**	**[-7.85, -1.20]**		
	wet - riparian	**-9.54**	**[-12.86, -6.22]**		
Daily fluctuation in temperature[1,4]	**riparian - shrub**	**-1.70**	**[-2.03, -1.37]**	0.67	0.67
	wet - shrub	**1.04**	**[0.71, 1.36]**		
	wet - riparian	**2.74**	**[2.41, 3.06]**		

Snow onset date[5]	**wet - riparian**	**14.60**	**[8.07, 22.67]**	0.52	0.70

[1] Natural log transformation of the response variable.

[2] Inverse transformation of the response variable.

[3] Square-root transformation of the response variable.

[4] Comparisons made in years 2017, 2020, 2021.

[5] Comparisons made in years 2017 to 2021, only in riparian and wet habitats since snow onset dates in wet and mesic are the same, and are almost the same in riparian and shrub.

References

Fauteux, D., and G. Gauthier. 2022. Density-dependent demography and movements in a cyclic brown lemming population. Ecology and Evolution 12:e9055.

S3.2 Supplementary analysis: principal component analysis (PCA)

Method

To explore the degree of association amongst snow variables, we performed a principal component analysis (PCA) with the R generic function prcomp (Venables and Ripley 2002). We used 5 snow variables (density, thermal conductivity and SSA of the basal layer, snow depth and maximal height of depth hoar) from 65 snow pits dug between 2014 – 2019. After extracting the principal components from the data set, we performed mixed effect linear models to investigate how the principal component scores along the two main axes varied between habitats, using year as a random effect.

Results

The first two axes of the PCA explain respectively 46% and 34% of the variation in the dataset. Positive values on the first axis (PC1) were characteristic of sites with a deep snow cover, a high depth hoar and a relatively dense basal snow layer (Fig. S3.10, Table S3.4). This association was expected as depth hoar tends to be thicker in deeper snowpack due to a greater quantity of snow available to transform into depth hoar. Also, deep snowpack slows down snow metamorphism by reducing the vertical temperature gradient, leading to denser depth hoar. As riparian is the habitat with the deepest snowpack of all, it is therefore not surprising to find out the PC1 scores are the highest in this habitat (Fig. S3.11a, Table S3.5).

Positive values on the second axis of the PCA (PC2) were characteristic of sites with a low thermal conductivity (k_{eff}) and a low specific surface area (SSA) of the basal snow layer. In the medium-high range of SSA values (i.e., 10-12 m^2 kg^{-1}), it is expected to observe this association as k_{eff} is a proxy for snow hardness and higher measurements correspond to depth hoar indurated from a wind slab. However, we would not expect such association in the lowest range of SSA measurements (i.e., ~8 m^2 kg^{-1}), which corresponds to depth hoar indurated from melt-freeze, with high k_{eff} measurements. Such melt-freeze layers are mostly found in riparian habitat, and this could explain why this habitat had mostly positive scores for PC2 compared with shrub and wet habitats (Fig. S3.11b, Table S3.5).

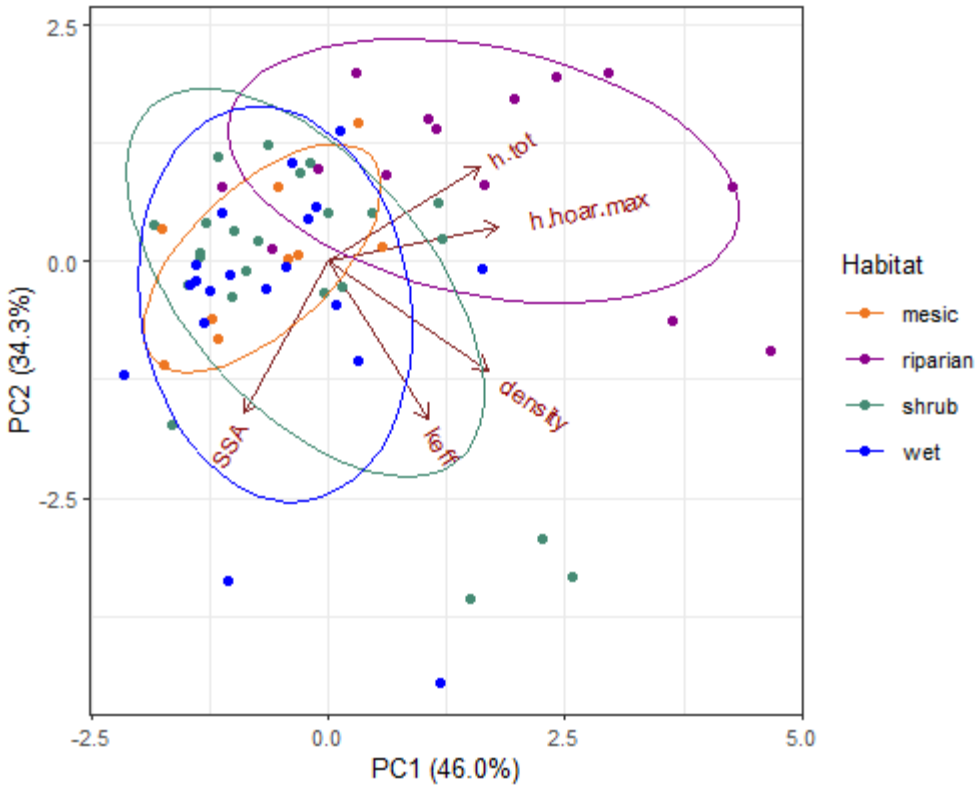


Figure S3.10 Principal component scores along the first two axes of snow measurements made at individual pits (dots) in four habitats (n = 65, 2014 – 2019). Ellipses define the region containing 95% of all samples in each habitat, arrows indicate correlation of each snow variable with the principal components and percentages on each axis refer to the variability explained by the principal component. List of abbreviation: h.tot = maximal snow depth, h.hoar.max = maximal height of the depth hoar, density = density of the basal layer, keff = thermal conductivity of the basal layer and SSA = specific surface area of the basal layer.

Table S3.4 Principal component coefficients of five snow variables sampled between 2014 – 2019 at Bylot Island on each axis of the analysis. Coefficients in bold indicate the major variables contributing to each PC axis.

Variables	PC1	PC2	PC3	PC4	PC5
basal k_{eff}	0.32	**-0.60**	**0.46**	0.00	**0.57**
basal density	**0.52**	-0.41	0.02	-0.11	**-0.74**
basal SSA	-0.27	**-0.58**	**-0.72**	-0.23	0.14
max height depth hoar	**0.55**	0.13	**-0.48**	**0.63**	0.21
max snow depth	**0.49**	0.36	-0.19	**-0.73**	0.25

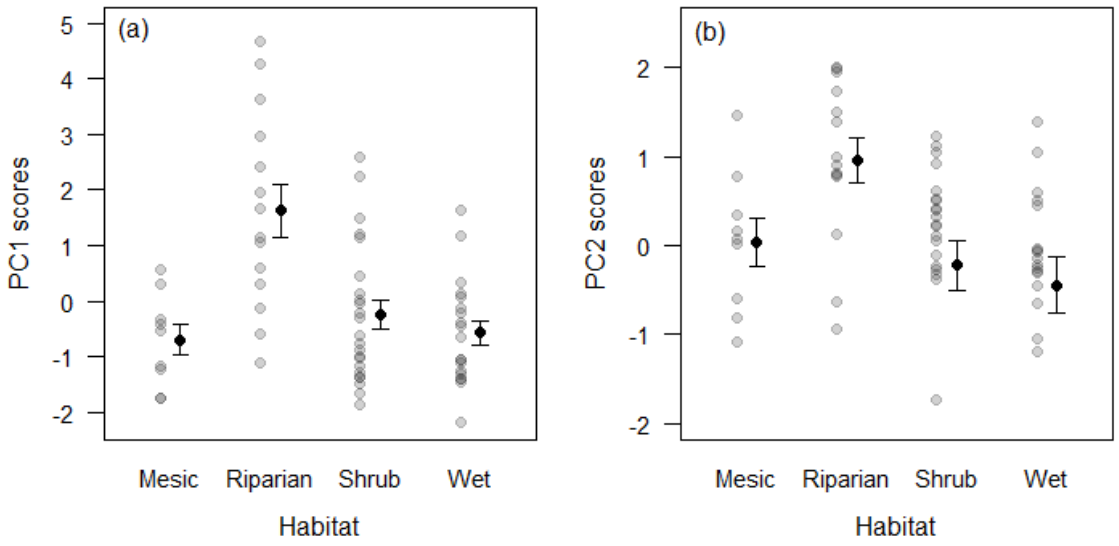


Figure S3.11 Scores of the (a) first axis and (b) second axis of a PC analysis summarizing five variables describing snow properties in four winter habitats used by lemmings at Bylot Island, 2014 – 2019. Black circles are the mean of the data, error bars represent SE and gray circles represent individual measurements (n_{mesic} = 9, $n_{riparian}$ = 14, n_{shrub} = 23, n_{wet} = 19).

Table 3.5 Coefficients of the models examining the influence of four habitats on PC scores (PC1 and PC2). Estimates in bold indicate that the 95% confidence interval did not include 0.

Principal component	Habitat	β	95% CI
PC1	**mesic - riparian**	**-1.72**	**[-2.60, -0.84]**
	shrub - riparian	**-1.37**	**[-2.08, -0.66]**
	wet - riparian	**-1.53**	**[-2.28, -0.78]**
	shrub - mesic	0.35	[-0.44, 1.15]
	wet - mesic	0.19	[-0.62, 1.01]
	wet - shrub	-0.16	[-0.79, 0.46]
PC2	mesic - riparian	-0.86	[-1.79, 0.07]
	shrub - riparian	**-0.95**	**[-1.70, -0.19]**
	wet - riparian	**-1.08**	**[-1.87, -0.29]**
	shrub - mesic	-0.09	[-0.94, 0.75]
	wet - mesic	-0.22	[-1.09, 0.65]
	wet - shrub	-0.13	[-0.80, 0.54]

References

Venables, W. N., and B. D. Ripley. 2002. Modern applied statistics with S. Fourth Edi. Springer-Verlag.

Annexe S4 – Documentation supplémentaire pour le Chapitre 4

S4.1 Yearly estimation of snow onset date

In this study, the snow onset date corresponds to the first date of the season when snow covered more than 80 % of our study area, without returning below 50 % of coverage. Partial melting is part of the processes we wished to include in this study.

We used MODIS images (Moderate Resolution Imaging Spectroradiometer; MOD10A1 snow product collection 6 extracted from https://modis.gsfc.nasa.gov/) between 2003 and 2019 as a first clue of the timing of snow onset. The satellite provides one image daily and analysis of these data over our 51 km^2 study area allows detection of the presence of snow on the ground. We obtained snow cover information at the pixel level (500 m) with the normalized-difference snow index (NDSI) (see collection 6 User Guise of Riggs and Hall (2015) for more information). Then NDSI pixels were transformed into binary classes using a threshold of 0.4 to calculate the daily snow cover fraction (i.e., NDSI $\geq$ 0.4 classified as snow covered (1) and NDSI < 0.4 classified as not snow covered (0)). This threshold of 0.4 is a standard value that is widely used to distinguish snow from other bright material like clouds, soils or rocks (Dozier 1989). However, estimating a snow onset date with this data does not always give an accurate result as there are often gaps between two usable images due to the presence of clouds (between 1 to 18-day gaps).

We used other cues to refine the snow onset dates derived from MODIS images. Since 1993, an automated station records hourly weather data at our study site. We used relative air humidity at 2 m, air temperature at 2 m, wind speed at 3 m and snow depth recorded hourly at the BYLCAMP station (CEN 2022) from 2000 to 2021 to help us narrow down our estimate of the snow onset date. In winter 2009-2010, no weather data was recorded at due to a malfunction of the weather station and between 2013 and 2016, the same applies to the snow depth gauge. In the latter years, we used snow depth recorded from another weather station located about 1.7 km away from the main one (TUNDRA; Domine 2021).

In years with uncertainties in the data (2005, 2007, 2011) or with malfunction of the weather station (2009), we also used weather data recorded in Mittimatalik (Pond Inlet), about 90 km from our main study area as a complement (extracted from the Environment and Climate Change Canada Historical Climate Data web site

https://climate.weather.gc.ca/index_e.html). Precipitation and other weather observations recorded in Mittimatalik were compared to weather data recorded on Bylot Island to see the concordance between the two datasets and add more certainty to the detection of snow precipitation events.

From 2016 to 2021, an automated camera deployed at the study site took one picture daily of the surrounding landscape, which allowed us to get a precise snow onset date for these years. Between 2016 and 2019, we compared snow onset dates estimated with our method (based on MODIS images and local weather data) to those obtained with the automated camera. Snow onset dates were the same in 2016 and 2018 and differed by 1 day in 2017 and 2019, which confirmed the reliability of our method.

In summary, we mixed several environmental cues to get the most accurate estimate of the snow onset date each year. Since this date influences other derived weather variables used in this study (melt-freeze, rain-on-snow and freezing rain), it was important to have the most accurate date possible. We provide below the annual snow onset date along with the criteria used (Table S1), and the graphs of weather and MODIS data used to make these inferences each year.

Table S4.1 Yearly estimates of snow onset date (onset date). The corresponding year of the winter, a description of the methods used to estimate the date (criteria used), as well as the corresponding figures (sources) are shown in the table.

Winter	Onset date	Criteria used	Source
2003-2004	October 6	- Oct 4: MODIS indicated a 10% snow cover. - Oct 6: MODIS indicated a 100% snow cover; snow onset occurred between these dates. - Oct 6: there is a humidity peak, air temperature is <0°C and the snow gauge detected a snow accumulation.	Fig S4.1
2004-2005	October 1	- Sept 29: MODIS indicated a 25% snow cover. - Oct 9: MODIS indicated a 100% snow cover; snow onset occurred between these dates. - Oct 1: there is a humidity peak, air temperature is <0°C and the snow gauge detected a snow accumulation.	Fig S4.2
2005-2006	September 26	- Sept 21: MODIS indicated a 50% snow cover. - Oct 6: MODIS indicated a 100% snow cover; snow onset occurred between these dates. - Sept 25-26: there is a humidity peak and air temperature is <0°C overnight. - Sept 25-29: the snow gauge detected a gradual accumulation with some noise despite low air humidity values. - Sept 27-28: a peak in wind speed occurred, suggesting that snow accumulated prior to this date was blown away. - Sept 26: snow precipitation was recorded in Pond Inlet (no data available on Sept 25).	Figs S4.3, S4.4 & S4.5
2006-2007	September 30	- Sept 28: MODIS indicated a 0% snow cover. - Oct 6: MODIS indicated a 100% snow cover; snow onset occurred between these dates. - Sept 30-Oct 1: there is a humidity peak, air temperature is <0°C and the snow gauge detected a snow accumulation.	Fig S4.6
2007-2008	September 13	- Sept 11: MODIS indicated a 18% snow cover. - Oct 14: MODIS indicated a 92% snow cover; snow onset occurred between these dates. - Sept 13: there is a humidity peak, air temperature is <0°C and the snow gauge detected a snow accumulation with some noise. - Sept 13: snow precipitation was recorded in Pond Inlet.	Figs S4.7, S4.8

2008-2009	September 15	- Sept 11: MODIS indicated a 0% snow cover. - Sept 15: MODIS indicated a 100% snow cover; snow onset occurred between these dates. - Sept 15: there is a humidity peak, air temperature is <0°C and the snow gauge detected a snow accumulation despite the noise.	Fig S4.9
2009-2010	September 21	- Sept 20: MODIS indicated a 0% snow cover. - Sept 22: MODIS indicated a 95% snow cover; snow onset occurred between these dates. - Sept 21: snow precipitation was recorded in Pond Inlet. - No weather data was recorded on Bylot Island that year.	Fig S4.10
2010-2011	September 30	- Sept 29: MODIS indicated a 10% snow cover. - Oct 1: MODIS indicated a 90% snow cover; snow onset occurred between these dates. - Sept 30: there is a humidity peak (above 90%), air temperature is <0°C and the snow gauge detected a snow accumulation.	Fig S4.11
2011-2012	September 15	- Sept 11: MODIS indicated a 0% snow cover. - Sept 22: MODIS indicated a 100% snow cover; snow onset occurred between these dates. - Sept 15: there is a humidity peak, air temperature is <0°C and the snow gauge detected a snow accumulation.	Fig S4.12
2012-2013	September 27	- Sept 25: MODIS indicated a 9% snow cover. - Sept 29: MODIS indicated a 100% snow cover; snow onset occurred between these dates. - Sept 27: there is a humidity peak, air temperature is <0°C and the snow gauge detected a snow accumulation.	Fig S4.13
2013-2014	October 12	- Oct 10: MODIS indicated a 19% snow cover. - Oct 14: MODIS indicated a 100% snow cover; snow onset occurred between these dates. - Oct 12: there is a humidity peak, air temperature is <0°C and the snow gauge detected a snow accumulation.	Fig S4.14
2014-2015	September 12	- Sept 9: MODIS indicated a 0% snow cover. - Sept 23: MODIS indicated a 100% snow cover; snow onset occurred between these dates. - Sept 12: there is a humidity peak, air temperature is <0°C and the snow gauge detected a snow accumulation.	Fig S4.15

		- Sept 14-16: there was probably a snow melt episode between these dates, but the melt was only partial according to snow gauge.	
2015-2016	September 20	- Sept 17: MODIS indicated a 20% snow cover. - Sept 21: MODIS indicated a 100% snow cover; snow onset occurred between these dates. - Sept 18-19: there are humidity peaks, but the temperature remained mainly >0°C, suggesting liquid precipitation. - Sept 20: there is a humidity peak and air temperature is <0°C overnight, suggesting snow precipitation.	Fig S4.16
2016-2017	September 9	- Sept 6: MODIS indicated a 11% snow cover. - Sept 10: MODIS indicated a 100% snow cover; snow onset occurred between these dates. - Sept 9: there is a humidity peak, air temperature is <0°C and the snow gauge detected a snow accumulation. - Sept 9: photos from the automated camera detected a snow accumulation. - Sept 18-20: there are humidity peaks with temperature >0°C, suggesting liquid precipitation. - Sept 19-20: photos from the automated camera detected a partial snow melting. - Sept 27-29: photos from the automated camera detected a rain-on-snow.	Fig S4.17
2017-2018	September 8	- Sept 5: MODIS indicated a 0% snow cover. - Sept 8: MODIS indicated a 100% snow cover; snow onset occurred between these dates. - Sept 8: there is a humidity peak, air temperature is <0°C and the snow gauge detected a snow accumulation. - Sept 8: photos from the automated camera detected a snow accumulation. - Sept 10-11: photos from the automated camera detected a partial snow melting.	Fig S4.18
2018-2019	September 16	- Sept 7: MODIS indicated a 0% snow cover. - Sept 25: MODIS indicated a 100% snow cover; snow onset occurred between these dates. - Sept 16: there is a humidity peak, air temperature is <0°C and the snow gauge detected a snow accumulation.	Fig S4.19

		- Sept 16: photos from the automated camera detected a snow accumulation. - Sept 17-19: the snow gauge detected a decrease in snow depth, mostly due to strong wind speed or to a partial melting. - Sept 18-19: photos from the automated camera detected a partial snow melting.	
2019-2020	September 30	- Sept 21: MODIS indicated a 0% snow cover. - Oct 6: MODIS indicated a 100% snow cover; snow onset occurred between these dates. - Sept 30: there is a humidity peak, air temperature is <0°C and the snow gauge detected a snow accumulation. - Sept 30: photos from the automated camera detected a snow accumulation.	Fig S4.20
2020-2021	September 23	- MODIS analysis is not available for that year. - Sept 23: photos from the automated camera detected a snow accumulation. - Sept 23: there is a humidity peak, air temperature is <0°C and the snow gauge detected a small snow accumulation.	Fig S4.21
2021-2022	October 8	- MODIS analysis is not available for that year. - Sept 30: there is a humidity peak, air temperature is <0°C and the snow gauge detected a snow accumulation. - Sept 30-Oct 4: air temperature is >0°C and there are humidity peaks, suggesting melting and rain-on-snow episodes. - Sept 30-Oct 4: photos from the automated camera detected a significant melting of the snow cover (<50% remaining). - Oct 8: there is a humidity peak, air temperature is <0°C and the snow gauge detected a small snow accumulation. - Oct 8: photos from the automated camera detected a snow accumulation.	Fig S4.22

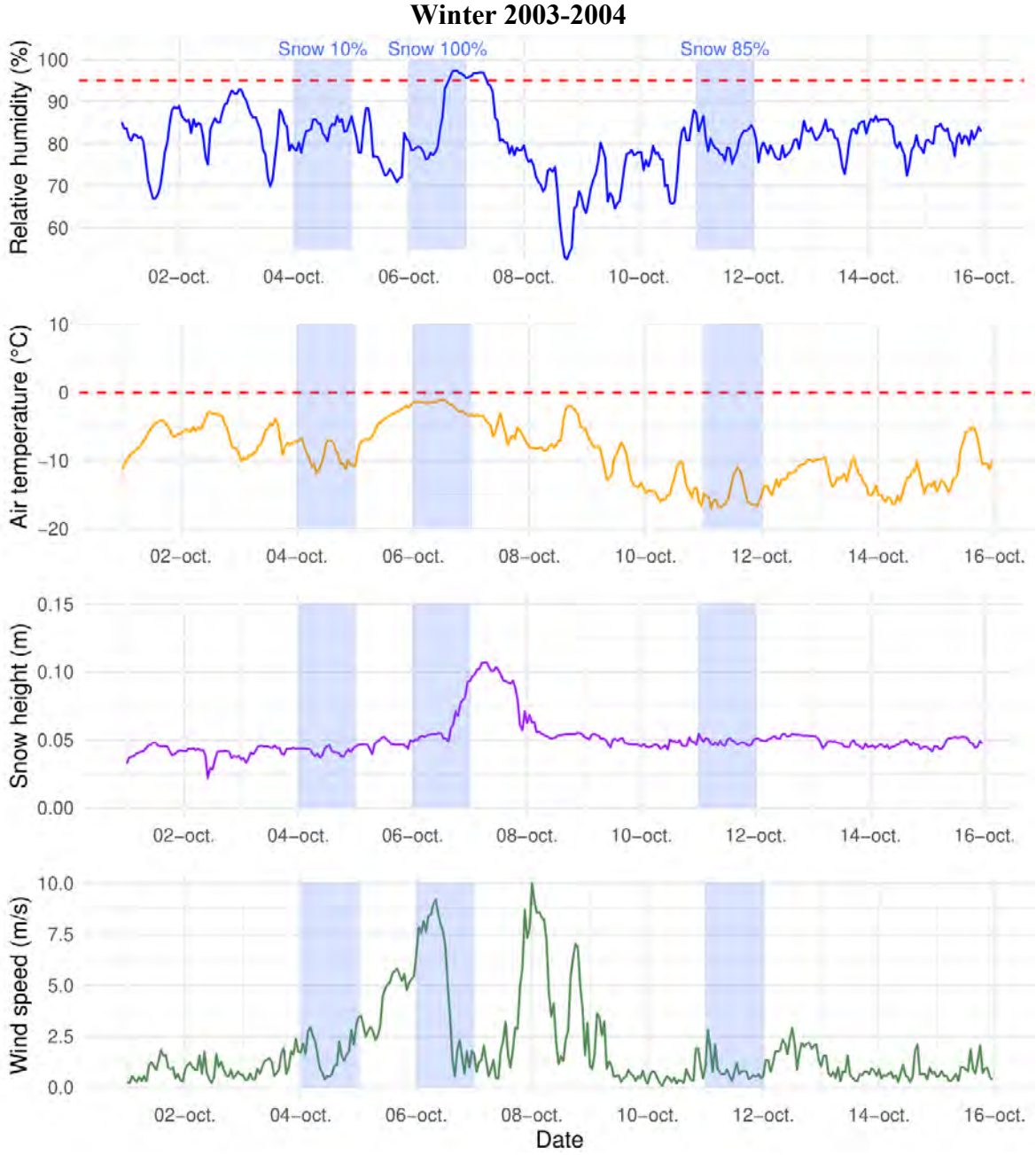


Figure S4.1 Weather conditions recorded during the period of snow onset in fall 2003. The blue boxes represent days with available MODIS images, and the percentage (%) of the study area covered by snow is indicated above the figure. The red dashed line on the relative humidity chart indicates the threshold above which we estimate a high risk of precipitation and on the air temperature chart it indicated 0°C.

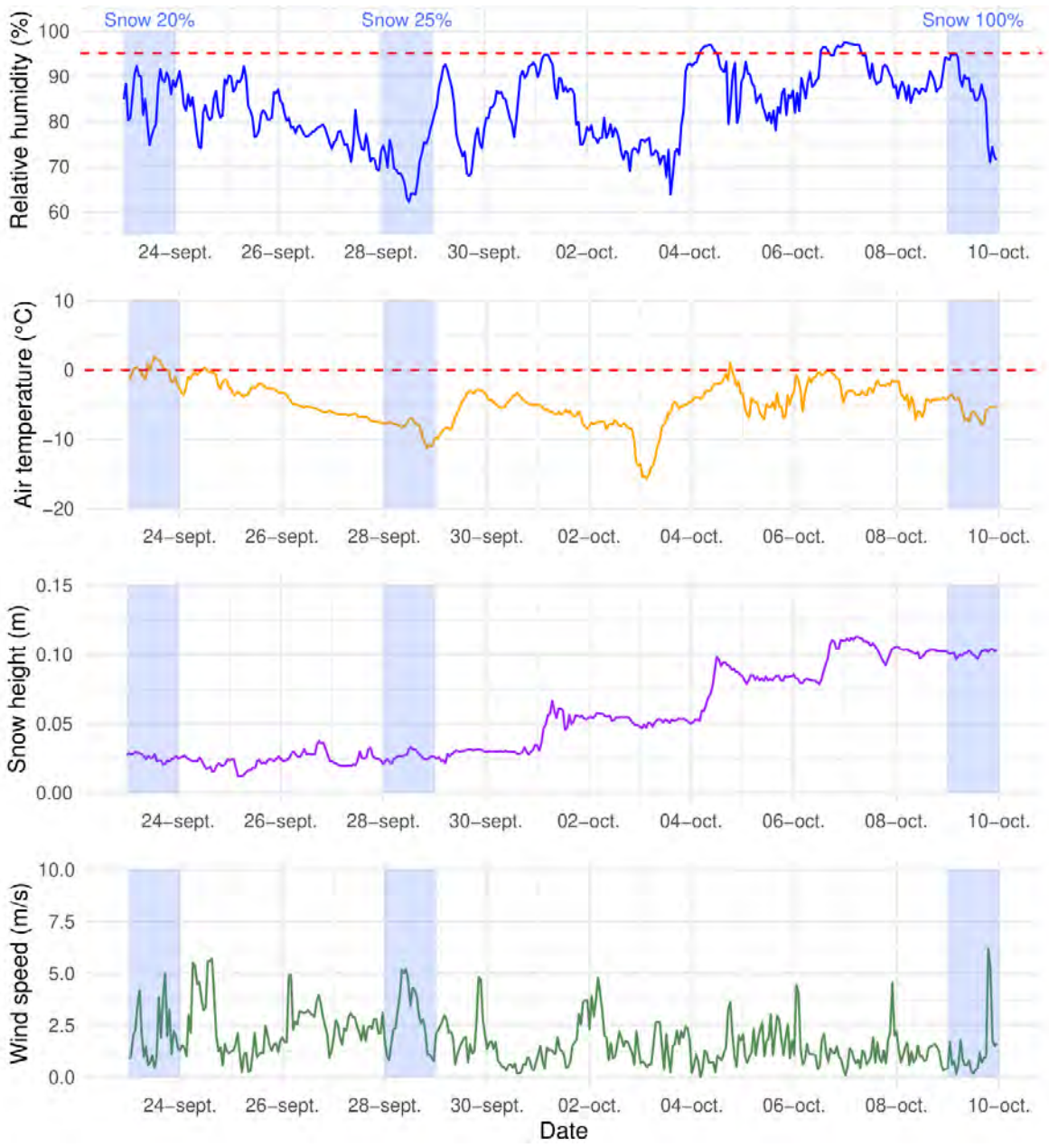


Figure S4.2 Weather conditions recorded during the period of snow onset in fall 2004. The blue boxes represent days with available MODIS images, and the percentage (%) of the study area covered by snow is indicated above the figure. The red dashed line on the relative humidity chart indicates the threshold above which we estimate a high risk of precipitation and on the air temperature chart it indicated 0°C.

Winter 2005-2006

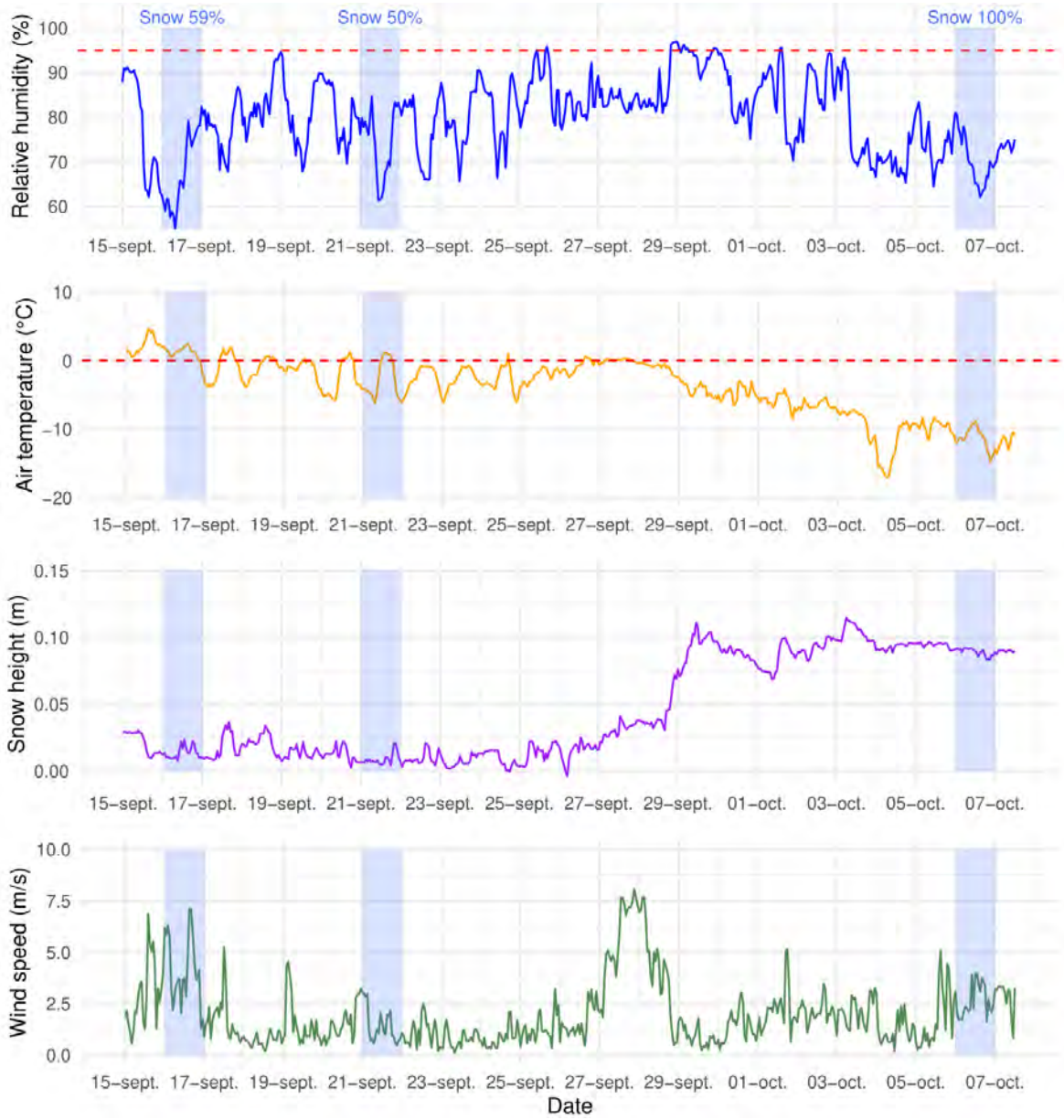


Figure 4.3 Weather conditions recorded during the period of snow onset in fall 2005. The blue boxes represent days with available MODIS images, and the percentage (%) of the study area covered by snow is indicated above the figure. The red dashed line on the relative humidity chart indicates the threshold above which we estimate a high risk of precipitation and on the air temperature chart it indicated 0°C.

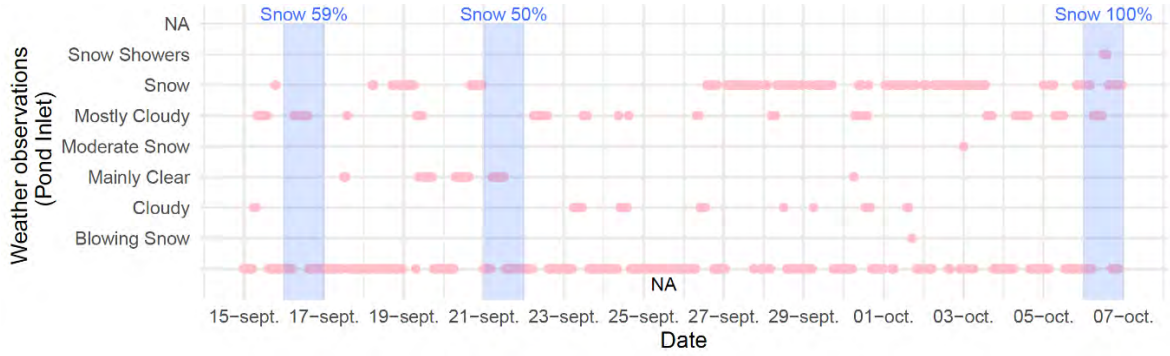


Figure S4.4 Weather observations from Pond Inlet in the period of snow onset in fall 2005. The blue boxes represent days with available MODIS images, and the percentage (%) of the study area covered by snow is indicated above the figure.

Figure S4.5 Total solid precipitation recorded in Pond Inlet in the period of snow onset in fall 2005. The blue boxes represent days with available MODIS images, and the percentage (%) of the study area covered by snow is indicated above the figure.

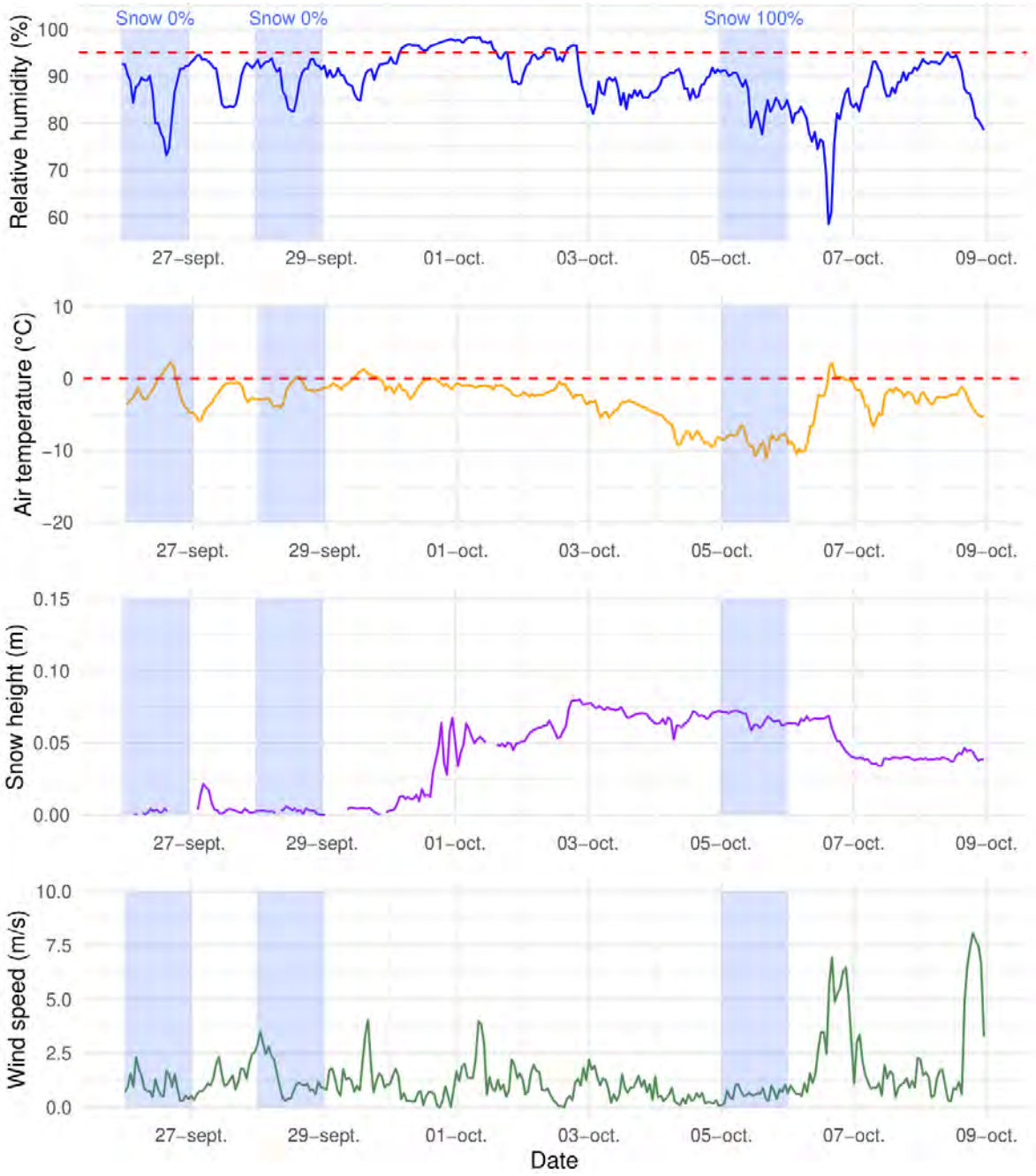


Figure S4.6 Weather conditions recorded during the period of snow onset in fall 2006. The blue boxes represent days with available MODIS images, and the percentage (%) of the study area covered by snow is indicated above the figure. The red dashed line on the relative humidity chart indicates the threshold above which we estimate a high risk of precipitation and on the air temperature chart it indicated 0°C.

Winter 2007-2008

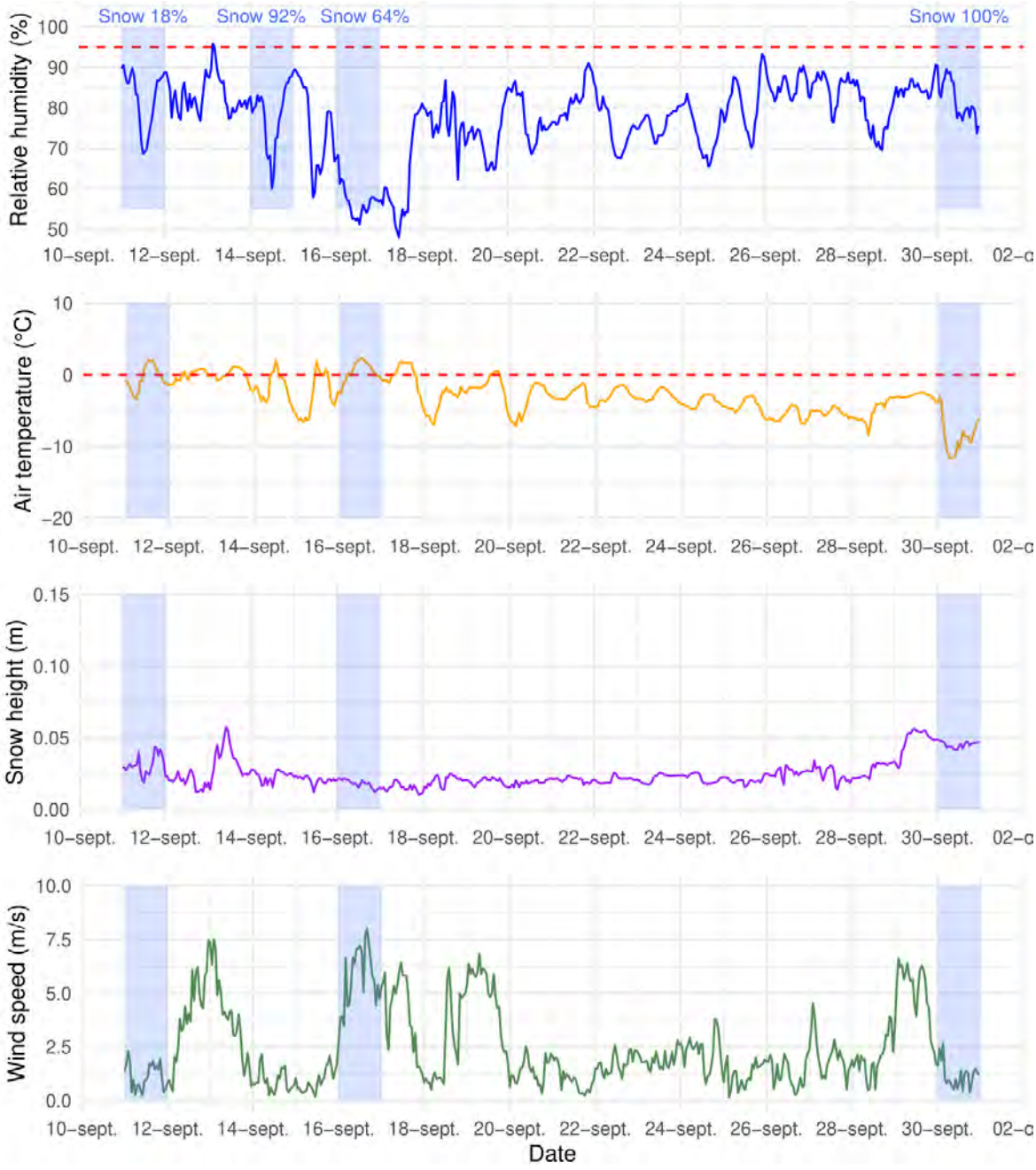


Figure S4.7 Weather conditions recorded during the period of snow onset in fall 2007. The blue boxes represent days with available MODIS images, and the percentage (%) of the study area covered by snow is indicated above the figure. The red dashed line on the relative humidity chart indicates the threshold above which we estimate a high risk of precipitation and on the air temperature chart it indicated 0°C.

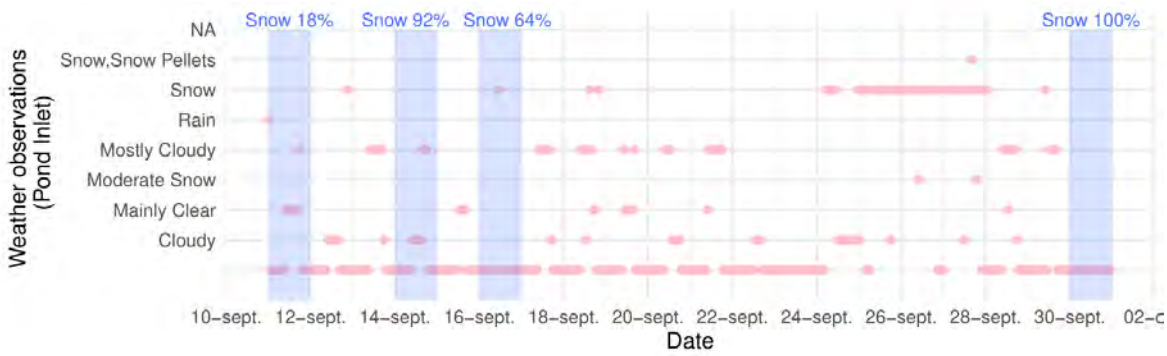


Figure S4.8 Weather observations from Pond Inlet in the period of snow onset in fall 2007. The blue boxes represent days with available MODIS images, and the percentage (%) of the study area covered by snow is indicated above the figure.

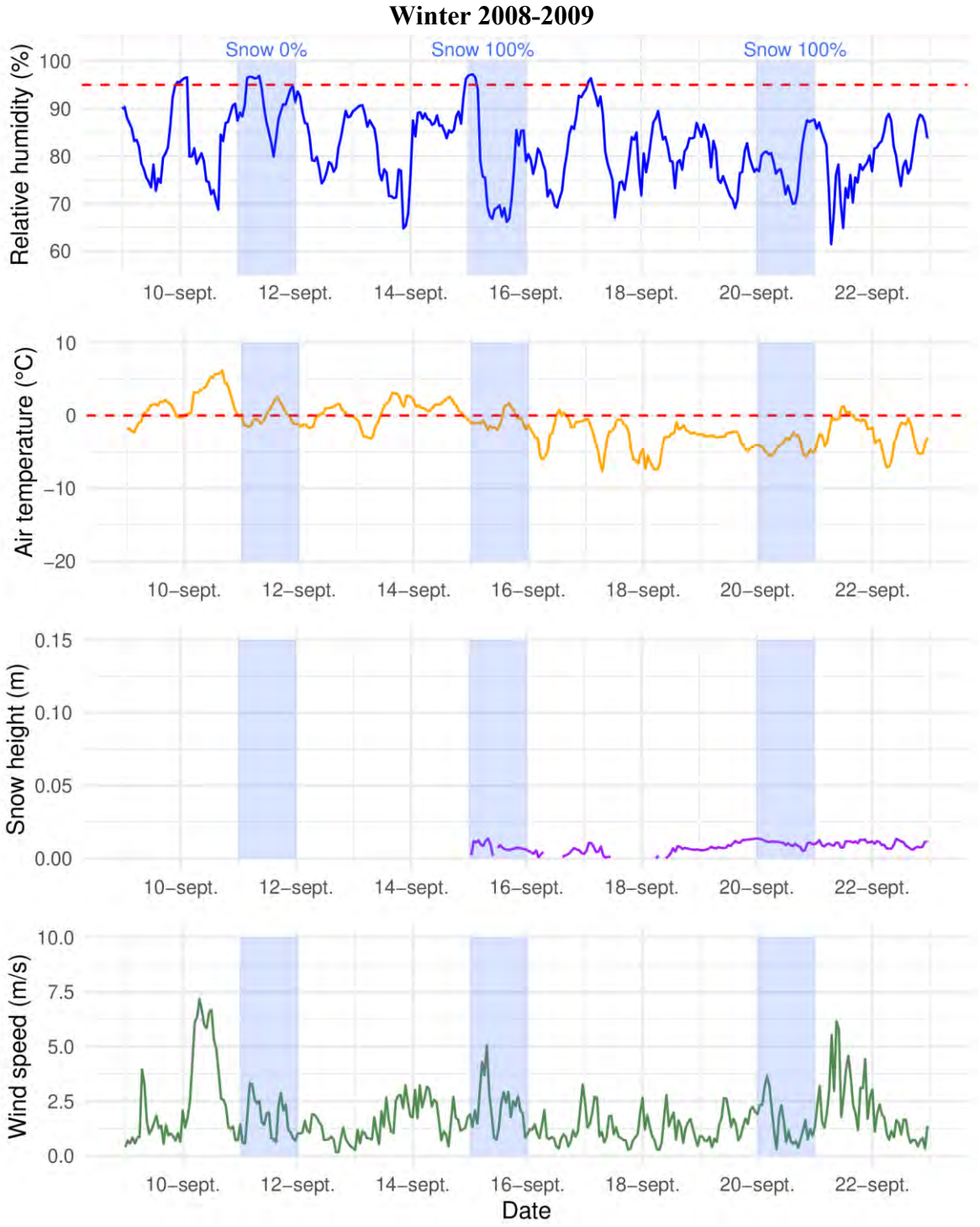


Figure S4.9 Weather conditions recorded during the period of snow onset in fall 2008. The blue boxes represent days with available MODIS images, and the percentage (%) of the study area covered by snow is indicated above the figure. The red dashed line on the relative humidity chart indicates the threshold above which we estimate a high risk of precipitation and on the air temperature chart it indicated 0°C.

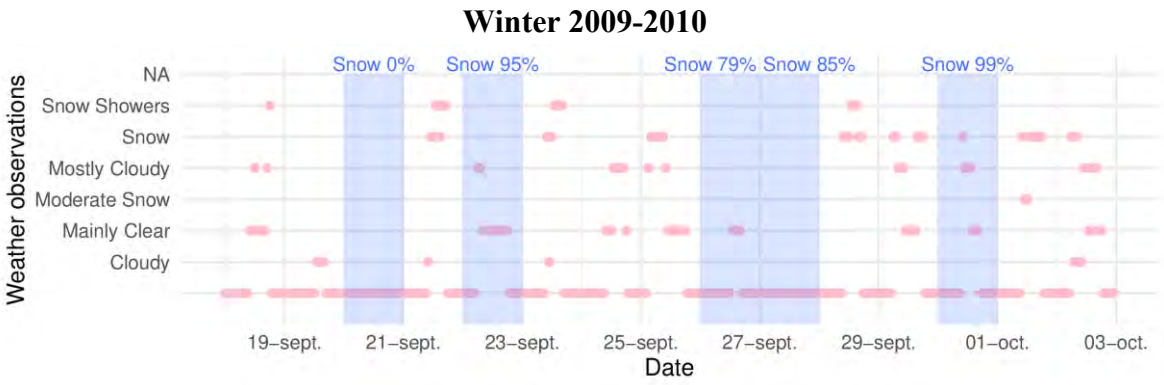


Figure S4.10 Weather observations from Pond Inlet in the period of snow onset in fall 2009. The blue boxes represent days with available MODIS images, and the percentage (%) of the study area covered by snow is indicated above the figure.

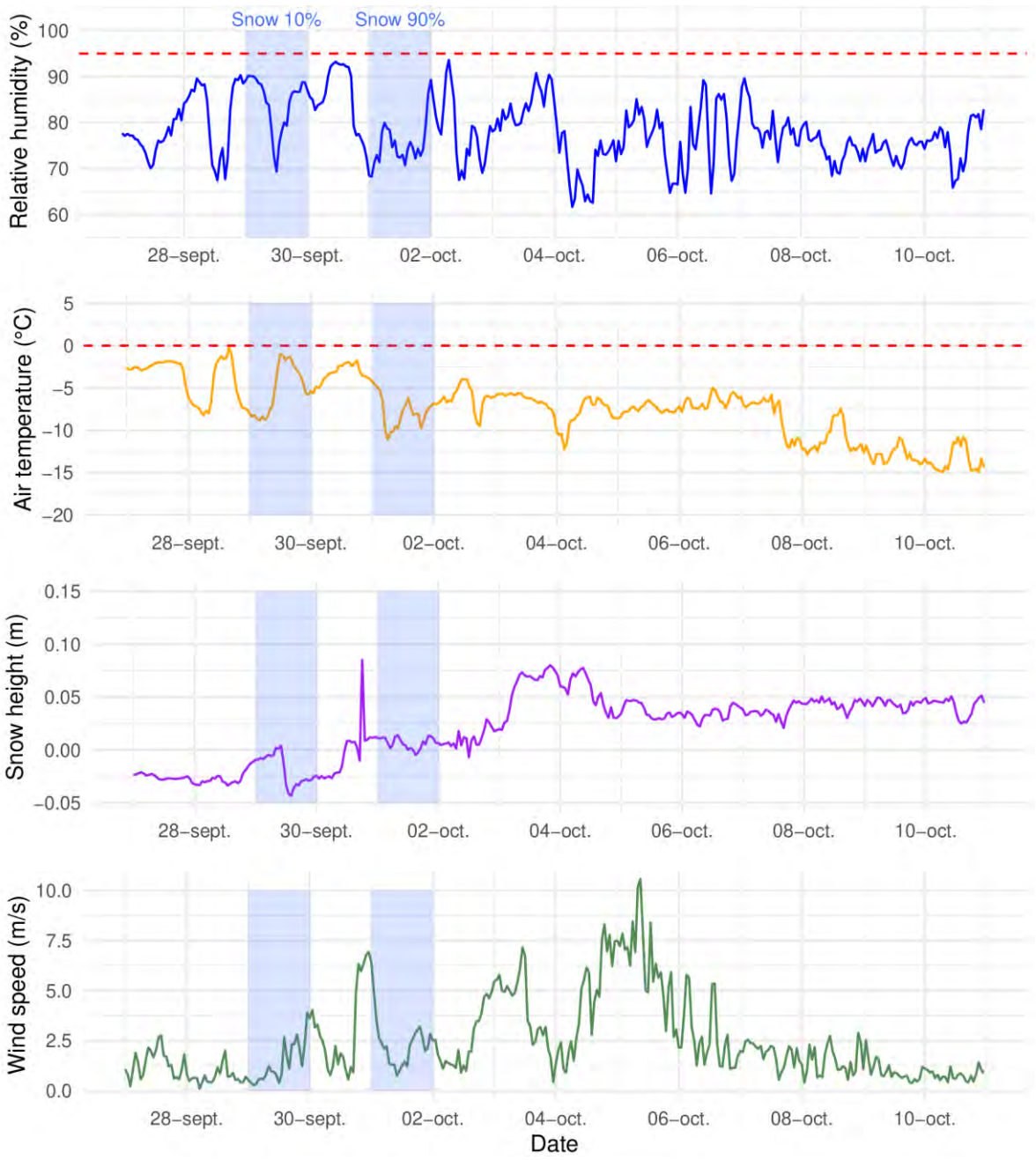


Figure S4.11 Weather conditions recorded during the period of snow onset in fall 2008. The blue boxes represent days with available MODIS images, and the percentage (%) of the study area covered by snow is indicated above the figure. The red dashed line on the relative humidity chart indicates the threshold above which we estimate a high risk of precipitation and on the air temperature chart it indicated 0°C.

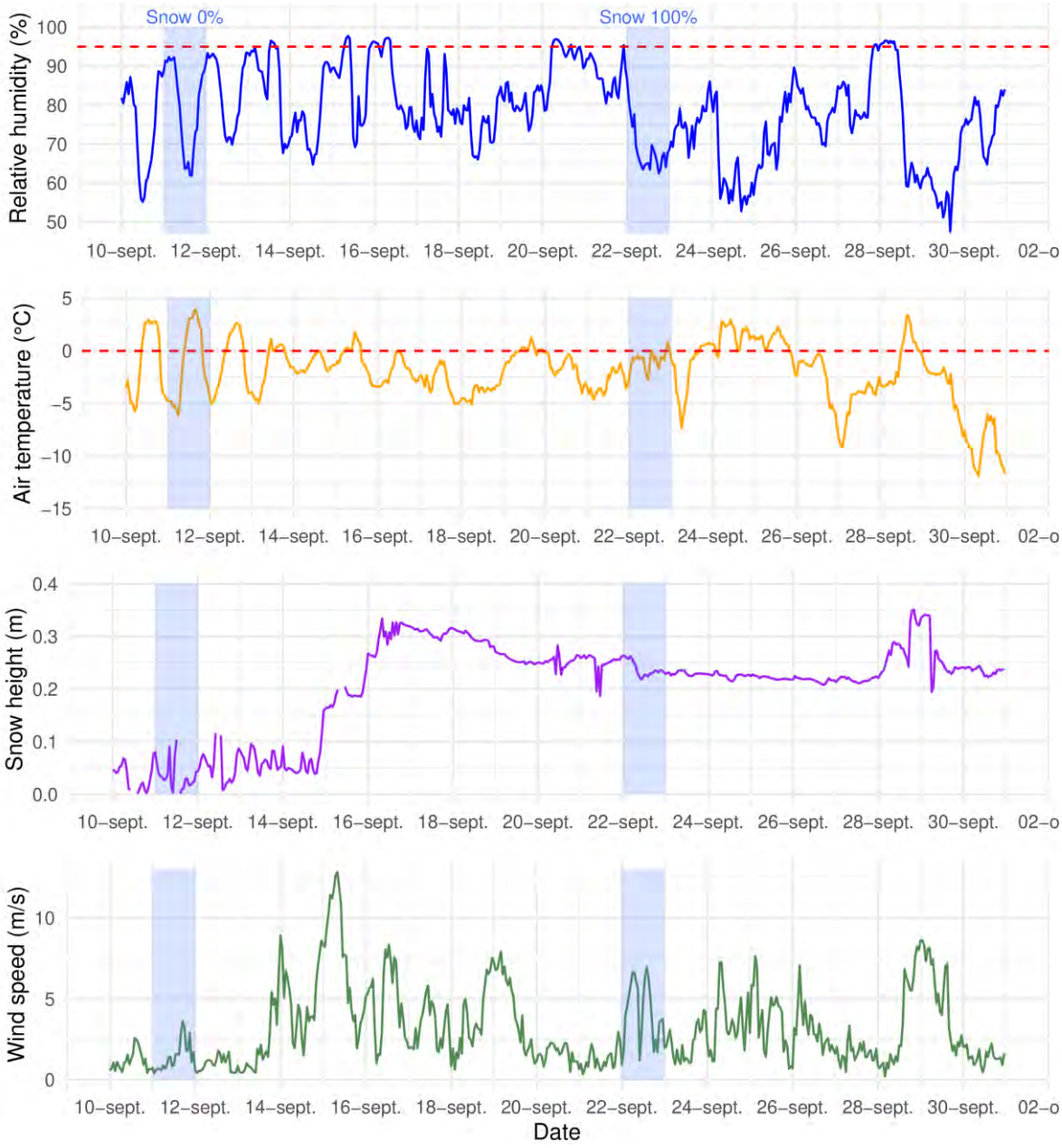


Figure S4.12 Weather conditions recorded during the period of snow onset in fall 2011. The blue boxes represent days with available MODIS images, and the percentage (%) of the study area covered by snow is indicated above the figure. The red dashed line on the relative humidity chart indicates the threshold above which we estimate a high risk of precipitation and on the air temperature chart it indicated 0°C.

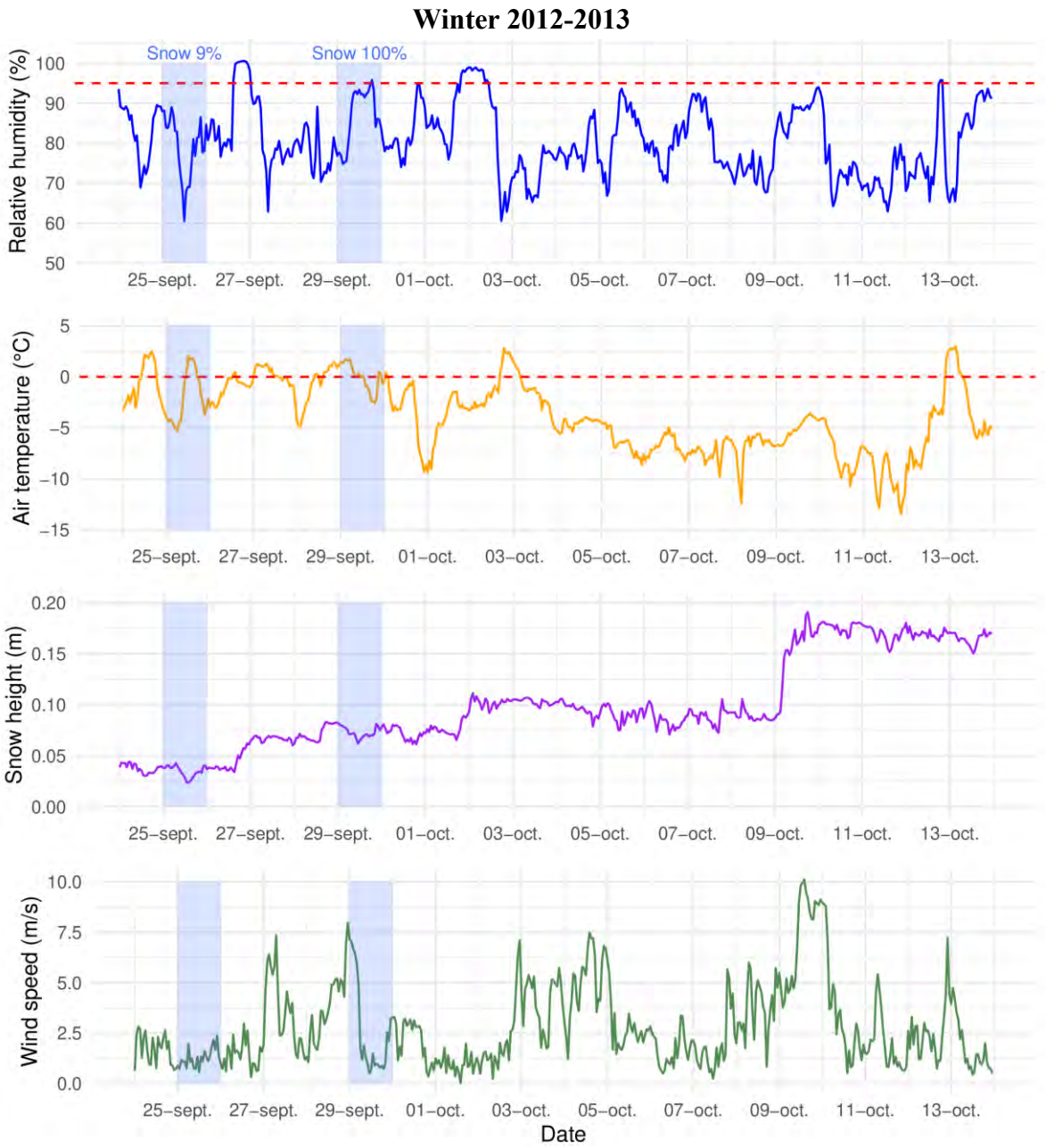


Figure S4.13 Weather conditions recorded during the period of snow onset in fall 2012. The blue boxes represent days with available MODIS images, and the percentage (%) of the study area covered by snow is indicated above the figure. The red dashed line on the relative humidity chart indicates the threshold above which we estimate a high risk of precipitation and on the air temperature chart it indicated 0°C.

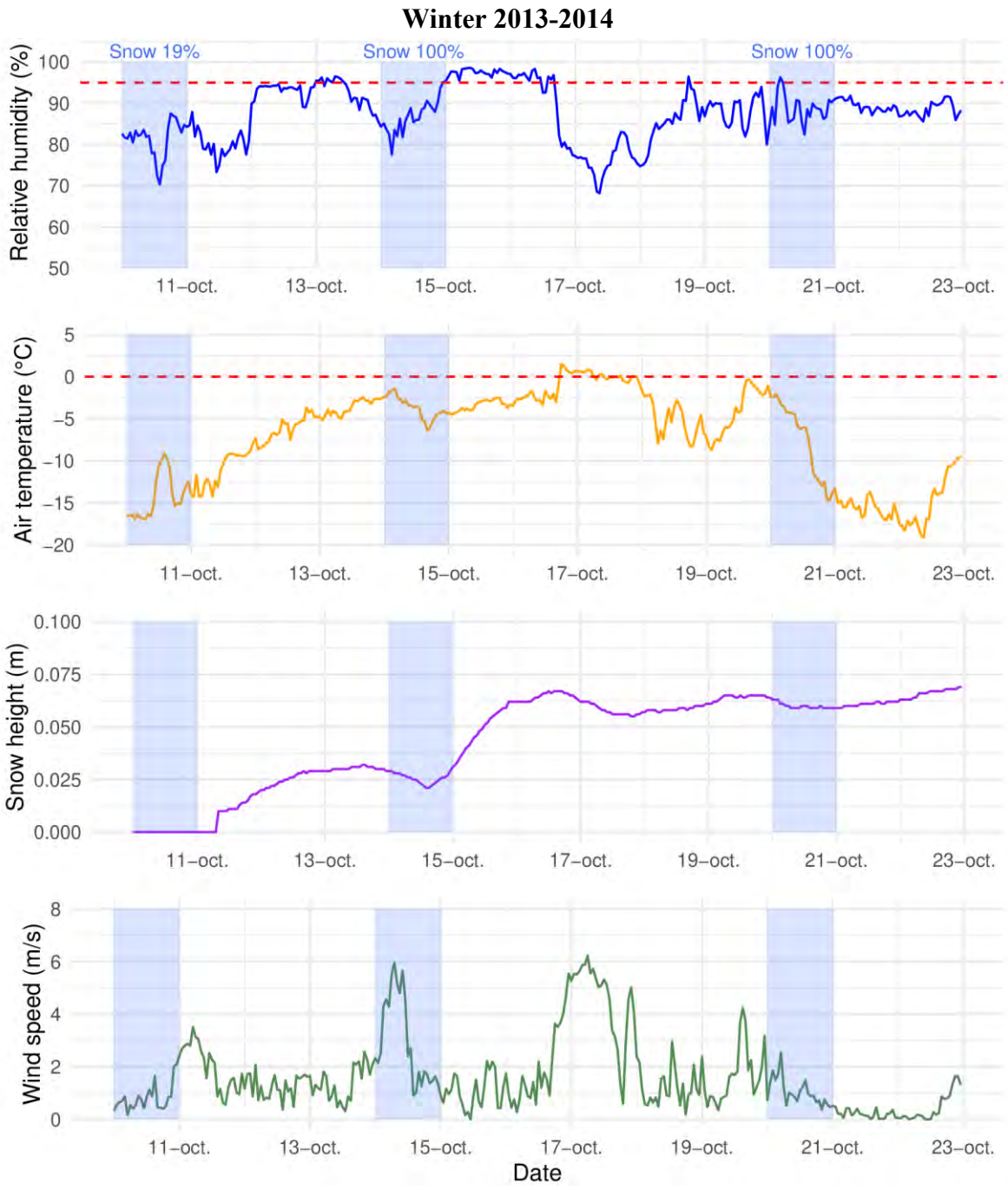


Figure S4.14 Weather conditions recorded during the period of snow onset in fall 2013. The blue boxes represent days with available MODIS images, and the percentage (%) of the study area covered by snow is indicated above the figure. The red dashed line on the relative humidity chart indicates the threshold above which we estimate a high risk of precipitation and on the air temperature chart it indicated 0°C.

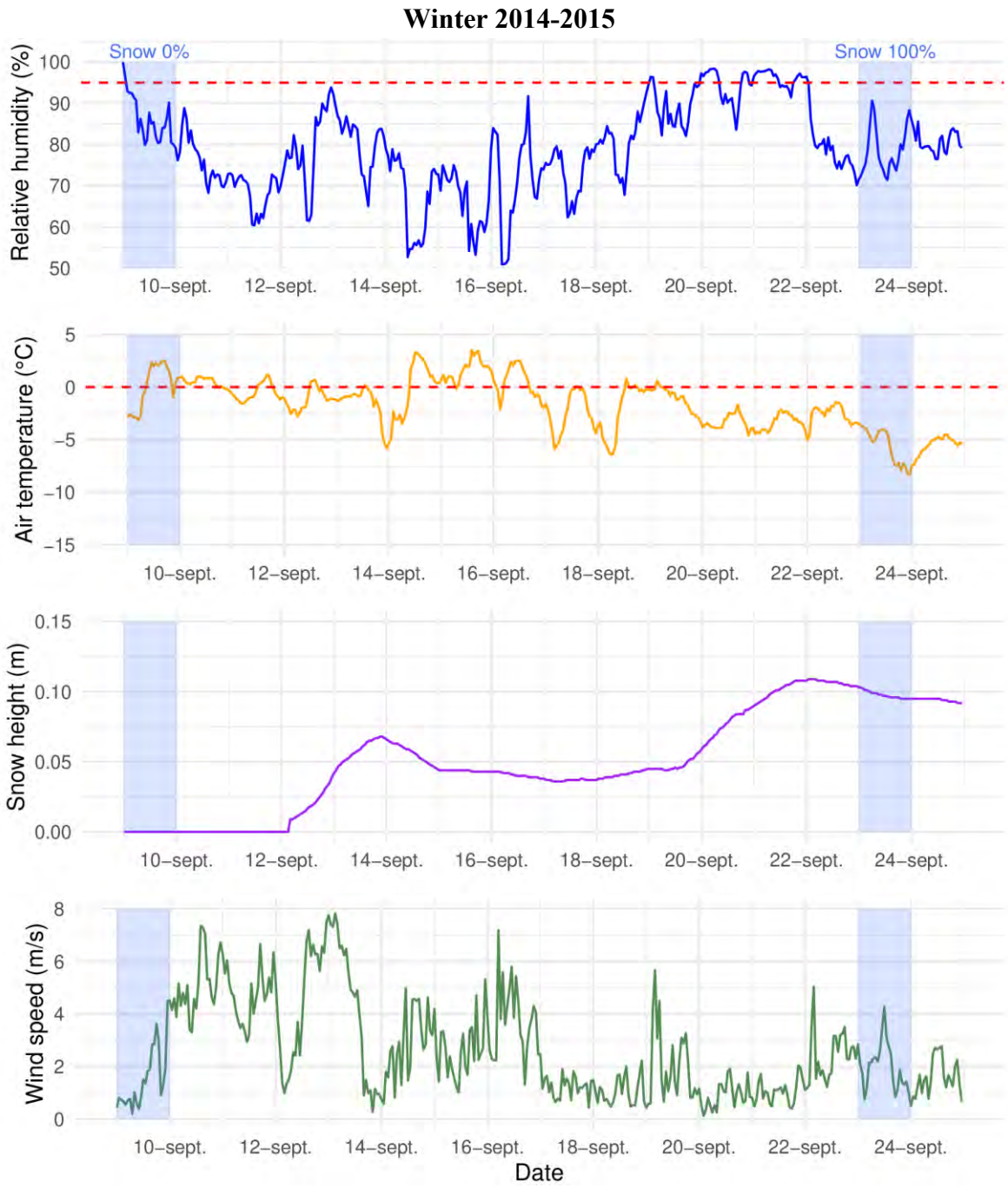


Figure S4.15 Weather conditions recorded during the period of snow onset in fall 2014. The blue boxes represent days with available MODIS images, and the percentage (%) of the study area covered by snow is indicated above the figure. The red dashed line on the relative humidity chart indicates the threshold above which we estimate a high risk of precipitation and on the air temperature chart it indicated 0°C.

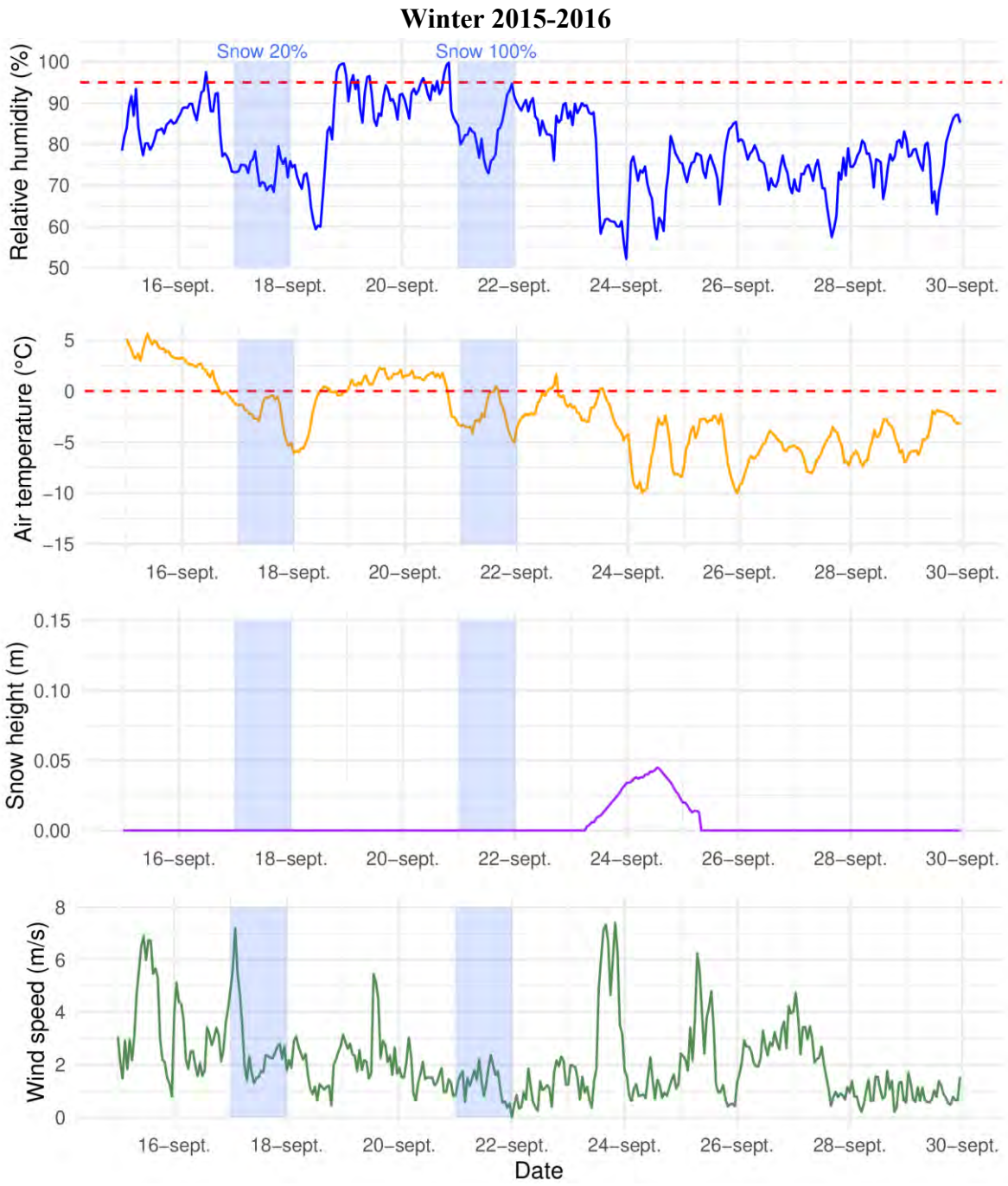


Figure S4.16 Weather conditions recorded during the period of snow onset in fall 2015. The blue boxes represent days with available MODIS images, and the percentage (%) of the study area covered by snow is indicated above the figure. The red dashed line on the relative humidity chart indicates the threshold above which we estimate a high risk of precipitation and on the air temperature chart it indicated 0°C.

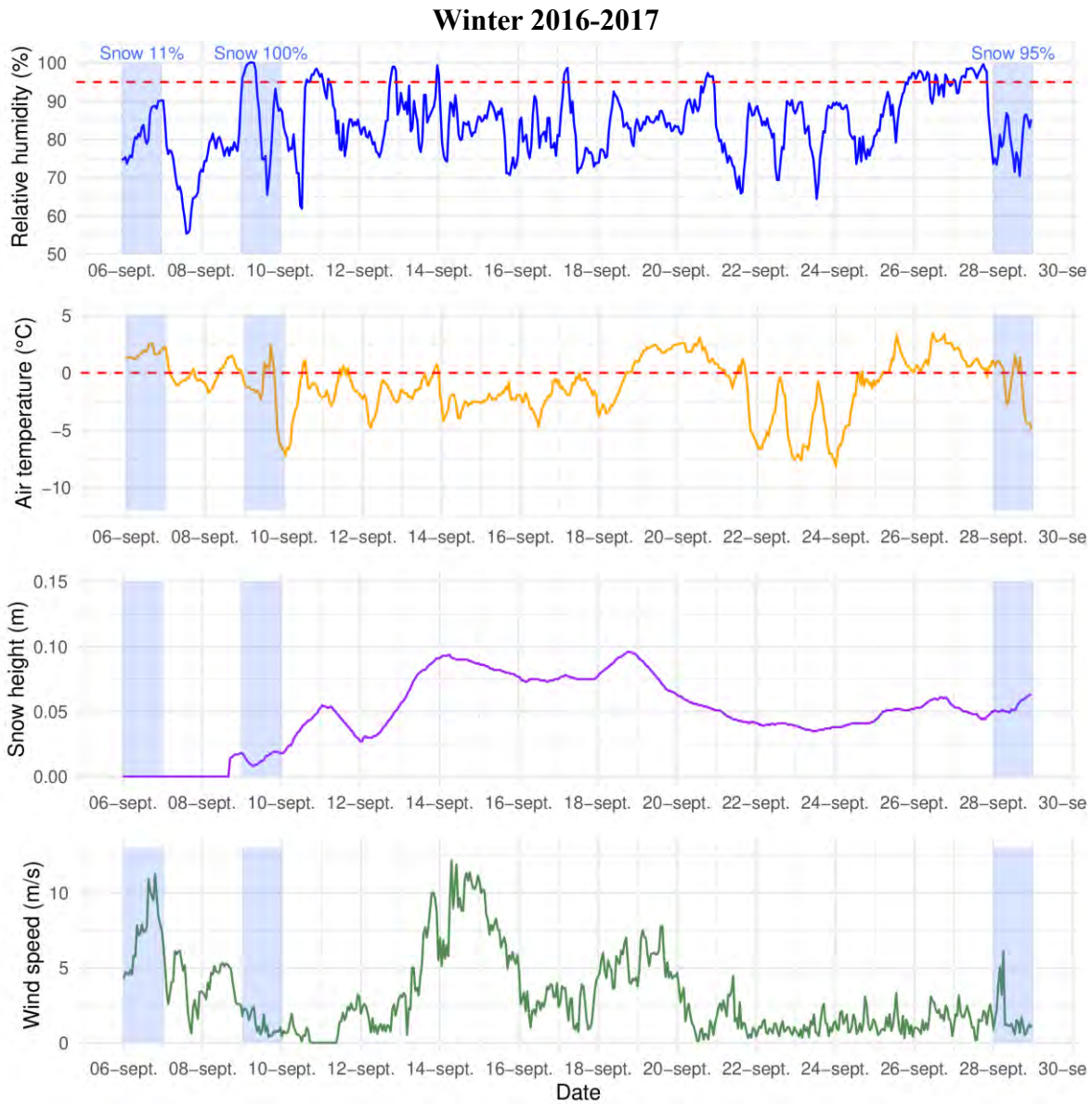


Figure S4.17 Weather conditions recorded during the period of snow onset in fall 2016. The blue boxes represent days with available MODIS images, and the percentage (%) of the study area covered by snow is indicated above the figure. The red dashed line on the relative humidity chart indicates the threshold above which we estimate a high risk of precipitation and on the air temperature chart it indicated 0°C. On September 9, there is a humidity peak, and the air temperature is below 0°C. Furthermore, the snow gauge also detected snow accumulation on that date.

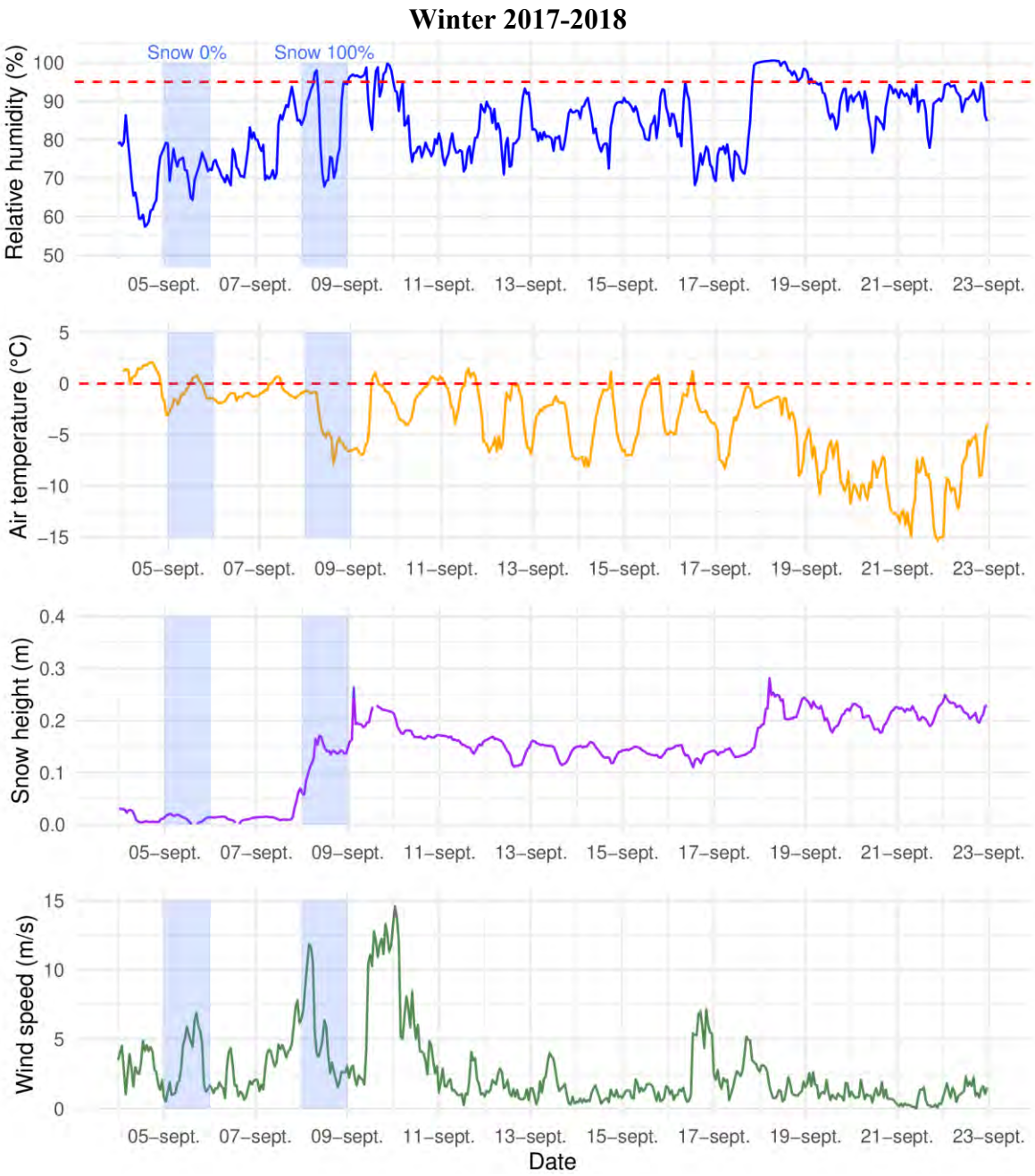


Figure S4.18 Weather conditions recorded during the period of snow onset in fall 2017. The blue boxes represent days with available MODIS images, and the percentage (%) of the study area covered by snow is indicated above the figure. The red dashed line on the relative humidity chart indicates the threshold above which we estimate a high risk of precipitation and on the air temperature chart it indicated 0°C.

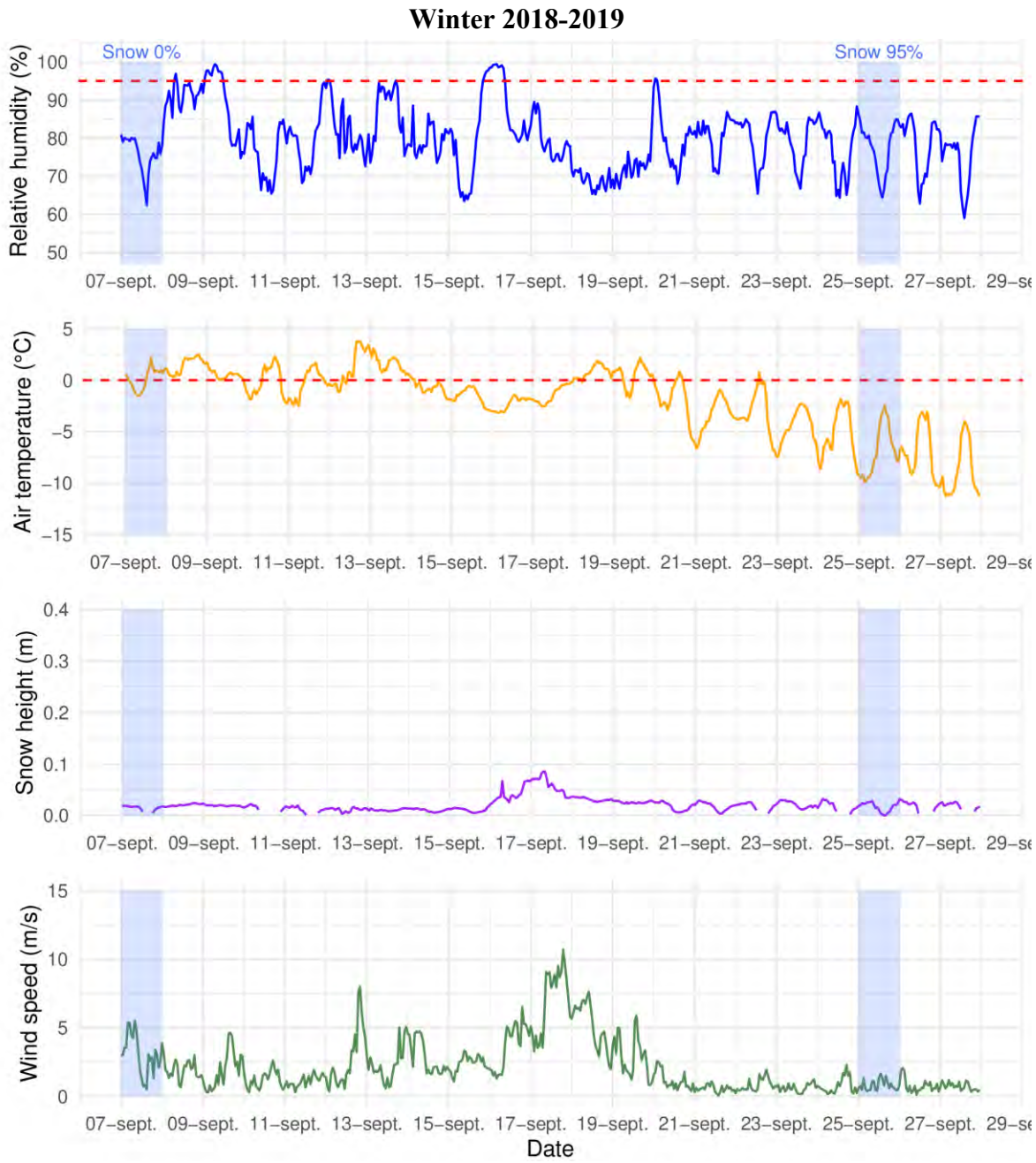


Figure S4.19 Weather conditions recorded during the period of snow onset in fall 2018. The blue boxes represent days with available MODIS images, and the percentage (%) of the study area covered by snow is indicated above the figure. The red dashed line on the relative humidity chart indicates the threshold above which we estimate a high risk of precipitation and on the air temperature chart it indicated 0°C.

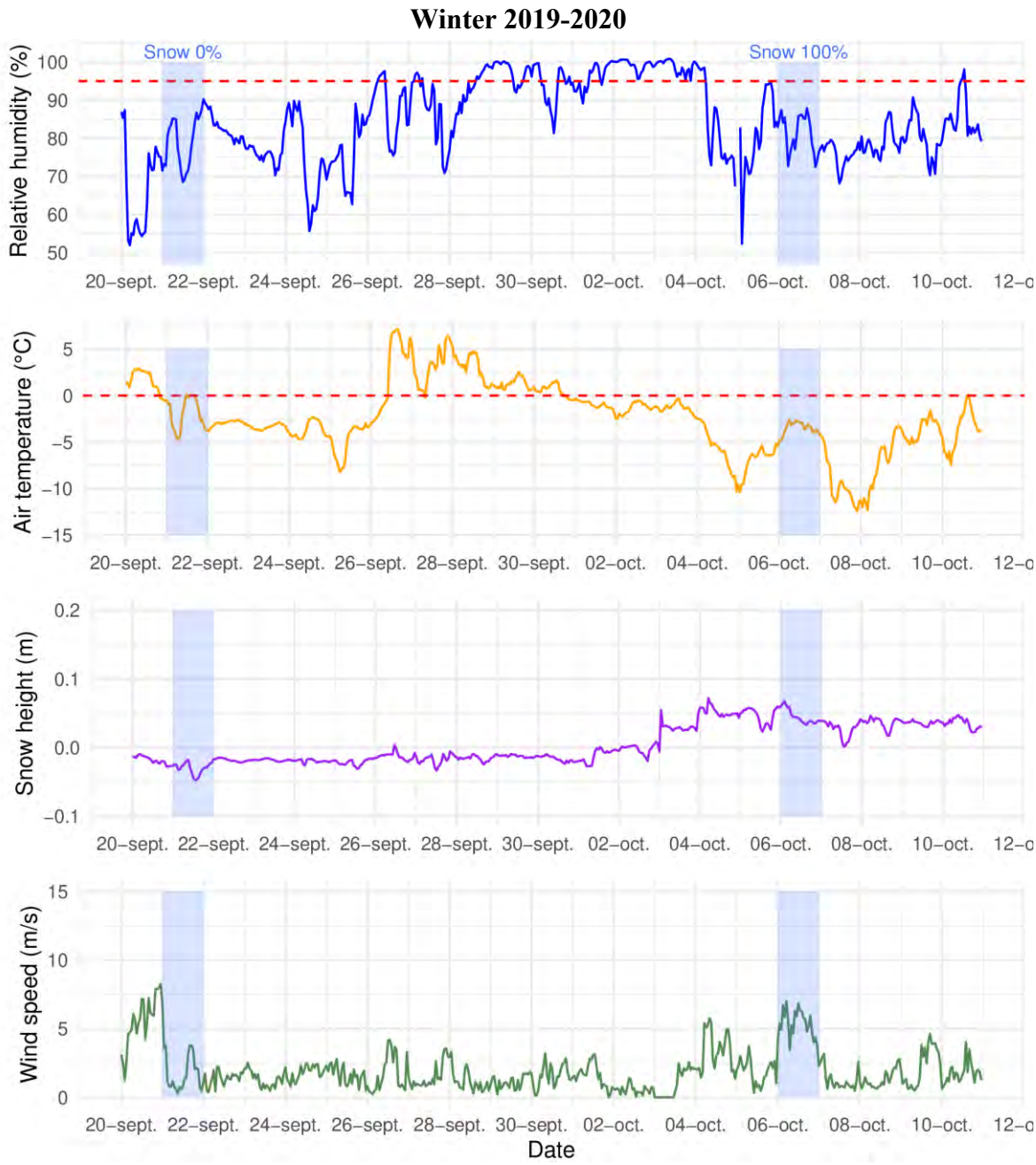


Figure S4.20 Weather conditions recorded during the period of snow onset in fall 2019. The blue boxes represent days with available MODIS images, and the percentage (%) of the study area covered by snow is indicated above the figure. The red dashed line on the relative humidity chart indicates the threshold above which we estimate a high risk of precipitation and on the air temperature chart it indicated 0°C.

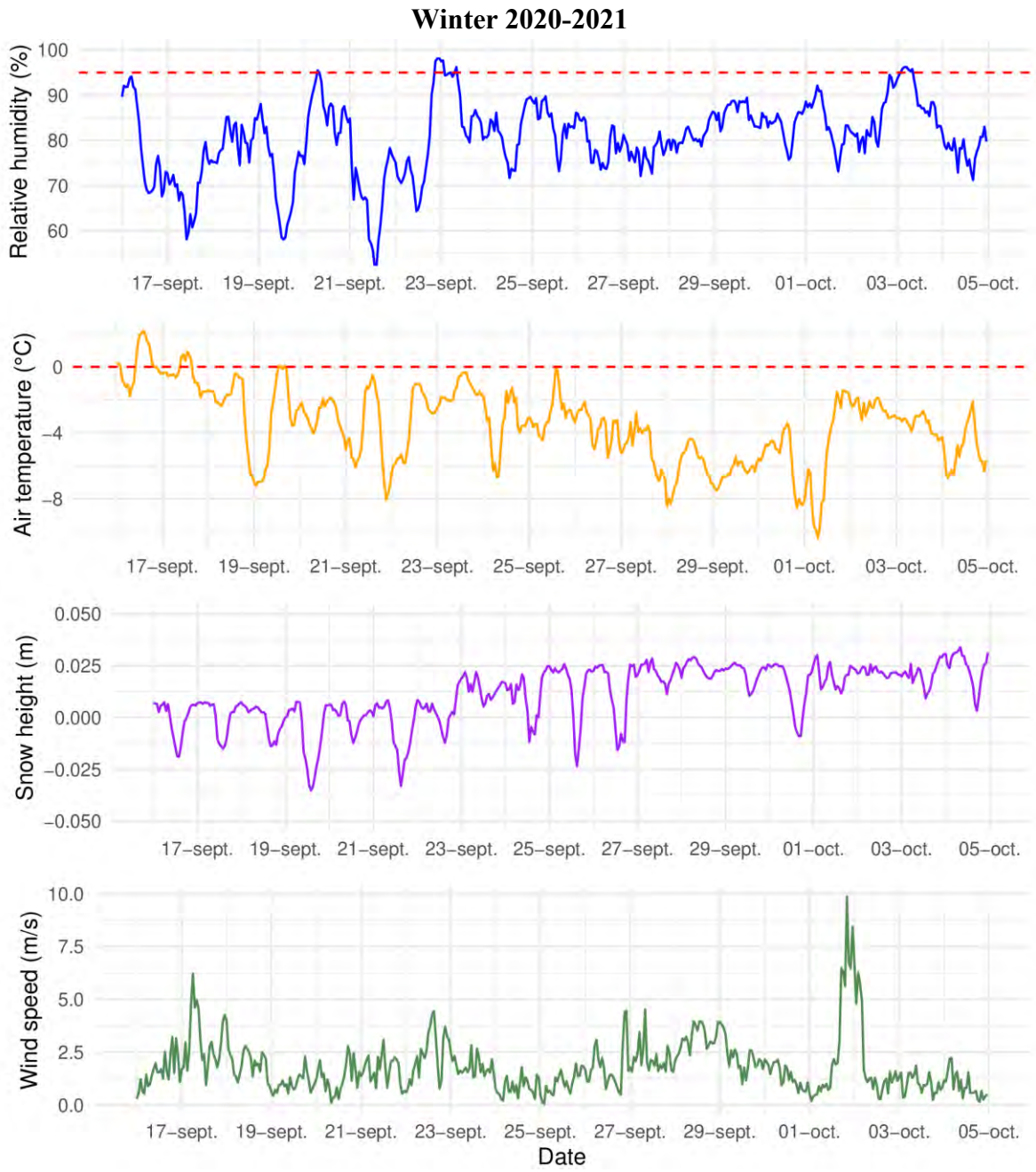


Figure S4.21 Weather conditions recorded during the period of snow onset in fall 2018. The red dashed line on the relative humidity chart indicates the threshold above which we estimate a high risk of precipitation and on the air temperature chart it indicated 0°C. MODIS analysis is not available for that year.

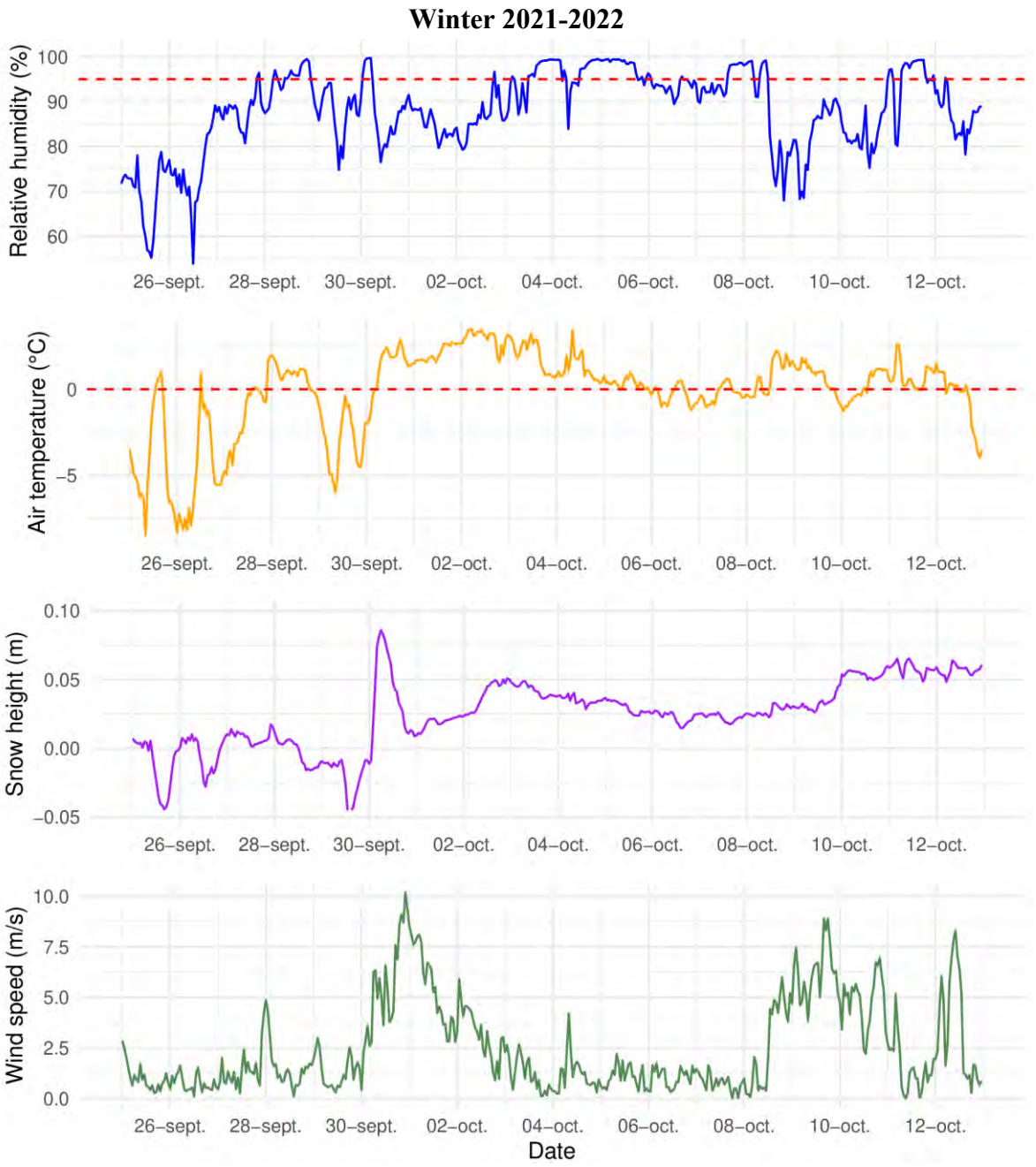


Figure S4.22 Weather conditions recorded during the period of snow onset in fall 2018. The red dashed line on the relative humidity chart indicates the threshold above which we estimate a high risk of precipitation and on the air temperature chart it indicated 0°C. MODIS analysis is not available for that year.

References

CEN. 2022. Données des stations climatiques de l'île Bylot au Nunavut, Canada, v. 1.12.0 (1992-2022). Nordicana D2, doi: 10.5885/45039SL-EE76C1BDAADC4890.

Domine, F., G. Lackner, D. Sarrazin, M. Poirier, and M. Belke-Brea. 2021. Données météorologiques, de neige et de sol de l'île Bylot, haut arctique canadien, pour forcer et tester des modèles de neige et de surfaces continentales, v. 1.100000 (2013-2019). Nordicana D86, doi: 10.5885/45693CE-02685A5200DD4C38.

Dozier, J. 1989. Spectral signature of alpine snow cover from the landsat thematic mapper. Remote Sensing of Environment 28:9–22.

Riggs, G., and D. Hall. 2015. MODIS Snow Products Collection 6 User Guide. https://nsidc.org/sites/nsidc.org/files/files/MODIS-snow-user-guide-C6.pdf.

S4.2 Supplementary material for Chapter 4

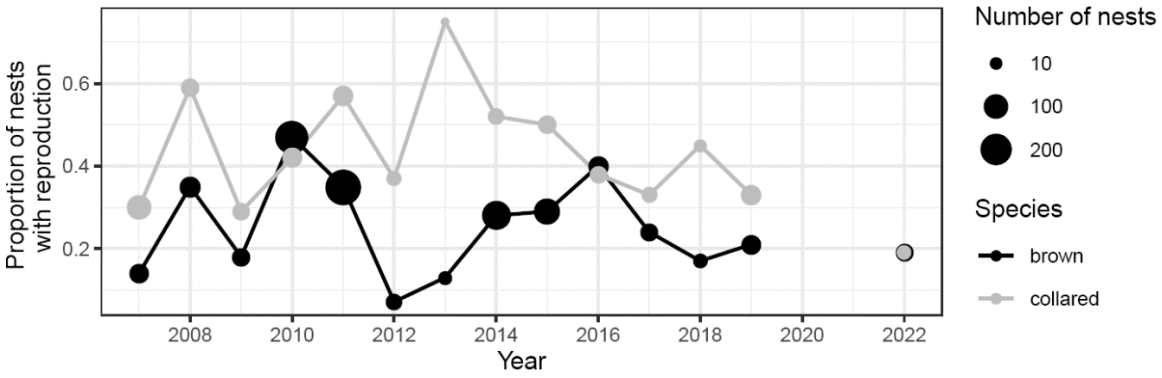


Figure S4.23 Proportion of nests of brown and collared lemming with reproduction during winters 2007 to 2019 in mesic and riparian habitats on Bylot Island. Each winter is referred to by the year when it ended.

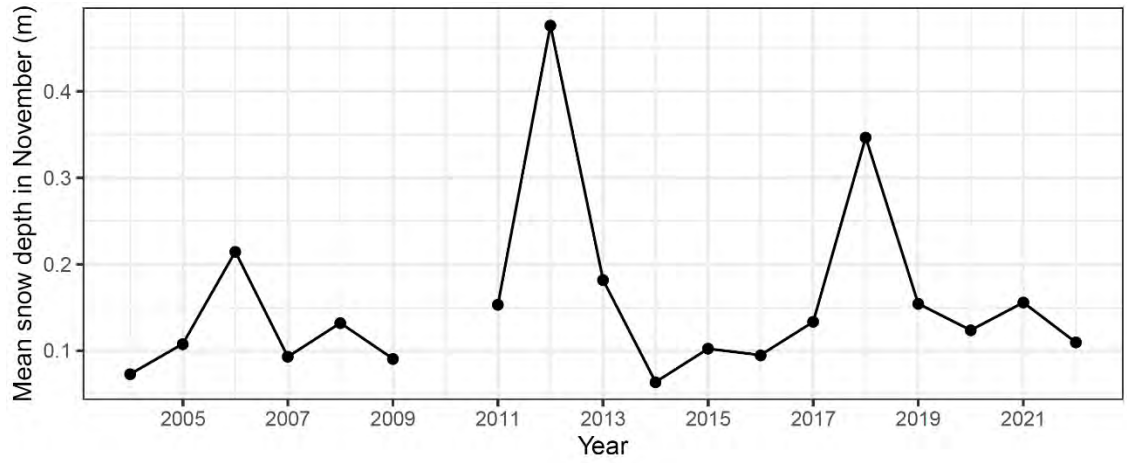


Figure S4.24 Mean snow depth in November from 2004 to 2022 on Bylot Island. Each winter is referred to by the year when it ended.

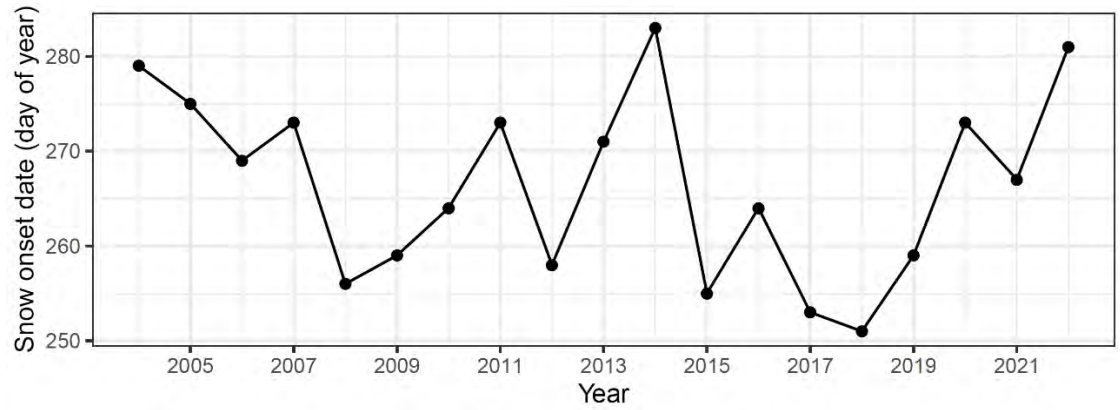


Figure S4.25 Snow onset dates during winters 2004 to 2022 on Bylot Island. Each winter is referred to by the year when it ended.

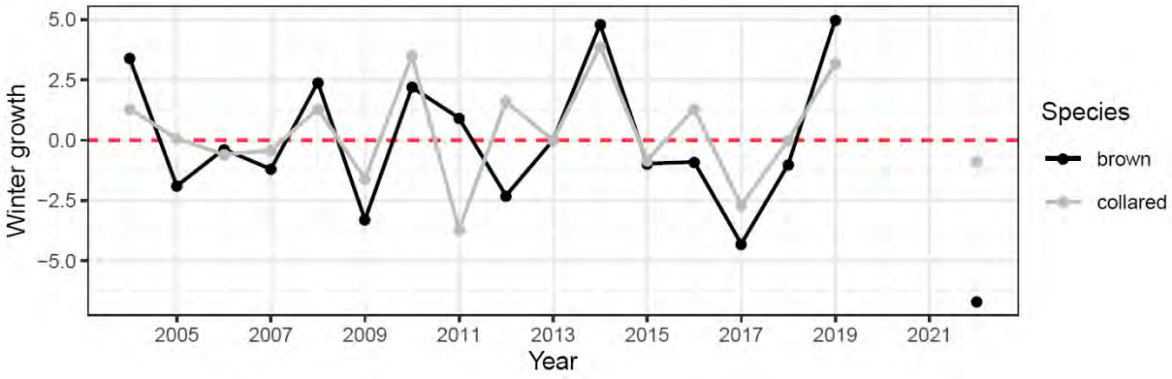


Figure S4.26 Winter population growth (*r*) of brown and collared lemmings from 2004 to 2022 on Bylot Island. Red line represents a null growth. Each winter is referred to by the year when it ended.

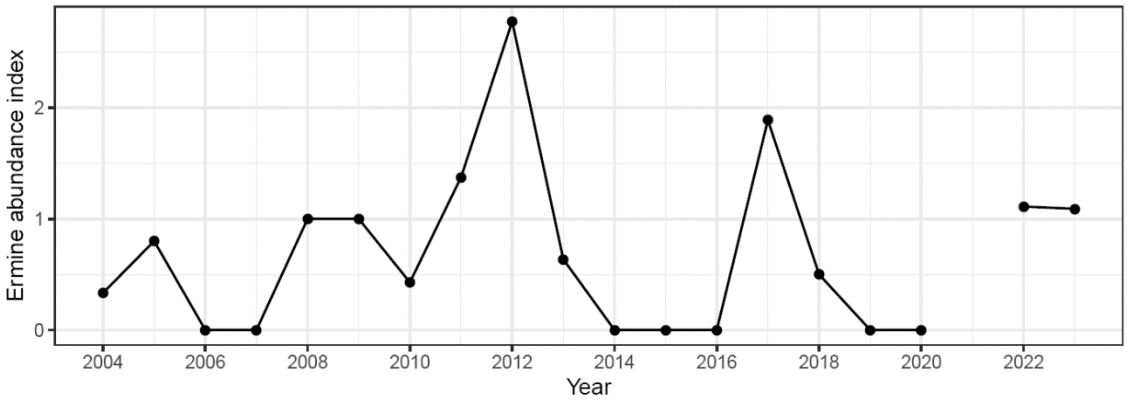


Figure S4.27 Index of ermine abundance during summers 2004 to 2022 on Bylot Island. Data from (Bolduc et al. 2023).

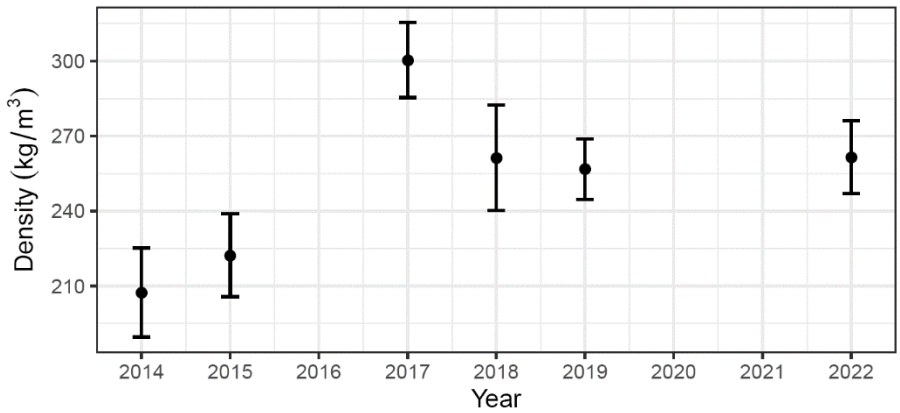


Figure S4.28 Mean density of the basal snow layer in riparian and mesic habitat during winters 2014 to 2022 on Bylot Island. Error bars represent SE. Each winter is referred to by the year when it ended.

Table S4.2 Coefficients of the models examining the influence of snow parameters (rain-on-snow (ros), melt-freeze (melt), freezing rain (fr), snow depth in November (depth) and snow onset (onset)) on annual proportion of lemming winter nests with reproduction, with additive or interactive effects of lemming species, lemming density in August of the previous year (density) and ermine abundance of the previous summer on Bylot Island, 2007 – 2022. The slope estimate (β), its 95% confidence interval (CI), the number of parameters in the model (k), the dispersion parameter (φ) and the adjusted R^2 are presented. Models appear in decreasing order of strength of support based on R^2. Conclusive fixed effects are in bold.

Model	Parameter	β	95% CI	φ	k	R2
ros + density + species	(Intercept)	-1.00	[-1.20, -0.76]	1.91	4	0.43
	log(ros)	**-0.23**	**[-0.38, -0.08]**			
	log(density)	0.09	[0.00, 0.18]			
	collared	**0.76**	**[0.40, 1.12]**			
ros + ermine + species	(Intercept)	-1.16	[-1.44, -1.76]	1.96	4	0.41
	log(ros)	**-0.26**	**[-0.42, -0.09]**			
	ermine	0.20	[-0.02, 0.43]			
	collared	**0.64**	**[0.31, 0.97]**			
ros*density + species	(Intercept)	-1.01	[-1.22, -0.76]	1.99	5	0.4
	log(ros)	**-0.23**	**[-0.39, -0.07]**			
	log(density)	0.10	[0.00, 0.20]			
	collared	**0.77**	**[0.39, 1.15]**			
	log(ros):log(density)	0.02	[-0.08, 0.11]			
fr + density + species	(Intercept)	-0.47	[-0.85, -4.76]	2.04	4	0.39
	log(fr)	**-0.32**	**[-0.56, -0.09]**			
	log(density)	0.10	[0.00, 0.19]			
	collared	**0.80**	**[0.42, 1.17]**			
ros*ermine + species	(Intercept)	-1.19	[-1.50, -1.76]	2.04	5	0.39
	log(ros)	-0.33	[-0.71, 0.06]			
	ermine	0.20	[-0.03, 0.43]			
	collared	**0.65**	**[0.31, 0.98]**			
	log(ros):ermine	0.05	[-0.19, 0.28]			
fr*density + species	(Intercept)	-0.50	[-0.90, -5.76]	2.12	5	0.37
	log(fr)	**-0.31**	**[-0.55, -0.07]**			
	log(density)	0.04	[-0.19, 0.28]			
	collared	**0.82**	**[0.43, 1.21]**			
	log(fr):log(density)	0.04	[-0.12, 0.20]			
ros + species	(Intercept)	-1.00	[-1.21, -0.76]	2.12	3	0.36
	log(ros)	**-0.20**	**[-0.36, -0.04]**			
	collared	**0.60**	**[0.26, 0.94]**			

melt + density + species	(Intercept)	-0.12	[-0.82, -1.76]	2.16	4	0.35
	log(melt)	**-0.24**	**[-0.43, -0.04]**			
	log(density)	0.06	[-0.04, 0.15]			
	collared	**0.73**	**[0.34, 1.12]**			
melt + species	(Intercept)	-0.10	[-0.80, -1.76]	2.18	3	0.34
	log(melt)	**-0.24**	**[-0.44, -0.05]**			
	collared	**0.64**	**[0.29, 1.00]**			
ros*species	(Intercept)	-0.99	[-1.21, -9.76]	2.21	4	0.34
	log(ros)	-0.19	[-0.40, 0.03]			
	collared	**0.59**	**[0.24, 0.95]**			
	log(ros):collared	-0.04	[-0.37, 0.29]			
melt + ermine + species	(Intercept)	-0.12	[-0.88, -1.76]	2.28	4	0.32
	log(melt)	**-0.24**	**[-0.45, -0.04]**			
	ermine	0.02	[-0.21, 0.25]			
	collared	**0.64**	**[0.28, 1.01]**			
melt*density + species	(Intercept)	-0.15	[-0.87, -1.76]	2.25	5	0.32
	log(melt)	**-0.23**	**[-0.43, -0.03]**			
	log(density)	0.14	[-0.35, 0.63]			
	collared	**0.72**	**[0.31, 1.12]**			
	log(melt):log(density)	-0.02	[-0.16, 0.11]			
fr + species	(Intercept)	-0.56	[-0.96, -5.76]	2.30	3	0.31
	log(fr)	**-0.26**	**[-0.50, -0.02]**			
	collared	**0.61**	**[0.26, 0.96]**			
melt*species	(Intercept)	-0.09	[-0.93, -0.76]	2.28	4	0.31
	log(melt)	**-0.25**	**[-0.49, -0.01]**			
	collared	0.63	[-1.05, 2.31]			
	log(melt):collared	0.00	[-0.44, 0.45]			
melt*ermine + species	(Intercept)	-0.59	[-2.42, -5.76]	2.35	5	0.3
	log(melt)	-0.12	[-0.60, 0.37]			
	ermine	0.41	[-0.98, 1.80]			
	collared	**0.64**	**[0.27, 1.01]**			
	log(melt):ermine	-0.10	[-0.46, 0.25]			
fr*species	(Intercept)	-0.61	[-1.13, -6.76]	2.39	4	0.28
	log(fr)	-0.23	[-0.56, 0.11]			
	collared	0.72	[-0.12, 1.56]			
	log(fr):collared	-0.07	[-0.56, 0.42]			
fr + ermine + species	(Intercept)	-0.58	[-1.04, -5.76]	2.40	4	0.28

	log(fr)	**-0.26**	**[-0.50, -0.01]**			
	ermine	0.03	[-0.20, 0.25]			
	collared	**0.61**	**[0.26, 0.97]**			
fr*ermine + species	(Intercept)	-0.48	[-1.09, -4.76]	2.48	5	0.26
	log(fr)	-0.32	[-0.67, 0.04]			
	ermine	-0.08	[-0.59, 0.42]			
	collared	**0.62**	**[0.25, 0.99]**			
	log(fr):ermine	0.07	[-0.21, 0.35]			
depth + density + species	(Intercept)	-0.80	[-1.18, -8.76]	2.63	4	0.21
	depth	-1.00	[-3.40, 1.39]			
	log(density)	0.07	[-0.04, 0.17]			
	collared	**0.66**	**[0.24, 1.07]**			
depth + ermine + species	(Intercept)	-0.80	[-1.18, -8.76]	2.64	4	0.21
	depth	-2.02	[-5.11, 1.08]			
	ermine	0.18	[-0.13, 0.49]			
	collared	**0.58**	**[0.20, 0.95]**			
depth + species	(Intercept)	-0.81	[-1.20, -8.76]	2.67	3	0.2
	depth	-0.90	[-3.29, 1.49]			
	collared	**0.55**	**[0.17, 0.92]**			
onset + density + species	(Intercept)	-2.50	[-7.50, -5.76]	2.66	4	0.2
	onset	0.01	[-0.01, 0.02]			
	log(density)	0.07	[-0.04, 0.18]			
	collared	**0.68**	**[0.25, 1.11]**			
depth*species	(Intercept)	-0.66	[-1.15, -6.76]	2.66	4	0.2
	depth	-2.10	[-5.53, 1.34]			
	collared	0.20	[-0.55, 0.95]			
	depth:collared	2.62	[-2.31, 7.55]			
depth*ermine + species	(Intercept)	-1.00	[-1.61, -0.76]	2.68	5	0.2
	depth	-0.16	[-5.26, 4.93]			
	ermine	0.30	[-0.12, 0.72]			
	collared	**0.57**	**[0.19, 0.96]**			
	depth:ermine	-0.98	[-3.20, 1.23]			
onset*ermine + species	(Intercept)	0.97	[-5.17, -9.76]	2.69	5	0.19
	onset	-0.01	[-0.03, 0.02]			
	ermine	-5.02	[-11.75, 1.71]			
	collared	**0.59**	**[0.21, 0.98]**			
	onset:ermine	0.02	[-0.01, 0.04]			
depth*density + species	(Intercept)	-0.73	[-1.19, -7.76]	2.71	5	0.19

	depth	-1.49	[-4.53, 1.54]			
	log(density)	0.11	[-0.08, 0.30]			
	collared	**0.63**	**[0.21, 1.06]**			
	depth:log(density)	-0.37	[-1.61, 0.86]			
onset + species	(Intercept)	-1.60	[-6.45, -6.76]	2.73	3	0.18
	onset	0.00	[-0.02, 0.02]			
	collared	**0.55**	**[0.17, 0.93]**			
onset*density + species	(Intercept)	-2.31	[-7.84, -3.76]	2.78	5	0.17
	onset	0.01	[-0.02, 0.03]			
	log(density)	0.30	[-2.21, 2.80]			
	collared	**0.69**	**[0.24, 1.14]**			
	onset:log(density)	0.00	[-0.01, 0.01]			
onset*species	(Intercept)	-2.41	[-8.36, -4.76]	2.82	4	0.15
	onset	0.01	[-0.02, 0.03]			
	collared	3.10	[-7.48, 13.67]			
	onset:collared	-0.01	[-0.05, 0.03]			
onset + ermine + species	(Intercept)	-1.79	[-6.79, -7.76]	2.83	4	0.15
	onset	0.00	[-0.02, 0.02]			
	ermine	0.05	[-0.19, 0.30]			
	collared	**0.56**	**[0.17, 0.95]**			

Table S4.3 Coefficients of the models examining the influence of snow parameters (rain-on-snow (ros), melt-freeze (melt), freezing rain (fr), snow depth in November (depth) and snow onset date (onset)) on winter population growth of lemmings, with additive or interactive effects of lemming species, lemming density in August of the previous year (density) and ermine abundance of the previous summer on Bylot Island, 2007 – 2022. The slope estimate (β), its 95% confidence interval (CI), the number of parameters in the model (k), and the adjusted R^2 are presented. Models appear in decreasing order of strength of support based on R^2. Conclusive fixed effects are in bold.

Model	Parameter	β	95% CI	k	R^2
ros + density	(Intercept)	-0.83	[-1.64, -0.01]	3	0.55
	ros	**-0.07**	**[-0.13, -0.02]**		
	log(density)	**-0.80**	**[-1.17, -0.43]**		
ros*density	(Intercept)	-0.75	[-1.59, 0.09]	4	0.55
	ros	**-0.07**	**[-0.14, 0.00]**		
	log(density)	**-0.74**	**[-1.14, -0.34]**		
	ros:log(density)	-0.03	[-0.12, 0.07]		
melt + density	(Intercept)	-0.47	[-1.65, 0.71]	3	0.52
	melt	**-0.01**	**[-0.03, 0.00]**		
	log(density)	**-0.87**	**[-1.19, -0.54]**		
melt*density	(Intercept)	-0.34	[-1.59, 0.92]	4	0.51
	melt	**-0.02**	**[-0.03, 0.00]**		
	log(density)	**-0.70**	**[-1.27, -0.14]**		
	melt:log(density)	0.00	[-0.01, 0.01]		
depth + density	(Intercept)	-0.66	[-1.85, 0.53]	3	0.50
	depth	-4.24	[-10.14, 1.66]		
	log(density)	**-0.95**	**[-1.36, -0.54]**		
depth*density	(Intercept)	-1.06	[-2.41, 0.30]	4	0.50
	depth	-1.57	[-5.27, 2.13]		
	log(density)	**-1.21**	**[-1.89, -0.54]**		
	depth:log(density)	1.59	[-1.61, 4.80]		
onset*density	(Intercept)	2.34	[-18.35, 23.03]	4	0.49
	onset	-0.01	[-0.12, 0.10]		
	log(density)	**4.95**	**[-5.66, 15.56]**		
	onset:log(density)	-0.02	[-0.06, 0.02]		
fr*density	(Intercept)	-1.02	[-1.99, -0.04]	4	0.48
	fr	-0.03	[-0.09, 0.03]		
	log(density)	**-0.79**	**[-1.25, -0.33]**		
	fr:log(density)	-0.03	[-0.07, 0.01]		
fr + density	(Intercept)	-1.14	[-2.11, -0.16]	3	0.47
	fr	-0.02	[-0.08, 0.05]		

	log(density)	**-0.89**	**[-1.33, -0.45]**		
onset + density	(Intercept)	-6.34	[-23.51, 10.82]	3	0.47
	onset	0.02	[-0.06, 0.10]		
	log(density)	**-0.91**	**[-1.36, -0.46]**		
ros*ermine	(Intercept)	1.07	[-0.02, 2.15]	4	0.28
	ros	-0.46	[-1.27, 0.35]		
	ermine	-1.00	[-2.55, 0.55]		
	ros:ermine	0.21	[-0.22, 0.64]		
depth*ermine	(Intercept)	2.13	[-0.09, 4.34]	4	0.23
	depth	-6.53	[-16.29, 3.22]		
	ermine	**-3.47**	**[-5.60, -1.34]**		
	depth:ermine	7.85	[-0.39, 16.09]		
ros + ermine	(Intercept)	0.78	[-0.30, 1.87]	3	0.22
	ros	**-0.10**	**[-0.20, 0.00]**		
	ermine	-0.72	[-2.30, 0.86]		
ros	(Intercept)	0.38	[-0.49, 1.25]	2	0.21
	ros	**-0.12**	**[-0.21, -0.04]**		
ros*species	(Intercept)	0.32	[-0.91, 1.56]	4	0.21
	ros	-0.17	[-0.70, 0.36]		
	collared	0.12	[-1.79, 2.02]		
	ros:collared	0.10	[-0.43, 0.63]		
ros + species	(Intercept)	0.12	[-1.08, 1.31]	3	0.20
	ros	**-0.12**	**[-0.20, -0.04]**		
	collared	0.52	[-1.17, 2.22]		
melt*ermine	(Intercept)	2.88	[0.43, 5.33]	4	0.18
	melt	-0.04	[-0.10, 0.01]		
	ermine	-3.24	[-6.76, 0.29]		
	melt:ermine	0.03	[-0.02, 0.08]		
onset*ermine	(Intercept)	-23.54	[-55.02, 7.93]	4	0.18
	onset	0.09	[-0.03, 0.21]		
	ermine	32.63	[-2.08, 67.35]		
	onset:ermine	-0.13	[-0.26, 0.00]		
fr + ermine	(Intercept)	1.13	[-0.10, 2.36]	3	0.15
	fr	-0.05	[-0.11, 0.02]		
	ermine	-1.25	[-2.68, 0.17]		
melt + ermine	(Intercept)	1.28	[-0.15, 2.70]	3	0.14

	melt	-0.01	[-0.04, 0.02]		
	ermine	-1.04	[-2.68, 0.60]		
depth + ermine	(Intercept)	0.28	[-1.24, 1.79]	3	0.14
	depth	5.15	[-4.38, 14.68]		
	ermine	**-1.72**	**[-3.02, -0.43]**		
fr*ermine	(Intercept)	0.97	[-0.46, 2.39]	4	0.13
	fr	-0.02	[-0.16, 0.12]		
	ermine	-1.10	[-2.93, 0.73]		
	fr:ermine	-0.02	[-0.13, 0.08]		
onset + ermine	(Intercept)	-1.76	[-25.01, 21.48]	3	0.10
	onset	0.01	[-0.10, 0.12]		
	ermine	-1.30	[-2.88, 0.28]		
melt*species	(Intercept)	1.60	[-0.41, 3.61]	4	0.10
	melt	-0.04	[-0.08, 0.01]		
	collared	-1.16	[-4.40, 2.08]		
	melt:collared	0.03	[-0.02, 0.08]		
melt	(Intercept)	1.02	[-0.41, 2.45]	2	0.09
	melt	**-0.02**	**[-0.04, 0.00]**		
melt + species	(Intercept)	0.76	[-0.93, 2.45]	3	0.07
	melt	**-0.02**	**[-0.04, 0.00]**		
	collared	0.52	[-1.23, 2.27]		
fr	(Intercept)	0.31	[0.76, 1.38]	2	0.04
	fr	-0.06	[-0.13, 0.02]		
fr + species	(Intercept)	0.05	[-1.35, 1.46]	3	0.01
	fr	-0.06	[-0.13, 0.02]		
	collared	0.52	[-1.36, 2.40]		
onset	(Intercept)	-9.40	[-33.12, 14.31]	2	-0.01
	onset	0.03	[-0.08, 0.15]		
fr*species	(Intercept)	0.13	[-1.43, 1.69]	4	-0.02
	fr	-0.07	[-0.18, 0.04]		
	collared	0.37	[-1.84, 2.58]		
	fr:collared	0.02	[-0.14, 0.18]		
depth	(Intercept)	0.15	[-1.50, 1.80]	2	-0.03
	depth	-1.84	[-10.40, 6.72]		
onset + species	(Intercept)	-9.67	[-33.68, 14.35]	3	-0.04
	onset	0.03	[-0.08, 0.15]		

	collared	0.52	[-1.44, 2.49]		
depth + species	(Intercept)	-0.11	[-2.02, 1.80]	3	-0.05
	depth	-1.84	[-9.94, 6.26]		
	collared	0.52	[-1.41, 2.46]		
depth*species	(Intercept)	0.33	[-2.05, 2.72]	4	-0.07
	depth	-4.65	[-13.85, 4.55]		
	collared	-0.36	[-3.94, 3.21]		
	depth:collared	5.62	[-9.63, 20.87]		
onset*species	(Intercept)	-11.87	[-46.38, 22.65]	4	-0.07
	onset	0.04	[-0.18, 0.26]		
	collared	4.92	[-60.78, 70.63]		
	onset:collared	-0.02	[-0.27, 0.23]		