







Université du Québec  
à Rimouski

**ANALYSE DE L'ACTIVITÉ PRINTANIÈRE  
AU-DESSUS DE LA NEIGE CHEZ LE LEMMING  
VARIABLE (*DICROSTONYX GROENLANDICUS*) DE L'ÎLE  
D'ELLESMERE**

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« Dans le domaine des idées, tout dépend de l'enthousiasme. Dans le monde réel, tout repose sur la persévérance. » – Johann Wolfgang von Goethe. Au Nord, dans tous ses parallèles.



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## RÉSUMÉ

Les petits mammifères vivant dans des climats froids sont confrontés à d'importantes pertes de chaleur et donc, à de fortes demandes énergétiques liées à la régulation de leur température corporelle. Cependant, le coût énergétique de la thermorégulation peut être réduit par des adaptations comportementales, telles que l'utilisation de l'espace sous-nival comme refuge thermique. À l'aide de caméras automatisées, nous avons suivi des lemmings variables (*Dicrostonyx groenlandicus*) à la limite septentrionale de leur aire de répartition, alors qu'ils faisaient des apparitions à la surface de la neige au printemps, afin d'évaluer l'effet des variables météorologiques sur l'occurrence de ce comportement. Nous avons émis l'hypothèse que les lemmings réduisent leurs dépenses énergétiques liées à la thermorégulation lorsqu'ils sont à la surface de la neige au printemps. Tel qu'attendu, la probabilité d'activité à la surface augmente avec la température de l'air, mais diminue avec le couvert nuageux et la vitesse du vent. De plus, la température opérative à la surface était plus élevée que celle sous la neige, tandis que les profils de neige montraient l'absence d'eau liquide dans le manteau neigeux. Ces résultats soutiennent que l'activité des lemmings à la surface au printemps est une stratégie de thermorégulation comportementale. Cependant, l'observation de plusieurs prédateurs dans la zone d'étude, combinée au comportement de vigilance observé chez les lemmings sur la neige, souligne les risques associés à cette exposition sur la neige. Nous suggérons donc que les lemmings sont confrontés à un compromis entre thermorégulation et risque de prédation. Étant donné la rareté de données sur l'écologie hivernale des lemmings, nous avons également exploité ce comportement pour recueillir des informations précieuses sur la phénologie de la mue et la reproduction. Globalement, nos résultats permettent de mieux comprendre le compromis complexe entre la thermorégulation et le risque de prédation chez les petits mammifères vivant dans des climats froids, et mettent en évidence certaines implications potentielles pour la dynamique des écosystèmes arctiques basée sur les interactions prédateur-proie.

Mots clés : Thermorégulation comportementale, Petits mammifères, Lemmings, *Dicrostonyx*, Risque de prédation, Compromis, Comportement anti-prédateur, Vigilance





## ABSTRACT

Small mammals inhabiting cold climates face high heat losses and thus, high energy demands for body temperature regulation. However, the energetic cost of thermoregulation can be reduced through behavioral adaptations, such as the use of the subnivean space as a thermal refuge. Using automated cameras, we monitored collared lemmings (*Dicrostonyx groenlandicus*) at the northern limit of their range, as they surfaced from their snow burrows in spring, to assess the effect of weather variables on the occurrence of this behavior. We hypothesized that lemmings reduce the energetic cost of thermoregulation when they come to the surface of the snow in spring. As expected, the likelihood of surface activity increased with air temperature, but decreased with cloud cover and wind speed. In addition, the operative temperature was higher above the snow than below, while snow profiles showed the absence of liquid water in the snowpack. These findings support that lemming surface activity in spring is a behavioral thermoregulation strategy. However, observations of several predators in the study area, combined with vigilance behavior observed in lemmings at the snow surface, stress the risks associated with such exposure on the snow. We therefore suggest that lemmings face a trade-off between thermoregulation and predation risk. Given that data on lemming winter ecology are scarce, we also exploited this behavior to gather valuable knowledge on molting phenology and breeding. Overall, our results provide insight into the complex trade-off between thermoregulation and predation risk in small mammals inhabiting cold climates, and highlight some potential implications for arctic ecosystem dynamics based on predator-prey interactions.

*Keywords:* Behavioral thermoregulation, Small mammals, Lemmings, *Dicrostonyx*, Predation risk, Trade-off, Antipredator behavior, Vigilance



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## INTRODUCTION GÉNÉRALE

La capacité de thermogénèse et la flexibilité comportementale des endothermes leur permettent de faire face à un grand éventail de pressions externes, incluant des conditions environnementales extrêmes et un fort risque de prédation (Lima & Dill, 1990; Terrien et al., 2011). Cette adaptabilité leur permet de réguler la quantité d'énergie qu'ils investissent pour répondre à différents besoins selon les ressources disponibles (Genoud, 1988; Beaver et al., 2017; Hume et al., 2020).

Les échanges énergétiques entre un animal et son environnement influencent plusieurs aspects de son écologie, tels que la sélection de son habitat (Huey, 1991), les comportements de recherche de nourriture (Mathot et al., 2009), ainsi que divers traits de son histoire de vie, comme la reproduction (Racey, 1987; Stearns, 1992). Ces interactions peuvent même influencer la répartition géographique des espèces (Root, 1988; Boratyński, 2021). Ces interactions entre les individus et leur environnement peuvent donc entraîner des répercussions sur la dynamique des populations et des écosystèmes (McNab, 1980).

Dans ce mémoire, j'explore les facteurs environnementaux qui influencent le comportement d'un mammifère en milieu naturel, en mettant l'accent sur ses besoins énergétiques associés à la thermorégulation. Pour ce faire, je définirai d'abord comment le budget énergétique et les conditions environnementales influencent les besoins des individus. Cette approche me permet ensuite d'examiner les implications écologiques des contraintes et compromis nécessaires au maintien de l'équilibre énergétique et à la survie des individus, en soulignant l'impact du risque de prédation et du froid comme contraintes majeures chez les proies endothermes.

## **1. LE BUDGET ÉNERGÉTIQUE DES ENDOTHERMES**

Le budget énergétique d'un animal désigne la quantité d'énergie qu'il acquiert, principalement via son alimentation, puis la manière dont cette énergie est répartie pour soutenir ses fonctions vitales, ses activités quotidiennes et, lorsque les dépenses sont inférieures à l'énergie assimilée, l'accumulation de réserves (Hudson & White, 1985; McNab, 2002). Bien que complexes à mesurer en milieu naturel, les dépenses énergétiques d'un individu peuvent être divisées en deux catégories de fonctions biologiques, soit 1) le métabolisme, 2) la production (croissance et reproduction) (Fig. 1A) (Hudson & White, 1985; McNab, 2002). La composante métabolique représente la plus grande partie du budget énergétique d'un endotherme et comprend à la fois les coûts liés à la maintenance (thermorégulation et autre maintenance de base) et aux activités (locomotion, interactions sociales, comportements anti-prédation, etc.) (McNab, 2002). Plusieurs facteurs influencent les dépenses énergétiques tels que la taille corporelle, le statut reproducteur ainsi que les comportements individuels et sociaux (Speakman, 1997). Le budget énergétique d'un individu en milieu naturel est également grandement influencé par les conditions environnementales puisque la régulation de la température corporelle représente une part importante des dépenses énergétiques (Walsberg, 1985; McNab, 2002; Norris & Kunz, 2012).

## **2. LA RÉGULATION DE LA TEMPÉRATURE CORPORELLE**

Chez les espèces endothermes, la température corporelle est activement maintenue à l'intérieur d'un intervalle donné grâce à l'équilibre entre la production de chaleur métabolique et les échanges (gains et pertes) de chaleur avec l'environnement (McNab, 2002). Les échanges thermiques entre un animal et son environnement, aussi appelés budget thermique, sont dictés par quatre mécanismes principaux soit 1) la radiation, 2) la conduction, 3) la convection et 4) l'évaporation (Fig. 1B) (Porter & Gates, 1969; Gates, 1980; McNab,

2002). La radiation constitue le transfert d'énergie par le biais d'ondes électromagnétiques entre deux objets qui ne sont pas en contact. L'énergie radiative peut être absorbée, réfléchie ou transmise (Birkebak, 1966; Porter & Gates, 1969; McNab, 2002). La conduction et la convection, quant à elles, sont les échanges de chaleur par contact direct entre un animal et une surface (conduction) ou par transport par le mouvement de l'air qui l'entoure (convection) (Birkebak, 1966; McNab, 2002; Norris & Kunz, 2012). La perte de chaleur sous forme d'évaporation d'eau, principalement par la respiration, constitue le quatrième et dernier mécanisme d'échange thermique (Birkebak, 1966; McNab, 2002).

Plusieurs facteurs environnementaux, tels que la température, la vitesse du vent, l'humidité et l'intensité de la radiation solaire, influencent donc simultanément les échanges énergétiques entre un animal et son environnement (Speakman, 1997). Plus précisément, le différentiel de température entre la surface corporelle et l'environnement immédiat de l'animal (air ou surface de contact) joue un rôle déterminant dans les échanges de chaleur par convection et par conduction, respectivement (Cena & Monteith, 1975; Gates, 1980; Reynolds, 1993; McNab, 2002). Plusieurs auteurs ont ainsi démontré qu'une augmentation de la vitesse du vent accroît les pertes de chaleur par convection chez les mammifères terrestres (Tregear, 1965; Heller, 1972; Chappell, 1980b, 1980a) et les oiseaux (Robinson et al., 1976; Walsberg et al., 1978). Le couvert nuageux et l'angle du soleil par rapport à l'horizon influencent quant à eux les échanges de chaleur par radiation (Gates, 1980; Norris & Kunz, 2012). Les propriétés physiques d'un animal influencent également son budget thermique. Par exemple, son rapport surface/volume (McNab, 2002; Tattersall et al., 2012) et l'isolation de son enveloppe externe (Scholander et al., 1950; Tregear, 1965) interagissent avec son environnement dans le transfert de chaleur. Les propriétés optiques de l'enveloppe de l'animal, influencées par la couleur et la texture, modifient également la quantité d'énergie solaire absorbée ou réfléchie par l'individu (Walsberg et al., 1978; McNab, 2002; Norris & Kunz, 2012). Il est donc essentiel de considérer les échanges thermiques et leurs effets sur le budget énergétique pour obtenir un portrait aussi complet que possible des interactions entre un animal et son environnement (Gates, 1980).

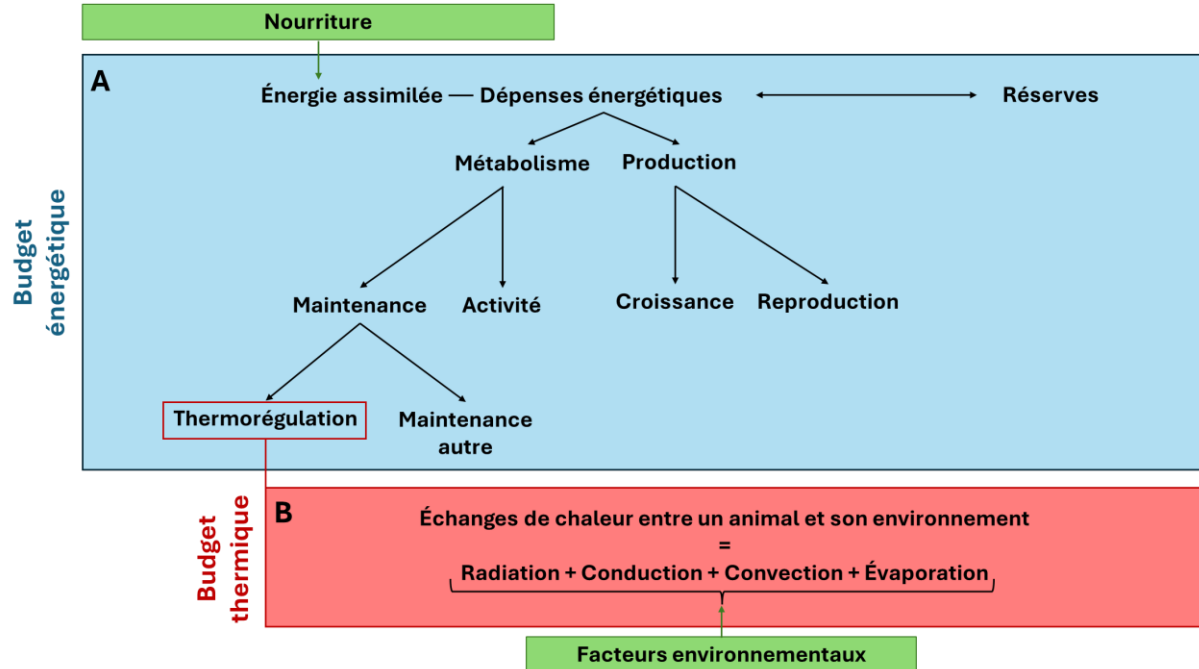


Figure 1. Schématisation des différentes composantes des budgets énergétiques et thermiques chez les endothermes. Schéma élaboré selon les définitions de Hudson & White (1985) et McNab (2002).

Plusieurs adaptations anatomiques, physiologiques et comportementales permettent aux individus de moduler les échanges de chaleur avec leur environnement et donc, d'équilibrer leur budget énergétique (Tattersall et al., 2012; Blix, 2016). La mue saisonnière, qui peut changer la couleur et la densité de la fourrure, est susceptible de modifier à la fois les pertes de chaleur par convection et les gains de chaleur par radiation (Hart, 1956; Walsberg, 1991; Zimova et al., 2018). Les adaptations physiologiques comprennent les changements du taux métabolique ou encore les modifications de la circulation périphérique afin de favoriser ou de limiter les pertes de chaleur (Heldmaier et al., 1990; McNab, 2002; Blix, 2016). Chez les mammifères exposés au froid, la production de chaleur par les cellules des tissus adipeux bruns et le frissonnement, c'est-à-dire la contraction asynchrone des muscles squelettiques, sont deux stratégies importantes pour maintenir la température corporelle (McNab, 2002; Cannon & Nedergaard, 2004). Les adaptations comportementales, quant à elles, varient considérablement selon l'environnement et l'espèce. Elles incluent notamment les modifications dans l'utilisation de l'espace ou le niveau d'activité (Hafez,

1964; Terrien et al., 2011; Mota-Rojas et al., 2021). Par exemple, le spermophile arctique (*Spermophilus parryi*) modifie son patron d'activité journalier en ajustant le temps passé dans son terrier selon les conditions météo et sa température corporelle (Long et al., 2005). L'utilisation d'un nid offre également une isolation qui favorise la conservation de la chaleur corporelle et réduit ainsi les dépenses énergétiques (Chappell, 1980b; Casey, 1981). L'adoption de certaines postures peut aussi prévenir l'hyper ou l'hypothermie en ajustant la dissipation de la chaleur corporelle (Bicca-Marques & Calegari-Marques, 1998; Dasilva, 1993; Terrien et al., 2011; Lopes & Bicca-Marques, 2017). L'exposition au soleil, ou « sun-basking » en anglais, est également une stratégie répandue chez plusieurs espèces de mammifères (Kelley et al., 2016; Coppola et al., 2019; Flôres et al., 2021) et d'oiseaux (Kennedy, 1969; Mueller, 1972; Cade, 1973). Elle permet d'augmenter la température corporelle par l'absorption de radiation solaire et ainsi diminuer les dépenses énergétiques liées à la thermorégulation (McNab, 2002; Warnecke et al., 2007). Ainsi, en réduisant la quantité d'énergie investie dans la thermorégulation, ces adaptations comportementales favorisent la survie dans des environnements thermiques contraignants (Terrien et al., 2011).

### **3. LES CONTRAINTES ET COMPROMIS ÉNERGÉTIQUES**

Un animal peut augmenter son apport alimentaire pour augmenter sa production de chaleur (Hafez, 1964; Terrien et al., 2011) ou encore pour répondre à des besoins énergétiques élevés autres que la thermorégulation. Par exemple, les femelles reproductrices peuvent augmenter leurs apports énergétiques pour compenser les coûts importants de la lactation (Gittleman & Thompson, 1988; Hamel & Côté, 2009). Toutefois, les animaux étant limités dans la quantité d'énergie qu'ils peuvent assimiler ou dépenser dans un intervalle de temps donné (Kirkwood, 1983; Weiner, 1992), ceux-ci doivent parfois faire des compromis entre différentes fonctions biologiques en raison de contraintes énergétiques (Stearns, 1992; Mathot & Dingemanse, 2015).

Parmi les compromis les plus étudiés, on retrouve ceux entre les coûts d'un événement de reproduction et les coûts de survie, de reproduction future, de croissance ou encore de maintien de la condition corporelle (Stearns, 1992). Par exemple, dans un contexte de ressources alimentaires limitées, les femelles cerfs de Virginie (*Odocoileus virginianus*) favorisent l'accumulation de réserves énergétiques afin d'augmenter leur survie à long terme plutôt que la croissance et la survie de leurs faons (Therrien et al., 2007). De même, plusieurs études suggèrent qu'un effort de reproduction soutenu chez les oiseaux peut entraîner une réduction de l'énergie investie dans la mue postnuptiale (Nilsson & Svensson, 1996; Echeverry-Galvis & Hau, 2013; Demers et al., 2023).

Des compromis peuvent également survenir lorsque les besoins en matière de thermorégulation sont élevés, puisque l'énergie utilisée pour la thermorégulation ne peut pas être investie pour combler d'autres besoins (Angilletta, 2009). Par exemple, les femelles campagnol des champs (*Microtus arvalis*) exposées à des températures élevées réduisent leur investissement dans la production de lait maternel, ce qui ralentit la croissance de leurs jeunes (Simons et al., 2011). La thermorégulation comportementale peut également interférer avec d'autres activités comme l'alimentation et la recherche de partenaire sexuel (Mason et al., 2017; Cunningham et al., 2021) ou encore le risque de prédation (Carr & Lima, 2012; Veldhuis et al., 2019), ce qui peut avoir des conséquences sur la survie des individus et la démographie de la population.

#### **4. LES EFFETS DES PRÉDATEURS SUR LE BUDGET ÉNERGÉTIQUE**

En plus des défis liés à la thermorégulation, le risque de prédation représente une forte pression de sélection chez de nombreux endothermes (Lima & Dill, 1990). La prédation influence entre autres la physiologie, la morphologie ainsi que les comportements des espèces proies (Lima, 1998b; Sheriff et al., 2009; Walters et al., 2017). En effet, les prédateurs, en plus de leurs effets létaux, peuvent également avoir des effets non létaux en altérant le comportement de leurs proies (Lima, 1998a; Creel & Christianson, 2008; Zanette



& Clinchy, 2019). Plusieurs adaptations comportementales permettant de limiter le risque de prédation sont possibles, telles que l'utilisation d'habitats refuges (Lagos et al., 1995; Creel et al., 2005; Sundell et al., 2012; Fardell et al., 2021) ou encore l'augmentation du niveau de vigilance (Laundré et al., 2001; Creel et al., 2017; Clermont et al., 2017).

Bien que ces stratégies anti-prédatrices peuvent augmenter la survie à court terme, elles représentent une contrainte importante dans le budget énergétique, soit en générant une dépense d'énergie supplémentaire ou en limitant l'acquisition de ressources. En effet, les comportements anti-prédateurs peuvent représenter un compromis qui réduit le temps passé à effectuer d'autres activités essentielles à l'équilibre du budget énergétique (Lima & Dill, 1990). De nombreuses études montrent par exemple qu'une augmentation du risque de prédation peut entraîner une diminution du temps d'alimentation des proies (Brown et al., 1988; Brown & Kotler, 2004; Verdolin, 2006). Quelques études ont également démontré que le risque de prédation peut limiter l'accès à des secteurs favorables à la thermorégulation (Yasué et al., 2003; Milling et al., 2017). À long terme, ces compromis peuvent entraîner des coûts reportés en modifiant la croissance des proies (Urban, 2007; Dmitriew, 2011), en limitant leur reproduction (Ylönen & Ronkainen, 1994; Sheriff et al., 2009; Creel et al., 2011) et en réduisant leur survie (McNamara & Houston, 1987; LaManna & Martin, 2016). Tout ceci peut avoir des répercussions sur la dynamique de leurs populations (Creel, 2018; Preisser et al., 2005).

## **5. LES CONTRAINTES ÉNERGÉTIQUES DANS LES ÉCOSYSTÈMES ARCTIQUES**

Les proies en milieux arctiques font face à de nombreuses contraintes simultanées, car le froid et la faible disponibilité des ressources s'ajoutent à la pression de prédation (Bliss, 2000; Blix, 2016). En effet, dans les environnements très nordiques, les coûts énergétiques associés à la thermorégulation sont particulièrement élevés et représentent une contrainte majeure au sein du budget énergétique (Heldmaier et al., 1990; McNab, 2002). Les compromis entre maintenir sa température corporelle, minimiser les risques de prédation et

optimiser la recherche de nourriture sont inévitables pour assurer la survie. Par exemple, une proie pourrait choisir de s'exposer à un plus grand risque de prédation pour remplir ses besoins en matière de thermorégulation. Ce compromis a été observé chez les carcajous (*Gulo gulo*) qui, malgré des risques accrus d'être tué par les loups, leurs congénères ou les humains lorsqu'ils sont à la surface de la neige, sélectionnent cet emplacement pour se reposer lorsque les conditions sont favorables à la thermorégulation (Glass, Breed, Liston, et al., 2021). Toutefois, contrairement au compromis entre le risque de prédation et l'acquisition de ressources alimentaires qui a largement été étudié (Brown & Kotler, 2004; Verdolin, 2006; Creel, 2018), les compromis entre la thermorégulation et le risque de prédation sont souvent négligés, en particulier chez les mammifères (mais voir Veldhuis et al., 2019).

Chez les espèces de petite taille, maintenir l'équilibre thermique et énergétique est particulièrement exigeant en raison de leur rapport surface-volume élevé qui favorise les pertes de chaleur (McNab, 1980; Norris & Kunz, 2012). De plus, leur petite taille limite la quantité de réserves que les individus peuvent accumuler et l'épaisseur de la couche de fourrure qu'ils peuvent produire et transporter (Blix, 2016).

## **6. MODÈLE D'ÉTUDE**

Je me suis intéressée aux contraintes des petits mammifères vivant en milieux froids et aux compromis qui en découlent, en utilisant le lemming variable (*Dicrostonyx groenlandicus*) comme modèle. Résidant à l'année dans le Haut-Arctique et possédant la répartition la plus nordique parmi les petits mammifères (Jarrel & Fredga, 1993; Gotthardt & McClory, 2006), cette espèce clé de la toundra (Krebs et al., 2003; Gauthier et al., 2004; Ims & Fuglei, 2005) est particulièrement confrontée aux défis liés au risque de prédation et à la thermorégulation.

Comme quelques autres espèces de petits mammifères, les populations de lemming variable présentent des cycles d'abondance (Oksanen et al., 2008; Krebs, 2011) qui

influencent la dynamique des écosystèmes arctiques. En effet, les fluctuations de densité de lemmings engendrent des réponses numériques (changement d'abondance) et fonctionnelles (consommation de proies alternatives) des prédateurs de la toundra tels que le renard arctique (*Vulpes lagopus*), l'hermine (*Mustela erminea*), le harfang des neiges (*Bubo scandiacus*), le labbe à longue queue (*Stercorarius longicaudus*), le goéland bourgmestre (*Larus hyperboreus*), voire le loup arctique (*Canis lupus arctos*) (Batzli et al., 1980; Gilg et al., 2006; Therrien et al., 2014). Les cycles d'abondance des lemmings peuvent ainsi influencer indirectement le recrutement d'autres espèces qui partagent les mêmes prédateurs, comme des passereaux, des limicoles ou des oies (Bêty et al., 2002; McKinnon et al., 2014).

Les lemmings variables traversent les longs hivers du désert polaire, qui durent 8 à 10 mois (Bliss, 2000), en demeurant actifs dans le manteau neigeux qui les protège en partie du froid et des prédateurs (Pauli et al., 2013; Berteaux et al., 2017). Cette espèce de lemmings est particulièrement bien adaptée à la vie sous-nivale, grâce à diverses adaptations morphologiques saisonnières telles que la croissance d'un pelage hivernal blanc de qualité isolante accrue (Reynolds, 1993) et d'une griffe modifiée lui permettant de creuser dans la neige et la glace (Brooks, 1970; Fuller et al., 1975; Kays & Wilson, 2009). Le manteau neigeux arctique est généralement composé de deux couches principales: la couche de neige durcie par le vent (« wind slab ») recouvrant une couche de neige plus friable appelée givre de profondeur (« depth hoar ») (Domine et al., 2018; Benson & Sturm, 1993; Domine et al., 2012; Sturm et al., 1995). Les lemmings se déplacent à travers la couche de givre de profondeur qui facilite les mouvements par sa plus faible densité (Poirier et al., 2019). Les conditions météorologiques hivernales, notamment les propriétés du couvert neigeux, influencent grandement la dynamique des populations de lemmings (Batzli et al., 1980; Reid & Krebs, 1996). En effet, une couche de neige épaisse de faible densité facilite l'accès à la nourriture, augmente la survie et permet la reproduction hivernale (MacLean et al., 1974; Korslund & Steen, 2006; Duchesne et al., 2011; Reid et al., 2012). Un succès reproducteur hivernal élevé serait d'ailleurs requis pour engendrer les phases d'augmentation du cycle de population (Millar, 2001; Ims et al., 2011; Bilodeau et al., 2013b; Fauteux et al., 2015).

## 7. SITE D'ÉTUDE

Mon site d'étude se situe sur le territoire de la Station des Forces canadiennes (SFC) Alert dans le Haut-Arctique canadien, au Nunavut ( $82^{\circ}30'05''$  N,  $62^{\circ}20'20''$  W), et est situé à 817 km du pôle Nord géographique (Fig. 2). La faune habitant ce territoire doit survivre dans un climat froid et sec typique du désert polaire. Annuellement, Alert reçoit en moyenne 17,4 mm de pluie et 184 cm de neige, avec une température pouvant descendre jusqu'à  $-40^{\circ}\text{C}$  en hiver (Environment and Climate Change Canada, 2013; Government of Canada, 2019). La courte période sans gel (28 jours) (Government of Canada, 2019) et une courte saison de croissance de 60 à 80 jours (Bliss, 2000) caractérisent aussi le site. La population de lemmings variable d'Alert fluctue en abondance (Julien et al., 2014), et les années 2019 et 2023 ont été des années typiques de forte abondance (D. Berteaux, données non publiées).

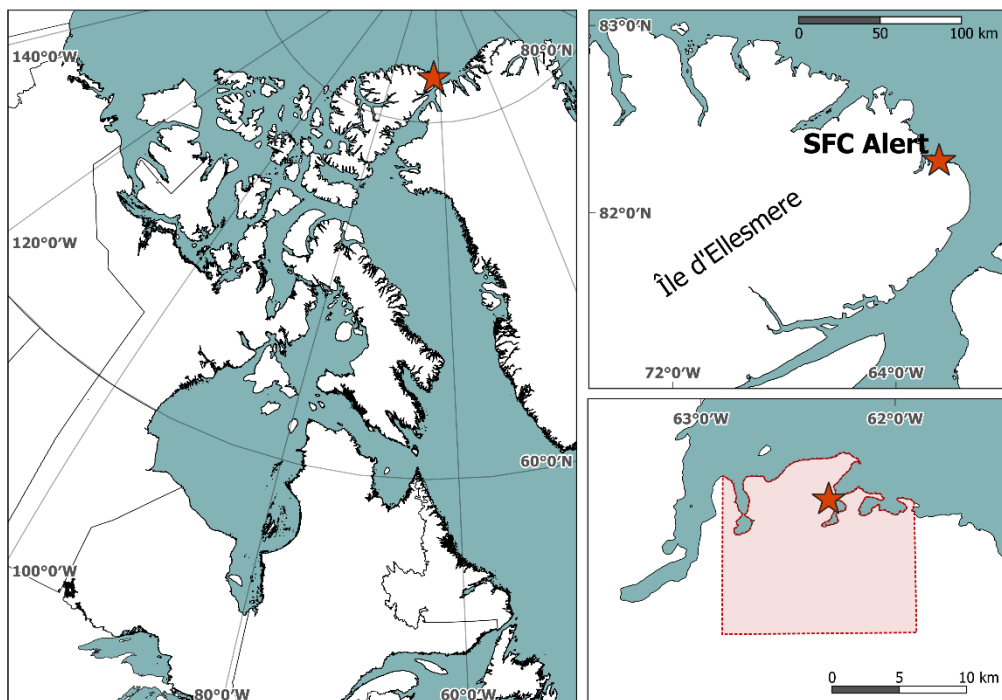


Figure 2. Localisation du site d'étude d'Alert (Nunavut, Canada). L'étoile montre la localisation de la Station des Forces canadiennes Alert et le polygone rouge montre la zone d'étude, soit la propriété du ministère de la Défense nationale où j'ai recueilli mes données.

## 8. OBJECTIF GÉNÉRAL

Étant donné l'effet protecteur du couvert neigeux contre de nombreux prédateurs, on pourrait croire que les lemmings auraient avantage à rester cachés sous la neige aussi longtemps que possible. Pourtant, des observations réalisées à différents sites, notamment à Barrow en Alaska (Rausch, 1950; Thompson, 1955; Batzli et al., 1980), à l'île Wrangel en Russie (Ehrich et al., 2020) et à Alert au Canada (D. Berteaux, données non publiées), montrent que les lemmings bruns (*Lemmus trimucronatus*) et les lemmings variables peuvent effectuer des sorties à la surface du couvert de neige au printemps alors que celui-ci est encore intact. Au moment de ces sorties, les lemmings variables ont déjà subi leur mue printanière et portent donc leur fourrure brune d'été (D. Berteaux, données non publiées) (Fig. 3). Cette activité à la surface est donc particulièrement surprenante étant donné l'apparence contrastée des lemmings sur le manteau neigeux, qui les rend facilement détectables par les prédateurs. Puisque l'écologie des lemmings est difficile à étudier lorsqu'ils demeurent sous la neige, leur activité au-dessus de la neige constitue en outre une opportunité unique pour explorer les compromis comportementaux et les stratégies de survie adoptés par des proies dans des conditions environnementales extrêmes.



Figure 3. Lemmings variables observés à la surface de la neige à Alert en 2019. Crédits photos : François Vézina (gauche), Émilie Desjardins (droite).

## 9. OBJECTIF SPÉCIFIQUE, HYPOTHÈSES ET PRÉDICTIONS

L'objectif spécifique de mon étude est d'expliquer l'activité du lemming variable à la surface de la neige au printemps, malgré le risque de prédation. J'ai émis l'hypothèse que les lemmings réduisent les coûts énergétiques associés à la thermorégulation lorsqu'ils se trouvent à la surface de la neige (**H1**). J'ai d'abord prédit que l'activité des lemmings en surface est positivement liée à la température de l'air (**P1a**), mais négativement liée au couvert nuageux (**P1b**) et à la vitesse du vent (**P1c**). J'ai également prédit que les lemmings sortent sur la neige lorsque la température opérative, c'est-à-dire la température environnementale combinant l'effet des trois variables météorologiques mentionnées précédemment, soit la température de l'air, le vent et la radiation solaire (Gagge, 1940; Bakken et al., 1985), est plus élevée à la surface de la neige qu'au niveau du sol (**P1d**). De plus, j'ai prédit qu'une fois au-dessus de la neige, les lemmings adoptent des comportements favorisant les transferts de chaleur positifs entre l'environnement et leur corps. Plus précisément, la proportion de temps passé immobile devrait être positivement liée au couvert nuageux (**P1e**), et les lemmings devraient privilégier une orientation du corps perpendiculaire aux rayons du soleil (**P1f**). Une hypothèse recoupant partiellement H1 est que les lemmings sortent à la surface de la neige pour éviter les conditions humides dans l'environnement sous-nival durant la fonte des neiges (**H2**), puisque ces conditions augmentent à la fois les risques de noyade (Rausch, 1950; Brooks, 1970; Jacob, 2003) et les pertes de chaleur (Webb & King, 1984). Par conséquent, j'ai prédit que l'activité des lemmings sur la neige coïnciderait avec l'accumulation printanière d'eau de fonte dans le manteau neigeux et au niveau du sol (**P2**).

Pour répondre à ma première hypothèse, j'ai quantifié l'activité des lemmings en suivant, à l'aide de caméras à déclenchement automatique, leurs sorties au-dessus de la neige aux entrées de 10 tunnels en 2019 et de 28 tunnels en 2023. Ces suivis ont été réalisés en mai et juin, avant la fonte de la neige, mais quand le jour est continu. J'ai également utilisé les données des stations météo d'Alert ainsi que celles fournies par des modèles taxidermiques permettant de mesurer la température opérative sur et sous la neige. Pour tester ma seconde hypothèse, j'ai réalisé des profils de neige afin de suivre l'évolution du manteau neigeux

durant toute la période de suivi des lemmings. Ces données m'ont permis d'expliquer les mécanismes comportementaux sous-jacents aux sorties apparemment risquées des lemmings à la surface de la neige, ainsi que les compromis énergétiques et écologiques qui en découlent.

# CHAPITRE 1

## LA FIÈVRE DU PRINTEMPS: LES LEMMINGS VARIABLES SE RÉCHAUFFENT AU-DESSUS DE LA NEIGE MALGRÉ LE RISQUE DE PRÉDATION

### 1.1 RÉSUMÉ EN FRANÇAIS DU PREMIER ARTICLE

Les petits mammifères vivant dans des climats froids sont confrontés à d'importantes pertes de chaleur et donc, à de fortes demandes énergétiques liées à la régulation de leur température corporelle. Cependant, des adaptations comportementales, telles que l'utilisation de l'espace sous-nival comme refuge contre les froids extrêmes, peuvent réduire le coût énergétique de la thermorégulation. À l'aide de caméras automatisées, nous avons suivi des lemmings variables (*Dicrostonyx groenlandicus*) à la limite septentrionale de leur aire de répartition, alors qu'ils sortaient à la surface de la neige au printemps, afin d'évaluer l'effet des variables météorologiques sur l'occurrence de ce comportement. Nous avons émis l'hypothèse que les lemmings, au printemps, bénéficient d'une réduction des coûts énergétiques liés à la thermorégulation lorsqu'ils sortent au-dessus de la neige. Tel qu'attendu, la fréquence de l'activité en surface augmente avec la température de l'air, mais diminue avec le couvert nuageux et la vitesse du vent. De plus, la température opérative à la surface était plus élevée que celle sous la neige, tandis que les profils de neige montraient l'absence d'eau liquide dans le manteau neigeux. Ces résultats soutiennent que l'activité des lemmings en surface au printemps est une stratégie de thermorégulation comportementale. Cependant, l'observation de plusieurs prédateurs dans la zone d'étude, combinée au comportement de vigilance observé chez les lemmings à la surface de la neige, souligne les risques associés à cette exposition sur la neige. Nous suggérons donc que les lemmings sont confrontés à un compromis entre thermorégulation et risque de prédation. Étant donné la rareté de données sur l'écologie hivernale des lemmings, nous avons également exploité ce comportement pour recueillir des informations précieuses sur la phénologie de la mue et la reproduction. Globalement, nos résultats permettent de mieux comprendre le compromis complexe entre la thermorégulation et le risque de prédation chez les petits mammifères vivant dans des climats froids, et mettent en évidence certaines implications potentielles pour la dynamique des écosystèmes arctiques basée sur les interactions prédateur-proie.

Cet article intitulé « *Spring fever: collared lemmings warm up above the snow despite predation risk* » sera soumis pour publication dans la revue scientifique « *Frontiers in Ecology and Evolution* ». En tant que première autrice, j'ai participé à l'élaboration de l'idée



originale et des hypothèses ainsi qu'à la récolte d'une partie des données. J'ai également bâti la base de données, réalisé les analyses et fait l'interprétation des résultats. Le présent article a été rédigé par moi-même, en collaboration avec le professeur Dominique Berteaux. Les auteurs ont contribué à l'idée originale et aux hypothèses (Dominique Berteaux) ainsi qu'à la récolte des données (Dominique Berteaux, Émilie Desjardins). Tous les auteurs ont participé au soutien logistique et à la révision du manuscrit.

## 1.2 SPRING FEVER: COLLARED LEMMINGS WARM UP ABOVE THE SNOW DESPITE PREDATION RISK

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## 1.3 ABSTRACT

Small mammals inhabiting cold climates face high heat losses and thus, high energy demands for body temperature regulation. However, behavioral adaptations, such as seeking refuge from extreme cold in the subnivean space, can reduce the energetic cost of thermoregulation. Using automated cameras, we monitored collared lemmings (*Dicrostonyx groenlandicus*) at the northern limit of their range, as they surfaced from their snow burrows in spring, to assess the effect of weather variables on the occurrence of this behavior. We hypothesized that lemmings reduce the energetic cost of thermoregulation when they come to the surface of the snow in spring. As expected, the frequency of surface activity increased with air temperature, but decreased with cloud cover and wind speed. In addition, the operative temperature was higher above the snow than below, while snow profiles showed the absence of liquid water in the snowpack. These findings support that lemming surface activity in spring is a behavioral thermoregulation strategy. However, observations of several predators in the study area, combined with vigilance behavior observed in lemmings at the snow surface, stress the risks associated with such exposure on the snow. We therefore suggest that lemmings face a trade-off between thermoregulation and predation risk. Given that data on lemming winter ecology are scarce, we also exploited this behavior to gather

valuable knowledge on molting phenology and breeding. Overall, our results provide insight into the complex trade-off between thermoregulation and predation risk in small mammals inhabiting cold climates, and highlight some potential implications for arctic ecosystem dynamics based on predator-prey interactions.

#### 1.4 INTRODUCTION

Regulating body temperature is essential to all endothermic animals. Such regulation requires energy for heat production or dissipation (McNab, 2002), but the energetic cost of thermoregulation can be reduced through behavioral adaptations (Terrien et al., 2011). For example, heat or cold-stressed animals can adjust their exposure to solar radiation by using thermal refuges or by sun-basking (Bicca-Marques & Calegario-Marques, 1998; Long et al., 2005; Warnecke et al., 2007). Thermal refuges can indeed offer very different operative temperatures, that is the fine-scale environmental temperature combining the effects of wind, radiation and air temperature (Gagge, 1940; Bakken et al., 1985), than the surrounding. Sun-basking is widespread in most taxonomic groups, including birds (Kennedy, 1969; Mueller, 1972) and mammals (e.g. Kelley et al., 2016; Coppola et al., 2019; Flôres et al., 2021), with some species even using body orientation to modulate heat gain from sun radiation (Maloney et al., 2005; Brown & Downs, 2007). Given the limited energy resources available to animals in the wild (Kirkwood, 1983; Weiner, 1992), minimizing the energetic costs of thermoregulation enables them to allocate more energy towards other essential biological functions such as foraging, growth, and reproduction (Stearns, 1992; Mathot & Dingemanse, 2015).

However, sunbathing in open areas may increase predation risk. For example, wolverines (*Gulo gulo*) trade the protection of the subnivean space against potential killing attempts by wolves (*Canis lupus*), conspecifics, and humans to rest on snow surfaces when weather facilitates thermoregulation (Glass et al., 2021). Conversely, during the snow season, pygmy rabbits (*Brachylagus idahoensis*) prioritize the protection offered by concealed

resting sites over the thermoregulatory benefits offered by open areas (Milling et al., 2017). Whereas the costs of predator avoidance on reproduction or foraging have been extensively studied in endotherms (Brown & Kotler, 2004; Verdolin, 2006; Creel, 2018), the thermoregulatory costs have been more often overlooked, especially in mammals (but see Veldhuis et al., 2019).

Thermoregulation is a major part of the daily energy expenditure of all endotherms (McNab, 2002), but due to their high surface-area-to-volume ratio, small mammals living in cold climates face unique challenges to maintain heat balance (Chappell, 1980a; Norris & Kunz, 2012). Collared lemmings (*Dicrostonyx groenlandicus*) exemplify this heat balance challenge, as they have the northernmost geographic distribution of all small mammals (Gotthardt & McClory, 2006; Jarrel & Fredga, 1993) and can be found in High Arctic polar deserts, where air temperature regularly reaches  $-40$  °C. They remain active year-round, and move, forage, build nests, and even breed during the harsh Arctic winters (MacLean et al., 1974; Stenseth & Ims, 1993a). Whereas snow cover provides protection against snow-surface predators like Arctic foxes (*Vulpes lagopus*) (Duchesne et al., 2011; Bilodeau et al., 2013a), lemmings also use subnivean burrows as thermal refuges (Berteaux et al., 2017; Pauli et al., 2013). Snow insulation generally protects them against the coldest air temperatures (Pomeroy & Brun, 2001; Reid et al., 2012), but, as spring progresses, the upper snow layers become warmer than the base layers, reversing the thermal gradient within the snowpack (Domine et al., 2016).

Snow properties, such as depth and density, play an important role in lemming survival and winter breeding success (Korslund & Steen, 2006; Duchesne et al., 2011; Reid et al., 2012), and thus in lemming abundance cycles (Millar, 2001; Bilodeau et al., 2013a; Fauteux et al., 2015). The Arctic snowpack typically consists of two main layers: a hard, wind-shaped layer overlaying a soft, friable layer at the base known as the depth hoar (Domine et al., 2002). Collared lemmings dig tunnels in the upper part of the depth hoar (Poirier et al., 2019), benefiting from remarkable adaptations to the subnivean life. This includes seasonal morphological changes such as a pre-winter molt into white fur which improves insulation

and camouflage (Hansen, 1959; Reynolds, 1993), and the development of oversized fore claws which facilitate digging into the snow (Fuller et al., 1975; Kays & Wilson, 2009).

As the snow offers a protective cover against predators, it would be expected that lemmings stay under the snow as long as they can, especially when they have turned brown after their spring molt. Yet, observations throughout the circumpolar North, including Barrow in Alaska (Batzli et al., 1980), Wrangel island in Russia (Ehrich et al., 2020; I. E. Menyushina, pers. comm.), and Alert in Canada (D. Berteaux, unpublished data) show that collared lemmings do surface while the snow cover is still intact. This surface activity is surprising given that *Dicrostonyx* lemmings are exposed to many surface predators, such as the arctic fox and the long-tailed jaeger (*Stercorarius longicaudus*) (Batzli et al., 1980; Gilg, 2002), and have developed sophisticated adaptations to decrease predation risk, such as the use of underground latrines (Boonstra et al., 1996). Given the above, our general objective was to explain why *Dicrostonyx* lemmings surface from snow in May-June, when snow cover is still present but continuous light considerably increases predation risk. We hypothesized that lemmings incur thermoregulatory benefits when coming to the snow surface (**H1**). We first predicted that lemming activity at the surface is positively related to air temperature (**P1a**), but negatively related to cloud cover (**P1b**) and wind speed (**P1c**). A related prediction was that lemming surface activity occurs when operative temperature is higher at the snow surface than at ground level (**P1d**). In addition, we predicted that once above the snow, lemmings adopt behaviors promoting positive heat transfers from the environment. Specifically, the proportion of time spent stationary should decrease with the increase of cloud cover (**P1e**), and lemmings should prioritize a body orientation perpendicular to sunrays (**P1f**). A partially overlapping hypothesis to **H1** is that lemmings select snow surface to avoid wet conditions in the subnivean environment during snowmelt (**H2**), as these conditions increase both risks of drowning (Rausch, 1950; Brooks, 1970; Jacob, 2003) and negative energy transfers to the environment (Webb & King, 1984). Accordingly, we predicted that lemming surface activity would coincide with the accumulation of meltwater in the snowpack and at ground level (**P2**).

## 1.5 MATERIAL AND METHODS

### Study area

We worked from 13 May – 12 June 2019 and 27 May – 14 June 2023 at Canadian Forces Station (CFS) Alert in the Canadian High Arctic, Nunavut (82°30'05" N, 62°20'20" W) (Fig. 4). Alert is a polar desert (Callaghan, 2005) characterized by low annual precipitations averaging 156 mm, cold winter temperatures reaching –40°C, a short growing season (60-80 days), and 24-h direct sunlight from early April to early September (Desjardins et al., 2021). Collared lemmings exhibit strong fluctuations in abundance at Alert (Julien et al., 2014), and 2019 and 2023 were typical years of high abundance characterized by high trapping success (D. Berteaux, unpublished data).

### Lemming predators

We assessed the presence of lemming predators in our study area by recording observations of Glaucous Gulls (*Larus hyperboreus*), Long-tailed Jaegers, Snowy Owls (*Nyctea scandiaca*), Arctic foxes and Arctic wolves (*Canis lupus arctos*) while performing other research tasks. Such incidental observations are a good indicator of wildlife abundance when observation effort is sufficient and wildlife visibility is high, as commonly experienced in the tundra (Fauteux et al., 2018; Bolduc et al., 2023).

### Weather

The CFS Alert airfield weather station (82°31' N, 62°17' W) measured hourly air temperature, wind speed and cloud cover. When values were missing, we used hourly air temperature, hourly wind speed and morning and evening cloud cover data from the Alert Environment and Climate Change Canada (ECCC) weather station (82°30' N, 62°20' W). Station personnel assessed cloud cover visually (10% increments) and we grouped this variable into four categories, namely Clear (0%), Mainly clear (10%-40%), Partially clear (50%-90%) and Overcast (100%). We used cloud cover and binary day/night categories as

indicators of solar radiation. The ECCC weather station estimated snow depth (cm) daily by averaging measurements from three snow depth gauges. Both stations are located within 3 km of the study sites described below.

### **Operative temperature**

From 27 May to 13 June 2023, we measured operative temperature at the bottom of the snowpack and at the snow surface. To do so, we recorded the internal temperature of 10 lemming-shaped 3-D printed hollow plastic models covered with lemming fur collected at Alert during a previous project. Models precisely replicated the shape, size, color, and fur texture of a collared lemming to accurately estimate the operative temperature (Bakken & Angilletta, 2014). We placed these models on the snow surface, each 1.5 m away from a lemming snow burrow entrance, to sample locations used by lemmings. We oriented each model randomly with respect to cardinal directions. We recorded their internal temperature at 6-minute intervals with iButton loggers (Model DS1922L, Alphasense Inc., precision  $\pm 0.001^{\circ}\text{C}$ ) positioned in their center. We measured the operative temperature under the snow by installing 10 additional iButton loggers at ground level. IButtons were fixed at the base of a wooden stake and inserted in the snowpack. Because wind and sun radiation are absent under the snowpack, we did not place these loggers inside plastic models.

### **Lemming behavior**

We conducted a camera-based sampling of lemming behavior in 2019 and 2023 before the snow-free season. On 13 May 2019, after opportunistically observing many lemmings at the surface of the snow, we placed an infrared triggered camera (Hyperfire 2, Reconyx, Holmen, Wisconsin, USA) near each of 10 snow burrow entrances. Each camera was mounted with a Universal Camera Mount (Reconyx, Holmen, Wisconsin, USA) on a wooden stake driven into the snow approximately 1 m from the burrow entrance. We placed cameras about 50 cm above the snow surface and centered their  $37.7^{\circ}$  field of view on the burrow entrance. We programmed cameras to take, after each triggering, a sequence of five pictures

at 2 frames per second followed by a 10-second video (hereafter, a triggered sequence). There was no delay between triggered sequences. Cameras remained active until posts collapsed due to local snow melt from 9 to 12 June (median date = 10 June) (Fig. 7). All burrows were located on the plain adjacent to the CFS Alert airfield, referred to below as site 1 (Fig. 4).

From 27 May – 3 June 2023, we placed 28 cameras (same methods as above) near 28 lemming burrow entrances at three sites where lemming snow burrows were abundant. Specifically, we monitored 12 burrows at site 1, which had already been used in 2019, and 8 burrows each at sites 2 and 3 (Fig. 4). Cameras remained active until local snow melt, which occurred from 5 to 14 June (median date = 14 June) depending on burrow (see Table S1 in Suppl. Mat.).

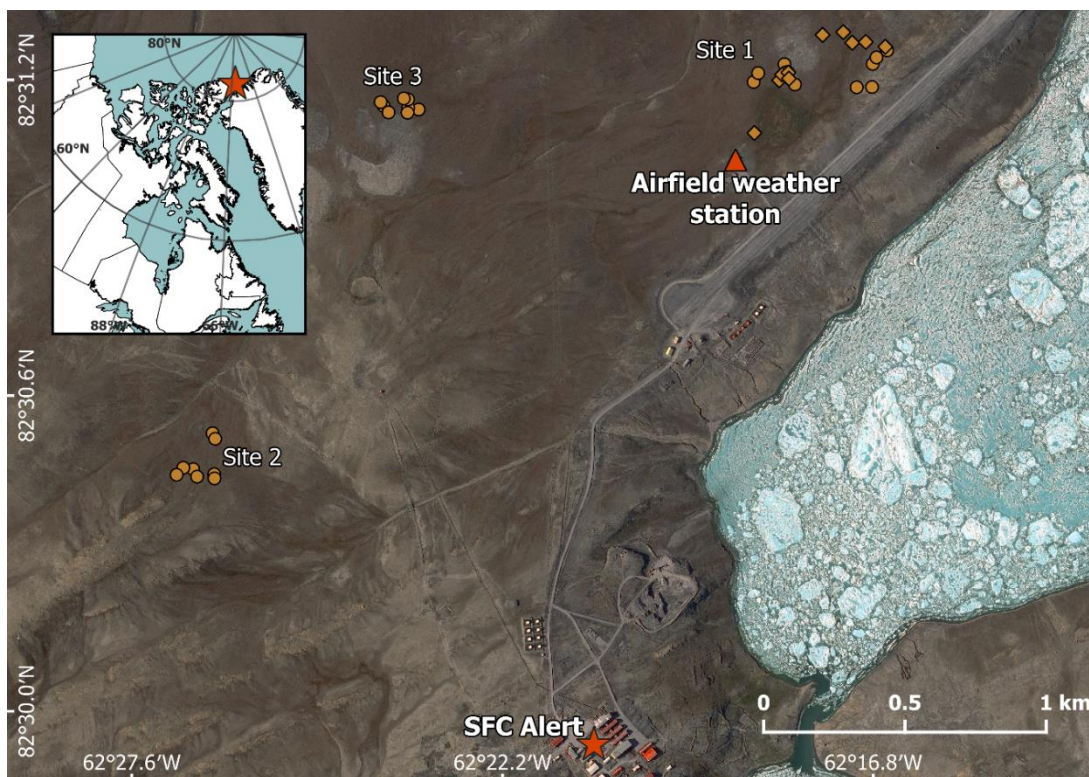


Figure 4. Location of the study area (insert) and locations of automated cameras (2019 – diamonds, 2023 – dots) at three sites near the Canadian Forces Station Alert in Nunavut, Canada. The satellite picture (WorldView-2/3) was taken on 15 July 2020. Red shapes show Canadian Forces Station Alert (star) and weather station (triangles) locations. Alert ECCC weather station is located just south of the CFS station and is, therefore, not visible on this map.



We calculated a lemming surface activity index (SAI), defined independently for each burrow and each 1-hour period of camera observation as:

$$SAI_{bh} = \sum_{t=1}^n L_t$$

Where:

$b$  is the considered burrow

$h$  is the considered 1-hour period of camera observation at burrow  $b$

$t$  is a triggered sequence within the 1-hour period of camera observation

$n$  is the total number of triggered sequences during the 1-h interval  $h$

$L_t$  is the number of lemmings observed in the  $t$ -th triggered sequence.

For example, a burrow would be assigned an index of 7 for a given 1-h period if we recorded 6 triggered sequences with 3 different lemmings observed in the first sequence, 0 in the second, and 1 in each of the remaining sequences. Several lemmings could appear on a given triggered sequence, and the same lemming could appear on many triggered sequences. Therefore, our lemming surface activity index reflects lemming activity at the snow surface around a given burrow during a given 1-hour period, rather than the number of individuals surfacing from the monitored burrow. We used the Timelapse2 software (Greenberg et al., 2019) to facilitate data extraction from pictures and videos. Since some cameras sometimes became inactive (e.g. when their supporting stake fell), we only considered burrows with an active camera when calculating an average hourly lemming surface activity index across burrows.

For each lemming observed in a triggered sequence, we assessed four individual-level variables, namely size (small, intermediate, adult), fur color (white, intermediate, brown), distance from burrow (at burrow entrance, close to burrow, far from burrow), and vigilance (not vigilant, vigilant, very vigilant) (Table 1 details category criteria for each variable). We sometimes observed feces and urine within 10-20 cm of the burrow entrance and rated such

latrines as absent (immaculate snow), small (snow surface covered by feces and urine < surface covered by an adult lemming) and large (surface covered > lemming size).

Table 1. Categories used to describe lemmings and their behavior when they surface from the snow at Alert, Nunavut, Canada. We assessed the vigilance index in 10-sec video recordings only when the lemming was visible for  $\geq 5$  sec.

Variable	Categories			
	0	1	2	Undetermined
<b>Size</b>	Size clearly inferior to adult size	Intermediate size	Adult size	---
<b>Fur color</b>	> 50% white	$\leq 50\%$ and > 5% white	$\leq 5\%$ white	Lemming partially hidden in burrow
<b>Maximal distance travelled from burrow</b>	Lemming visible but partially hidden in burrow	Lemming travelled < 1m from burrow entrance	Lemming travelled $\geq 1$ m from burrow entrance	Burrow not visible (rare)
<b>Vigilance index</b>	Not vigilant (head down)	Vigilant (head up or intermittent locomotion, no scan of surroundings)	Very vigilant (scans of surroundings)	Lemming visible during < 5 sec

We established activity budgets of lemmings observed above the snow using the 10-sec videos recorded in 2019. We extracted data from videos using the BORIS software (Friard & Gamba, 2016) and the behavioral classification of Table 2. We calculated activity budgets above the snow after excluding periods during the 10-sec videos when lemmings were invisible because they were in their burrow. During video recordings characterized by high solar radiation (assessed as a visible lemming shadow), we classified lemming orientation with respect to the sun according to Fig. 5.

Table 2. Behavioral classification of collared lemmings observed above the snow at Alert, Nunavut, Canada.

Category	Subcategory	Description
<b>Stationary</b>	Entirely visible	Lemming immobile outside burrow or relocates within 1 body length during video recording
	Partially visible	Lemming remains partially hidden in burrow
<b>Moving</b>	Walks or runs	Lemming walks or runs, continuously or intermittently. Relocates at > 1 body length during video recording
	Interacts	Lemming interacts with $\geq 1$ individual
	Other	Lemming digs, feeds, or performs other rare behavior
<b>Undetermined</b>	In burrow	Lemming under snow surface
	Outside field of view	Lemming outside burrow but out of field of view

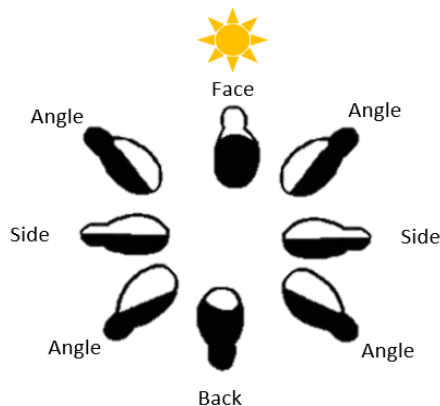


Figure 5. Classification of the orientation of a lemming with respect to the sun (adapted from Brown & Downs, 2007).

### Snow properties

From 29 May to 20 June 2023, we visited each site approximately every three days and dug 2 or 3 snow pits per site per visit, for a total of 34 snow pits (site 1: 9 pits, site 2: 17 pits, site 3: 8 pits). We produced a snow stratigraphy at each snow pit. Based on the size and shape of snow grains and the relative hardness of each snow layer, we differentiated depth hoar crystals from other types of snow crystals such as those from the wind slab, small rounded grains, faceting rounded crystals, melt-freeze polycrystals or crystals from the melt-freeze

crust (Pielmeier & Schneebeli, 2002; Fierz et al., 2009). We measured snow relative hardness every 10 cm from ground to snow surface using the De Quervain hand hardness test (Fierz et al., 2009). This allowed us to identify the main snow layers, evaluate the onset of snow melt, and observed the potential accumulation of water at ground level and in the snowpack. We also measured the total thickness of the snowpack and the thickness of the main layers.

## **Statistical analyses**

### ***Effect of weather on lemming surface activity***

We assessed the effects of environmental variables (air temperature, cloud cover, wind speed; **P1a-c**) on the lemming surface activity index after combining data from 2019 and 2023. We did so using a generalized additive mixed model (GAMM) from the *mgcv* package version 1.8-42 (Wood, 2017) with a log-link function and assumed Tweedie distribution. GAMMs are suitable when the relationship between explanatory and response variables is nonlinear, as observed here with temperature. We estimated the smoothing parameter for temperature using restricted maximum likelihood (REML). We chose a  $k$  basis dimension for temperature, following *gam.check* diagnostic information (Wood, 2017). We included burrow ID as a random factor (random intercept and slope) to control for unequal sample sizes between burrows. We also included a day/night binary variable alongside cloud cover as an indicator of solar radiation intensity, which varies with the sun's angle in the sky. This approach allowed us to account for some of the variations in solar radiation between cloudy days and clear nights. We considered 6:00 - 18:00 as day and 18:00 - 6:00 as night to reflect the daily variation in light intensity. We did not include in our final analysis the year of observation and the interaction between air temperature and wind speed, as their effects on model fit were not significant or negligible. We checked correlations between explanatory variables prior to model selection using a Pearson correlation matrix from the *GGally* package version 2.1.2 (Schloerke et al., 2021), and we assessed model assumptions visually. We used the Akaike Information Criterion (AIC) for model selection (Zuur et al., 2007).

### ***Operative temperature***

We compared mean operative temperature above and under the snowpack (**P1d**) using the nonparametric *Wilcoxon signed-rank test* from the *rstatix* package version 0.7.0 (Kassambara, 2021) because paired t-test assumptions were not met. As a complement to **P1b** and **P1d** testing, we also compared mean snow surface operative temperatures during daytime and nighttime using the same method.

### ***Effect of weather on lemming behavior above the snow***

We used a chi-squared test from *stats* package version 4.1.1 (R Core Team, 2021) to examine whether the observed distribution of stationary behavior duration in each category of cloud cover differed from random (**P1e**). We also used a chi-squared test to assess if lemmings, when stationary above the snow, selected a particular orientation with respect to the sun (**P1f**).

We performed all statistical analyses in R version 4.1.1 (R Core Team, 2021) and present summary statistics as mean  $\pm$  SD. Research techniques were approved by the Animal Care Committee of Université du Québec à Rimouski (permit # CPA-77-19-209) and the Government of Nunavut (Permit # WL 2018-020).

## **1.6 RESULTS**

### **Lemming predators**

Seven observers contributed to the predator observations during both 2019 and 2023 monitoring periods (13 May – 12 June 2019 and 27 May – 14 June 2023). The average daily observation effort for each observer was  $2.5 \pm 1.2$  hours in 2019 and  $2.6 \pm 1.0$  hours in 2023 (yielding a total of 407 and 250 hours of observations, respectively, across all observers). This allowed us to confirm the presence of most snow-surface predators in the study area during our lemming monitoring periods. These predators included the Glaucous Gull (first

observed on 14 May in 2019 and 23 May in 2023), Long-tailed Jaeger (28 May 2019, 1 June 2023), Snowy Owl (9 May 2019, observed only after the monitoring period in 2023), Arctic fox (26 May 2019, observed only after the monitoring period in 2023) and Arctic wolf (9 May 2019, 22 May 2023).

## **Weather**

Snow cover during the monitoring periods varied from 7 to 18 cm ( $14.9 \pm 2.4$  cm,  $n = 31$  days) in 2019 and from 30 to 50 cm ( $42.4 \pm 6.0$  cm,  $n = 19$  days) in 2023. (Fig. 6A, B). The start of snowmelt marked the end of our lemming monitoring periods on 12 June 2019 and 14 June 2023, but complete snowmelt took 5 days in 2019 and 14 days in 2023. Air temperature during our study periods varied from  $-14.9$  °C to  $7.7$  °C ( $-4.0 \pm 4.6$  °C) in 2019 and from  $-13.3$  °C to  $6.0$  °C ( $-2.3 \pm 3.3$  °C) in 2023, whereas wind speed ranged from 0 km/h to 55 km/h ( $10.2 \pm 10.5$  km/h) in 2019 and 0 km/h to 72 km/h ( $16.7 \pm 5.8$  km/h) in 2023 (Fig. 6A, B).

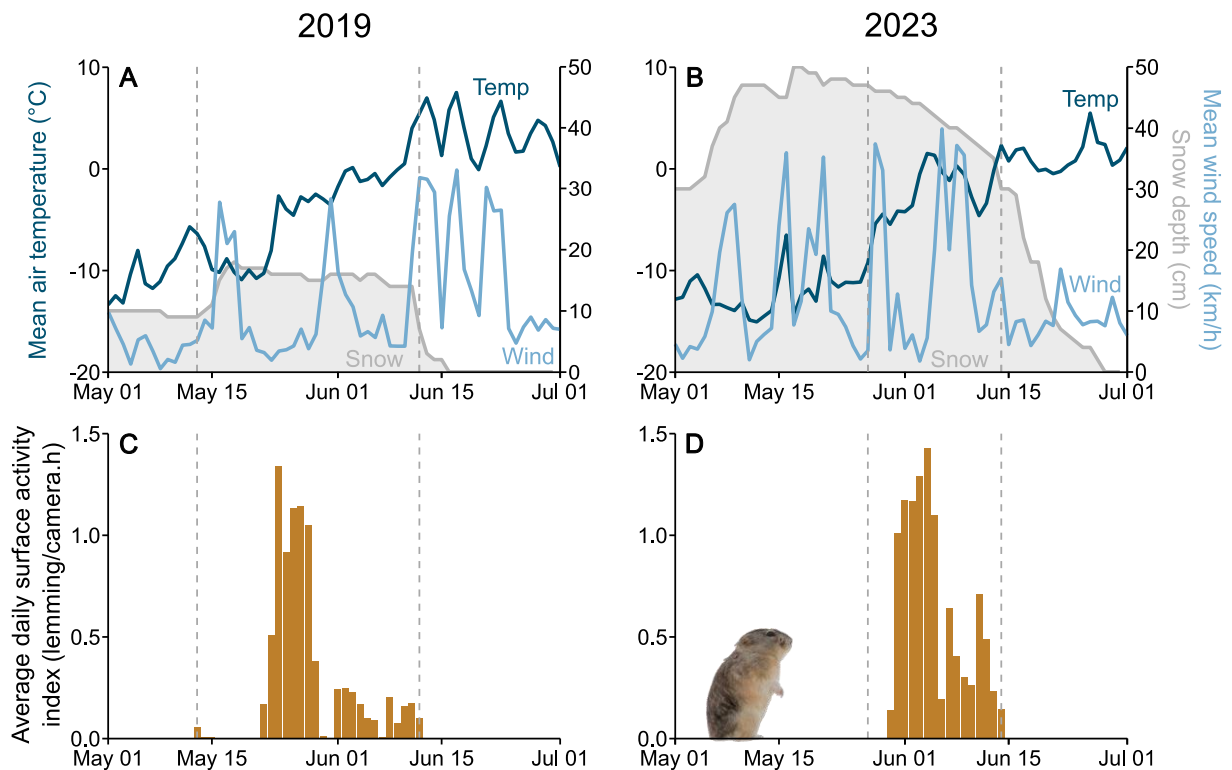


Figure 6. Daily mean ambient temperature, wind speed, and snow depth at Alert (Nunavut, Canada) from 1 May to 1 July 2019 (A) and 2023 (B). Average daily lemming surface activity index, i.e. total number of lemmings detected per day, divided by number of hours of camera activity, during monitoring periods in 2019 (C) and 2023 (D). Dashed vertical lines indicate when the camera monitoring of lemming activity above the snow started (13 May 2019 and 27 May 2023) and ended (12 June 2019 and 14 June 2023). One site was monitored in 2019 and 3 sites were monitored in 2023.

### Operative temperature

Operative temperature was clearly higher at the snow surface ( $6.1 \pm 3.9^\circ\text{C}$ , range  $-4.2 - 17.6^\circ\text{C}$ ) than at ground level ( $-5.4 \pm 2.6^\circ\text{C}$ , range  $-11.8 - 0.4^\circ\text{C}$ ) ( $n = 4096$ ;  $r = 0.87$ ;  $p < 0.001$ , Fig. 7), thus supporting **P1d**. It is noteworthy that 1) 95.3 % of mean operative temperatures measured at the snow surface were  $> 0^\circ\text{C}$ , compared to 1.1 % at ground level, 2) that operative temperature above the snow was subject to greater variations ( $21.8^\circ\text{C}$  difference;  $-4.2 - 17.6^\circ\text{C}$ ) than temperature at the base of the snowpack ( $12.2^\circ\text{C}$  difference;  $-11.8 - 0.4^\circ\text{C}$ ), and 3) that operative temperature above the snowpack was higher during the

day ( $8.0 \pm 3.8^\circ\text{C}$ , range  $-0.9 - 17.6^\circ\text{C}$ ) than during the night ( $4.2 \pm 3.0^\circ\text{C}$ , range  $-4.2 - 13.0^\circ\text{C}$ ) ( $n_{\text{(day/night)}} = 2056/2040$ ;  $r = 0.477$ ;  $p < 0.001$ ).

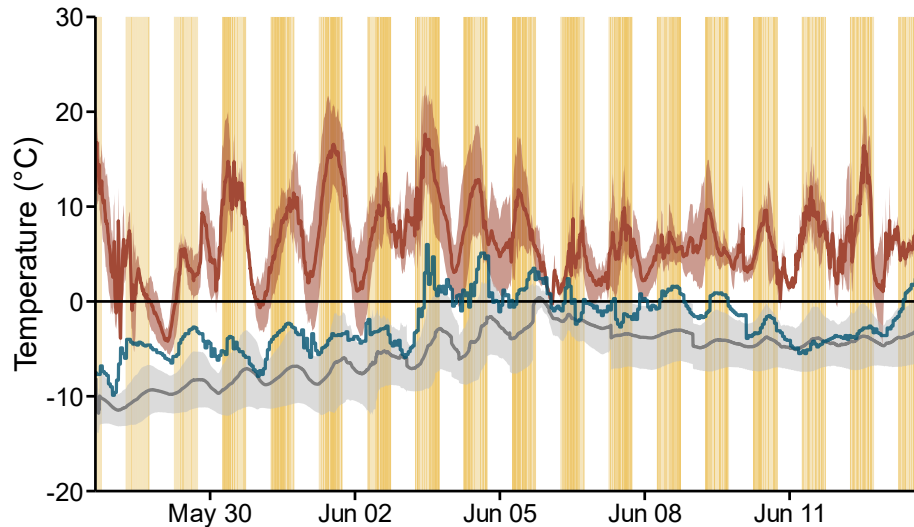


Figure 7. Mean operative temperature ( $\pm$  SD) recorded at the surface of the snowpack (dark red) and at ground level (grey) between 27 May and 13 June 2023 at site 1, Alert (Nunavut, Canada). Hourly air temperature from the weather stations appears in blue for reference, whereas yellow bands indicate daytime periods (from 6:00 to 18:00), when daily temperatures are highest although Alert receives 24-h direct sunlight in May and June.

### Lemming detection and observations

Our monitoring effort represented 294 camera-days in 2019 (10 burrows monitored over  $29.4 \pm 1.6$  days, range 31.0 – 27.9 days) and 332 camera-days in 2023 (28 burrows monitored over  $11.9 \pm 2.9$  days, range 5.8 – 17.4 days). This yielded 1,995 lemming observations in 2019 and 4,615 lemming observations in 2023 (2,020 and 4,845 triggered sequences, respectively). We did not detect any predator attacks on lemmings, although long-tailed jaegers ( $n = 8$ ), glaucous gull ( $n = 3$ ) and ermines ( $n = 2$ ) were observed in triggered sequences in 2023. During the 2019 monitoring period, lemming surface activity peaked between 23 and 29 May when 77.7% of all lemming observations occurred (Fig. 6C), while during the 2023 monitoring period, lemming surface activity peaked between 31 May and 5 June when 75.4 % of all lemming observations occurred (Fig. 6D). Most (86.8%) triggered sequences contained 1 lemming, but some contained 0 (9.1%), 2 (3.9%), 3 (0.2%) or even 4



(0.02%). Lemmings were usually of adult size (63.8%), but 8.5% had a size clearly inferior to that of adults and 27.6% had an intermediate size. A majority (67.9%) of observed lemmings wore their brown summer fur, but some (18.3%) showed white spots and 5.2% had over half of their body still covered by white winter fur. Fur color could not be assessed in 8.6% of cases. Latrines at the surface of the snow were observed at 33 of the 38 monitored burrows (26 burrows had a lot, and 7 a little urine and/or feces). Most observed lemmings (68.1%) stayed within 1 m of their burrow entrance.

### **Effect of weather on lemming surface activity**

Air temperature, cloud cover, daytime and wind speed all significantly influenced how many lemmings were observed at the snow surface, as shown by the best model explaining variations in lemming surface activity before snowmelt in 2019 and 2023 (deviance explained = 48.5%,  $R^2 = 0.21$ ,  $p < 0.001$  for all weather variables; see Table 3). Specifically, more lemmings surfaced from the snow with increasing temperatures (**P1a**), although this effect disappeared at temperatures  $> -4.4 \pm 0.7$  °C (Fig. 8A). Also as expected, lemming surface activity was positively affected by less cloudy skies (Fig. 8B) and daytime (Fig. 8D) (**P1b**). Regarding the effect of cloud cover, overcast conditions strongly restrained lemming surface activity but, once some direct solar radiation was available, the percentage of cloud cover seemed to have little to no effect. As expected, wind speed rather negatively affected lemming surface activity (**P1c**) (Fig. 8C).

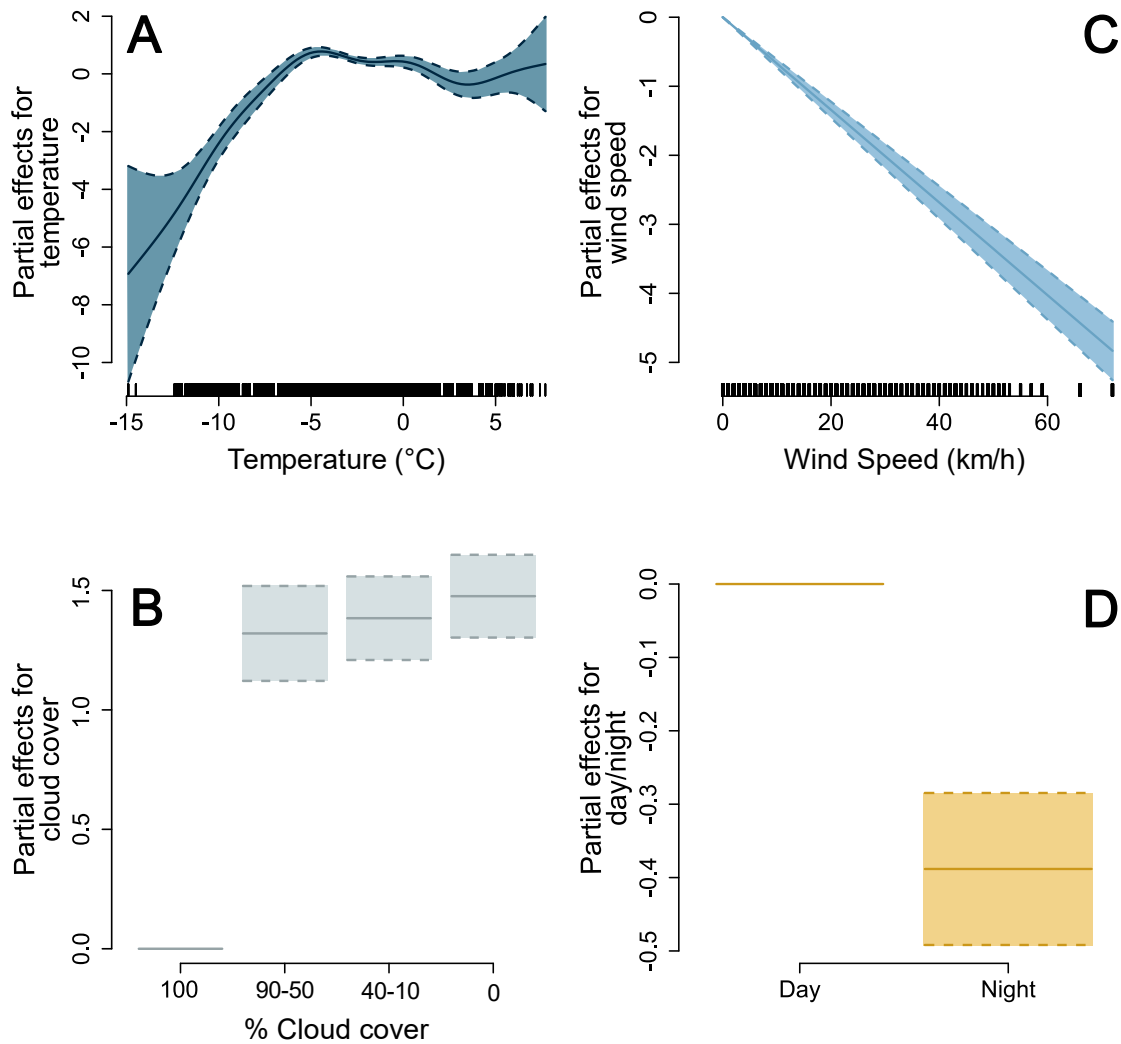


Figure 8. Partial effects of environmental (A: temperature, B: cloud cover, C: wind) and binary day/night (D) predictors of lemming activity above the snow in May – June 2019 and 2023. Effects generated from our best generalized additive model (see Table 3). In panels A and B, where partial effects of continuous variables are represented, dashed lines around shadowed areas represent 95% confidence intervals, whereas marks on the x-axis represent the distribution of observations.

Table 3. Significance of parametric coefficients and smoothing terms for the five best generalized additive models explaining variations in lemming surface activity before snowmelt in 2019 and 2023 at Alert, Nunavut Canada. Models included 3 environmental variables and one day/night binary variable as potential predictors of lemming surface activity.

Rank	Explanatory variables	Estimate	SE	T value	P	k (p)	edf	Ref.df	F	P	Deviance explained (%)	R <sup>2</sup>	AIC	df
1	(Intercept)	-2.956	0.282	-10.487	< 0.001	-	-	-	-	-	48.5	0.21	13367.11	76.76
	Wind.Sp	-0.067	0.003	-22.735	< 0.001	-	-	-	-	-				
	Cloud cover [50%; 90%]	1.320	0.099	13.285	< 0.001	-	-	-	-	-				
	Cloud cover [10%; 40%]	1.384	0.087	15.819	< 0.001	-	-	-	-	-				
	Cloud cover [0% ; 10%[	1.476	0.087	17.036	< 0.001	-	-	-	-	-				
	Circ_stateNight	-0.388	0.052	-7.499	< 0.001	-	-	-	-	-				
	S(Temperature)	-	-	-	-	9 (0.52)	6.788	7.607	35.295	< 0.001				
	S(Burrow)	-	-	-	-	38 (n.a.)	35.262	35.084	37.000	< 0.001				
S(Burrow, Temperature)	-	-	-	-	38 (n.a.)	24.780	25.841	37.000	0.02					
2	Intercept	-3.106	0.282	-11.001	< 0.001	-	-	-	-	-	48.0	0.19	13421.91	75.60
	Wind speed	-0.068	0.003	-22.719	< 0.001	-	-	-	-	-				
	Cloud cover [50%; 90%]	1.319	0.100	13.217	< 0.001	-	-	-	-	-				
	Cloud cover [10%; 40%]	1.329	0.088	15.181	< 0.001	-	-	-	-	-				
	Cloud cover [0% ; 10%[	1.419	0.087	16.364	< 0.001	-	-	-	-	-				
	S(Temperature)	-	-	-	-	9 (0.25)	6.545	7.409	35.729	< 0.001				
	S(Burrow)	-	-	-	-	38 (n.a.)	35.074	37.000	288.718	< 0.001				
	S(Burrow, Temperature)	-	-	-	-	38 (n.a.)	25.936	37.000	123.074	0.02				
3	(Intercept)	-2.590	0.270	-9.588	< 0.001	-	-	-	-	-	45.0	0.16	13703.08	68.22
	Wind.Sp	-0.070	0.003	-23.237	< 0.001	-	-	-	-	-				
	Cloud cover [50%; 90%]	1.557	0.100	15.534	< 0.001	-	-	-	-	-				
	Cloud cover [10%; 40%]	1.469	0.089	16.550	< 0.001	-	-	-	-	-				
	Cloud cover [0% ; 10%[	1.590	0.087	18.235	< 0.001	-	-	-	-	-				
	Circ_stateNight	-0.373	0.053	-7.098	< 0.001	-	-	-	-	-				
	S(Burrow)	-	-	-	-	38 (n.a.)	35.258	37.000	199.454	< 0.001				
	S(Burrow, Temperature)	-	-	-	-	38 (n.a.)	24.045	38.000	134.800	< 0.001				
4	(Intercept)	-1.872	0.276	-6.777	< 0.001	-	-	-	-	-	45.0	0.17	13716.52	75.09
	Wind.Sp	-0.075	0.003	-24.128	< 0.001	-	-	-	-	-				
	Circ_stateNight	-0.289	0.052	-5.550	< 0.001	-	-	-	-	-				
	S(Temperature)	-	-	-	-	9 (0.82)	7.364	8.076	40.938	< 0.001				
	S(Burrow)	-	-	-	-	38 (n.a.)	35.010	37.000	324.850	< 0.001				
	S(Burrow, Temperature)	-	-	-	-	38 (n.a.)	26.681	37.000	168.045	0.002				
5	(Intercept)	-2.009	0.276	-7.290	< 0.001	-	-	-	-	-	44.7%	0.17	13746.24	73.92
	Wind.Sp	-0.075	0.003	-24.130	< 0.001	-	-	-	-	-				
	S(Temperature)	-	-	-	-	9 (0.14)	7.225	7.975	41.389	< 0.001				
	S(Burrow)	-	-	-	-	38 (n.a.)	35.008	37.000	322.716	< 0.001				
	S(Burrow, Temperature)	-	-	-	-	38 (n.a.)	26.630	37.000	174.242	0.002				

## Effect of weather on lemming behavior above the snow

Using 1,722 videos collected in 2019 and containing at least one lemming (for a total of 4.78 hours of recording), we found that lemmings were stationary during 65 % of the time spent above the snow (entirely visible: 48 %, partially visible: 17 %). Lemmings were moving 15 % of the time while social interactions (2%) and other behaviors (1%) were rare. The remaining 17% of the time corresponds to lemmings being out of the field of view of the camera. In the 1,354 recordings where lemmings were visible for  $\geq 5$  seconds, signs of vigilance were detected in 94.5 % of triggered sequences (vigilant: 70.6%, very vigilant: 23.9%). An absence of lemming vigilance characterized only 1.4% of triggered sequences (vigilance level was undetermined in 4.1 % of sequences).

There was weak evidence that the occurrence of lemming stationary behavior was associated with cloud cover when individuals were entirely visible ( $P = 0.07$ ;  $X^2 = 6.96$ ;  $df = 3$ ; mean difference between observed and expected total durations =  $31.4 \pm 38.1$  sec), and no evidence that the occurrence of lemming stationary behavior was associated with cloud cover when individuals were partially visible ( $P = 0.64$ ;  $X^2 = 1.69$ ;  $df = 3$ ; mean difference between observed and expected total durations =  $22.7 \pm 8.9$  sec), thus mostly contradicting **P1e**. Similarly, stationary lemmings did not select a specific body orientation with respect to the direction of sunrays ( $P = 0.13$ ;  $X^2 = 5.65$ ;  $df = 3$ ), contradicting **P1f**.

## Snow properties

In the 35 snow pits dug in 2023, we found no liquid water or melt-freeze ice crust in the snowpack or at the ground surface, which contradicts **P2**. Even if the thickness of the snowpack varied locally (range 19.0 – 85.0 cm, mean  $43.0 \pm 18.7$  cm), we observed a general structure of the snowpack with two main layers. The bottom layer consisted of the depth hoar (soft, low-density snow composed of large snow grains) whereas the top layer consisted of a harder, denser snow often composed of smaller and more rounded grains (Fig. 9). Mean depth hoar thickness was  $7.3 \pm 3.8$  cm (range 0.0 – 15.0 cm). The first observation of melt-freeze

polycrystals and ice in the snowpack occurred on 14 June (9 days after the end of the peak surface activity period), which marked the end of the lemming monitoring period.

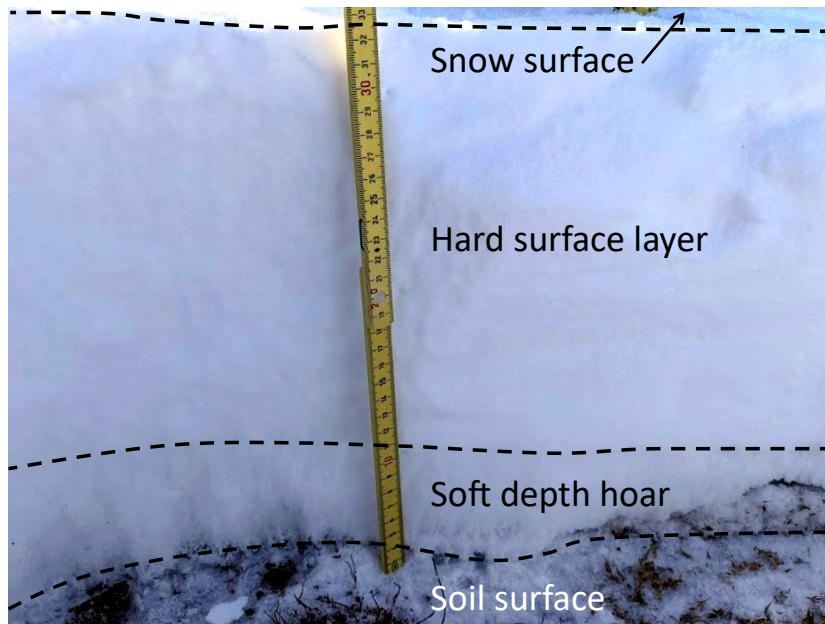


Figure 9. General stratigraphy of the snowpack in Alert in May and June 2023, before snowmelt. The structure shows two main layers: a thick hard surface layer made of small compact rounded grains on top and, at the bottom, a thinner, soft depth hoar made of large and loosely bounded grains of snow.

## 1.7 DISCUSSION

Collared lemmings in the Canadian High Arctic were observed spending time above the snow during spring, when their fur had turned brown, daylight was continuous, and multiple surface predators were active. The likelihood of this behavior increased with air temperature and daytime, yet decreased with cloud cover and wind speed. Higher operative temperatures were recorded at the snow surface compared to ground level during this period of surface activity, with no liquid water present in or below the snowpack. These findings support our hypothesis that lemmings surface in spring primarily for thermoregulatory purposes, despite the associated predation risks. Conversely, the data do not support the hypothesis that lemmings surface to disperse before the onset of snowmelt, as most of them

stayed in close vicinity of their burrow entrance, or to escape wet conditions below the snow surface. We further discuss the intricate aspects of thermoregulation observed, with emphasis on the many potential trade-offs between thermoregulation and predation risk, with some consideration of foraging behavior.

### **Thermoregulatory strategies of small mammals in cold, sunny, and risky environments**

We anticipated a positive effect of air temperature above the snow on lemming surface activity (**P1a**), as higher temperatures should reduce the thermal gradient between the environment and the lemming's body, thereby decreasing heat loss (Birkebak, 1966; Gates, 1980; Tattersall et al., 2012). Similar correlations between air temperature and time spent outside the burrow, along with a positive impact on body temperature, have been observed in Arctic ground squirrels (Long et al., 2005). Conversely, in cooler conditions, lemmings expend more energy and allocate more time to foraging (Maier & Feist, 1991). However, lemming activity plateaued when temperatures reached approximately  $-4^{\circ}\text{C}$ . This stabilization could be explained by two non-mutually exclusive hypotheses. First, under the surface activity constraint hypothesis, every lemming might have been surfacing at  $-4^{\circ}\text{C}$ , with daily time spent above the snow possibly maxing out due to competing demands such as foraging and sleep, leaving no room for the average surface activity index to increase further beyond  $-4^{\circ}\text{C}$ . Second, the predation risk hypothesis suggests that despite warmer temperatures, the arrival of new migratory predators, such as long-tailed jaegers (noted in 2019 and 2023, see Fig. S1, S2), could have offset the benefits of thermoregulation, thus halting any further increase in surface activity beyond  $-4^{\circ}\text{C}$  due to an unfavorable balance between thermoregulatory benefits and predation risks.

Solar radiation significantly contributes to the thermal energy budget of lemmings by enhancing heat gains (Chappell, 1980b; Norris & Kunz, 2012). Maximizing daytime activity outside the snow is beneficial for lemming thermoregulation, as solar radiation peaks when the sun is highest. However, cloud cover can reduce the body temperature gains achieved during basking (Warnecke et al., 2007; Terrien et al., 2011), though lemmings still benefit

from surfacing whenever some solar radiation penetrates the clouds (**P1b**). Both temperature and solar radiation are critical factors influencing the activity patterns of many rodent species across arctic and other habitats (Walsberg, 1988; Vispo & Bakken, 1993; Ellison et al., 1994; Eifler & Slade, 1998; Bozinovic et al., 2000; Long et al., 2005). Wind, on the other hand (**P1c**), increases convective heat loss and thus the energetic cost of thermoregulation (Chappell, 1980b). It may also impair lemmings' ability to detect predators as windy conditions can affect prey's olfactory, visual or auditive detection (Cherry & Barton, 2017). While solar radiation and wind speed interact, impacting radiative heat gain as wind speed increases (Chappell, 1980b), we were unable to include this interaction in our analysis due to our indirect assessment of radiation via cloud cover and day/night categories. Our measures of operative temperatures at the snow surface (**P1d**), however, served a similar function and further supported our general hypothesis that lemming surface activity promoted thermoregulatory benefits. Other explanatory variables, such as precipitations and visibility, could also enhance our understanding of lemming behavior, as snowfall likely hinders heat gains at the surface of the snow, and low visibility impairs predator detection. However, the temporal resolution of the precipitation and visibility data from the weather stations was insufficient for inclusion in our model and contained numerous missing values. Humidity inside and outside the burrows could also be a valuable variable for future research, as moisture decreases the insulating effectiveness of fur (Moen & Gilbert, 1973), which might also drive lemming surface activity for thermoregulatory purposes.

Collared lemmings use well-drained elevated areas in summer and lower habitat with deeper snow accumulation and higher plant density in winter (Batzli et al., 1980; Stenseth & Ims, 1993b). Lemmings must proceed to this seasonal shift of habitat before low habitats are flooded by heavy snowmelt in early summer (Batzli et al., 1980). However, during our monitoring period, which ended with the onset of snowmelt, lemmings at the snow surface were mostly stationary near their burrow entrance (**P1e**). Although surfacing above the snow might allow them to gather valuable pre-dispersal information, the lack of active dispersal and rare occurrences of other behaviors on the snow suggests that surface activity at this time

serves as an energy saving mechanism. Lemmings on the snow were likely sun-basking to decrease the energetic demands of thermoregulation through passive heating via solar radiation (Terrien et al., 2011). Supporting this interpretation, Chappell (1980b) found using heated metal casts that lemmings concealed within their subnivean burrows faced higher thermoregulation costs compared to those exposed to sunlight. Surprisingly, however, lemmings did not orient their bodies perpendicular to the sunrays (**P1f**), as would be expected for maximizing energy absorption from solar radiation. Such orientation is known to maximize body surface exposure to sunlight, increasing solar heat gain, and has been observed in other species (Berry, 1984; Maloney et al., 2005; Brown & Downs, 2007; Hetem et al., 2011; Norris & Kunz, 2012).

This paradox leads to four non-mutually exclusive hypotheses. First, the posture hypothesis suggests that lemmings might use body posture to reduce thermoregulation costs once out on the snow. For example, Wyoming ground squirrels (*Urocitellus elegans*) do not adjust their solar orientation but use posture as a behavioral thermoregulation strategy (Byman, 1985). We observed various postures in stationary lemmings, such as standing on all fours or on their hind legs, which may have thermoregulatory functions. Second, the wind hypothesis posits that lemming orientation could be influenced by wind direction, as wind can decrease radiative heat gain and increase convective heat loss based on body orientation (Heller, 1972; Fortin et al., 2000). Third, the snow reflection hypothesis considers the high albedo of snow, which reflects 50-90% of solar radiation (Pomeroy & Brun, 2001; Gardner & Sharp, 2010). Lemmings might benefit from the high reflectivity of the surrounding snow, thus lessening the need to orient their bodies directly towards the sun. Finally, the predation hypothesis arises from our observation that lemmings frequently changed their body orientation while scanning their surroundings, a sign of vigilance. Vigilance, common in many mammal species, serves primarily to detect predators (Quenette, 1990). Thus, while the predation risk at the snow surface was low enough to allow lemmings to surface, it might still be high enough to prevent them from maintaining an optimal orientation for sun-basking. Further research on energy input from solar radiation and predation risk at Alert is essential to explore these hypotheses.



In early June 2023, snow stratigraphy at Alert featured a soft depth hoar layer covered by a harder surface layer, aligning with observations from late April 2000 in the same area (Domine et al., 2002) and mirroring patterns typical of other Arctic regions (Benson & Sturm, 1993; Sturm et al., 1995; Domine et al., 2012, 2018). Contrary to findings at other sites for lemmings (Rausch, 1950; Menyushina, Pers. Comm. 2021) and voles (Korslund & Steen, 2006), wet conditions in the subnivean environment were not a factor for lemming surface activity at Alert (**P2**). This demonstrates that, while snow melt may facilitate lemming's activity at the snow surface in spring, it is not a prerequisite for such a behavior.

### **Other observations**

#### *Assessing predation risk*

We confirmed the presence of several avian and terrestrial predators in Alert during the monitored period of lemming activity at the snow surface, including jaegers and wolves which were observed capturing lemmings on the snow (R. Demers, E. Desjardins, D. Berteaux, unpublished data). Given that many predators rely on visual cues to locate their prey (Martin, 2017), it is clear that lemmings on the snow surface faced heightened predation risk. However, the automated cameras did not capture any attack from predators on lemmings. The small numbers of burrow entrances monitored (10 burrows in 2019, and 28 in 2023) compared to the abundance of burrows available might reduce the probability of capturing such predatory behaviors. This could also indicate a low risk of predation for lemmings staying close to their burrow entrance, which could favor the surfacing behavior of lemmings in Alert. One limitation of our qualitative predation risk assessment is that we observed ermines in Alert after the study period in both 2019 and 2023, suggesting they were present in spring as well. Since ermines primarily hunt under the snow, lemmings may reduce their exposure to ermines by remaining on the snow surface. Thus, increasing exposure to surface predators may decrease vulnerability to subnivean predators (Kotler et al., 1992), making trade-offs between thermoregulation and predation risk even more complex to assess. This is compounded by the fact that ermines can also hunt on the surface, and foxes and

wolves are capable of catching lemmings below the snow. A comprehensive quantification of predation risk is challenging in natural conditions, but including this variable as a predictor in our model would likely explain additional variation in the timing and intensity of lemming surface activity.

### *Phenology of spring molt*

The onset of spring molt in lemmings is initiated by the increase in light availability (Maier & Feist, 1991; Nagy et al., 1993), which inhibits the secretion of melatonin and stimulates the secretion of prolactin, responsible for the production of brown fur (Gower et al., 1993). Temperature, on the other hand, appears to influence the rate of molt in several northern species such as snowshoe hare and collared lemming (Zimova et al., 2018). As daylight returns in the last days of February and 24-h continuous sunlight starts in early April in Alert, most lemmings observed in May and June had already been through their spring molt. However, summer brown fur provides more visibility and less insulation than its winter white counterpart (Reynolds & Lavigne, 1988; Maier & Feist, 1991; Reynolds, 1993). Given that snowmelt in 2019 and 2023 did not occur later than the long-term average, and considering the typical minimum air temperatures of around  $-15^{\circ}\text{C}$  during our study, it is puzzling why the studied population did not evolve a later summer molt. Particularly, this adaptation could potentially reduce the observed color mismatch between lemming fur and the snowy background, which likely increases predation risk (Caro, 2005; Zimova et al., 2016; Atmeh et al., 2018; Otte et al., 2024). One hypothesis involves thermoregulatory benefits for lemmings with brown fur exposed to solar radiation. Specifically, small mammals, including lemmings, with brown pelage have been demonstrated to expend less energy maintaining body temperature while sun-basking than those with white pelage (Chappell, 1980b). Therefore, under spring conditions where the ground remains snow-covered and temperatures are low, yet solar radiation is strong, the energetic benefits of brown fur may outweigh the higher insulation and lower visibility associated with white fur. Staying in the close vicinity of their burrow entrance when on the snow surface might also be a behavioral

adaptation to limit the predation risk heightened by this color mismatch. This could further explain the absence of predation events detected by the automated cameras.

### *Latrines*

Lemming burrow entrances, often marked by urine and feces, were easily detectable, even when we were riding our snowmobiles. This visibility suggests that predators such as jaegers, foxes, and wolves could also easily spot locations where lemmings exited from the snow. However, summer observations in the Northwest Territories of Canada reveal that collared lemmings conceal their feces (and presumably urine) in underground latrines, likely to evade detection by predators (Boonstra et al., 1996). It is intriguing that lemmings adopt this concealment strategy during the summer but not in the winter when tracks are more visible against the white snow. To explain this apparent discrepancy, it's notable that while lemmings at Alert use underground latrines in summer, our experiments using white plastic cardboards placed near summer burrows showed that they still occasionally excrete small quantities of urine and feces above ground (D. Berteaux, pers. obs.). Therefore, the 'indoor plumbing' reported by Boonstra et al., (1996) may not ensure a completely clean floor, suggesting that our winter observations might not be as contradictory as they initially seem.

### *An even more intricate trade-off*

While sun-basking on the snow surface, lemmings reduce the amount of energy invested in thermoregulation. However, this behavior also comes at the cost of reduced energy acquisition through foraging. Endotherms, particularly arctic mammals, can rely on physiological adaptations such as shivering and heat production by brown adipose tissues to maintain their body temperature (McNab, 2002; Cannon & Nedergaard, 2004). Since collared lemmings increase their food intake at cooler temperatures (Maier & Feist, 1991; Nagy & Negus, 1993) to meet the high energetic demands of physiological heat production (McNab, 2002), it is worth questioning why they trade foraging time under the snow protective cover for the potential risks associated with behavioral thermoregulation at the

surface. One possible explanation lies in the quality of available food resources. While the extent to which lemmings deplete the available plant biomass through winter grazing remains debated (Moen et al., 1993 showed a significant decrease, whereas Bilodeau et al., 2014 found no effect), the quality of the remaining vegetation by the end of winter may be greatly reduced. When food quality is insufficient to meet metabolic needs, lemmings may benefit from reducing foraging time and sacrificing protective cover in favor of energy-saving behaviors such as sun-basking. Sun exposure may also provide additional benefits, such as hormonal regulation (Gower et al., 1993) or the synthesis of vitamins unavailable in their diet (Hickie et al., 1982), which could further encourage the surfacing behavior.

### *Population dynamics*

Monitoring lemming activity above the snow has provided new insights into their winter population dynamics. Observations of up to four lemmings surfacing from the same snow burrow, including individuals significantly smaller than adults, indicate that lemmings reproduced during the winters of 2019 and 2023. This reproductive activity aligns with the high lemming abundance observed at Alert during the subsequent summers of 2019 and 2023, as evidenced by incidental observations, trapping, and monitoring of predator reproduction (D. Berteaux, unpublished data). Collared lemmings are known to reproduce under favorable winter conditions (Stenseth & Ims, 1993a; Krebs et al., 1995; Millar, 2001), and such winter reproduction is crucial for the rapid population increases leading to peak density years (Millar, 2001; Ims et al., 2011; Fauteux et al., 2015). Given that data on winter reproduction are scarce, spring observations above the snow are a valuable source of new knowledge. A next step is to investigate whether spring surface activity also occurs in years of low lemming abundance, and what this activity might reveal about the age structure, molt phenology, or lemming behavior across the various phases of the lemming cycle.

## **Conclusion**

With the now widespread availability of infrared-triggered cameras, we were able for the first time to closely study the spring activity of lemmings at the snow surface. Thermoregulatory costs significantly contribute to the energy expenditure of small arctic mammals (Chappell, 1980b; McNab, 2002) and, interestingly, collared lemmings appear to accept to expose themselves to surface predators in exchange for thermoregulatory benefits. While similar trade-offs have been noted in other mammal species (Brown & Downs, 2005; Glass et al., 2021), their implications on predator-prey dynamics in the Arctic tundra, where collared lemmings are a central piece of the food web (Batzli et al., 1980), need to be explored.

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## 1.9 SUPPLEMENTARY MATERIAL

Table S4. Overview of monitoring effort aimed at quantifying lemming activity above the snow in 2019 and 2023 at Alert, Nunavut, Canada. We give for each observed burrow the period over which lemming activity was monitored, the number of triggered sequences that were generated by automatic cameras, and various measures describing the presence of lemmings on pictures and videos forming triggered sequences.

Site, Year	Burrow ID	Monitoring period (dates)	Length of activity period (days)	Number of triggered sequences	N triggered sequences with lemmings	Proportion of triggered sequences with lemmings (%)	Number of lemming observations
Site 1, 2019	12	2019-05-13 to 2019-06-12	31.0	24	20	83.3	22
	13	2019-05-13 to 2019-06-12	31.0	5	5	100.0	5
	14	2019-05-13 to 2019-06-12	30.7	602	576	95.7	586
	15	2019-05-13 to 2019-06-12	31.0	425	386	90.8	391
	16	2019-05-13 to 2019-06-09	27.9	30	28	93.3	28
	17	2019-05-13 to 2019-06-12	31.0	109	104	95.4	104
	18	2019-05-13 to 2019-06-09	27.9	340	336	98.8	381
	19	2019-05-13 to 2019-06-09	27.9	42	38	90.5	38
	20	2019-05-13 to 2019-06-09	27.9	417	397	95.2	413
	21	2019-05-13 to 2019-06-09	27.9	26	25	96.2	27
Subtotal 2019	10 burrows	13 May to 12 June	294.2	2,020	1,915	94.8	1,995
Site 1, 2023	2	2023-05-27 to 2023-06-12	15.8	431	412	95.6	437
	8	2023-05-27 to 2023-06-14	17.39	65	12	18.5	12
	9 - 03	2023-05-27 to 2023-06-02*	5.8	14	9	64.3	9
	9 - 12	2023-06-02 to 2023-06-12	10.0	384	341	88.8	349
	10 - 01	2023-05-27 to 2023-06-02*	5.8	3	3	100	3
	10 - 11	2023-06-02 to 2023-06-14	11.6	5	5	100	5
	11	2023-05-27 to 2023-06-14	17.4	146	139	95.2	139

	12	2023-05-27 to 2023-06-12	15.8	36	30	83.3	31
	13	2023-05-27 to 2023-06-08	11.8	38	30	78.9	30
	14	2023-05-27 to 2023-06-08	11.8	17	10	58.8	10
	15	2023-05-27 to 2023-06-12	15.8	616	553	89.8	588
	16	2023-05-27 to 2023-06-05	9.0	12	11	91.7	11
Site 2, 2023	17	2023-05-31 to 2023-06-14	13.3	11	9	81.8	10
	18	2023-05-31 to 2023-06-14	13.3	74	71	95.9	94
	19	2023-05-31 to 2023-06-14	13.3	24	18	75.0	20
	20	2023-05-31 to 2023-06-14	13.3	73	54	74.0	55
	21	2023-05-31 to 2023-06-14	13.3	469	387	82.5	399
	23	2023-06-02 to 2023-06-14	11.3	16	10	62.5	10
	26	2023-06-02 to 2023-06-14	11.4	2	2	100.0	2
	27	2023-06-02 to 2023-06-14	11.3	44	43	97.7	44
Site 3, 2023	28	2023-06-03 to 2023-06-14	10.3	69	67	97.1	70
	30	2023-06-03 to 2023-06-14	11.0	5	3	60.0	3
	31	2023-06-03 to 2023-06-14	10.3	72	69	95.8	69
	33	2023-06-03 to 2023-06-14	10.3	12	11	91.7	11
	36	2023-06-03 to 2023-06-14	10.3	44	39	88.6	39
	38	2023-06-03 to 2023-06-14	10.4	100	91	91.0	96
	40	2023-06-03 to 2023-06-14	10.4	8	5	62.5	5
	41	2023-06-03 to 2023-06-14	10.4	34	32	94.1	33
Subtotal 2023	28 burrows	27 May to 14 June	332.0	2,824	2,466	87.3	2,584
Total 2019- 2023	38 burrows		626.2	4,843	4,381	90.5	4,579

\*The cameras were moved to another burrow entrance, due to a lack of signs of activity

Figure S10. Average daily avian (purple) and terrestrial (green) predator index (A), i.e. total number of incidental observations of lemming predators detected per day, divided by mean daily observational effort (hours) for one observer, from 13 May to 12 June 2019. The predator index of 2019 shows the arrival of avian migratory predators throughout our study period. Daily mean ambient temperature and average daily lemming surface activity index are presented in B as reference. The dashed red line in B represents the  $-4.4^{\circ}\text{C}$  mark, where the effect of temperature on lemming surface activity plateaued.

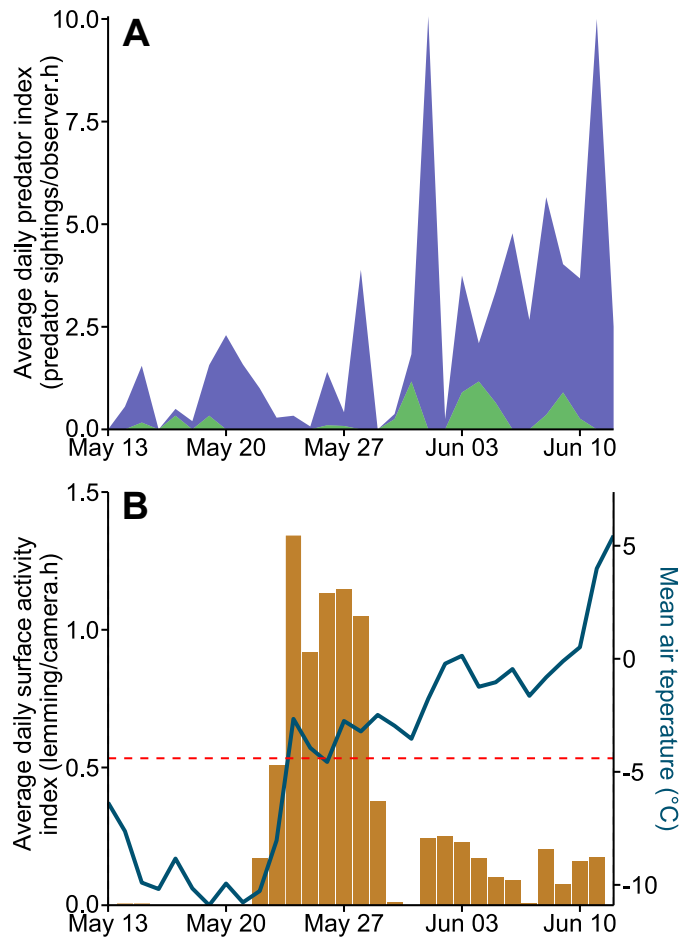
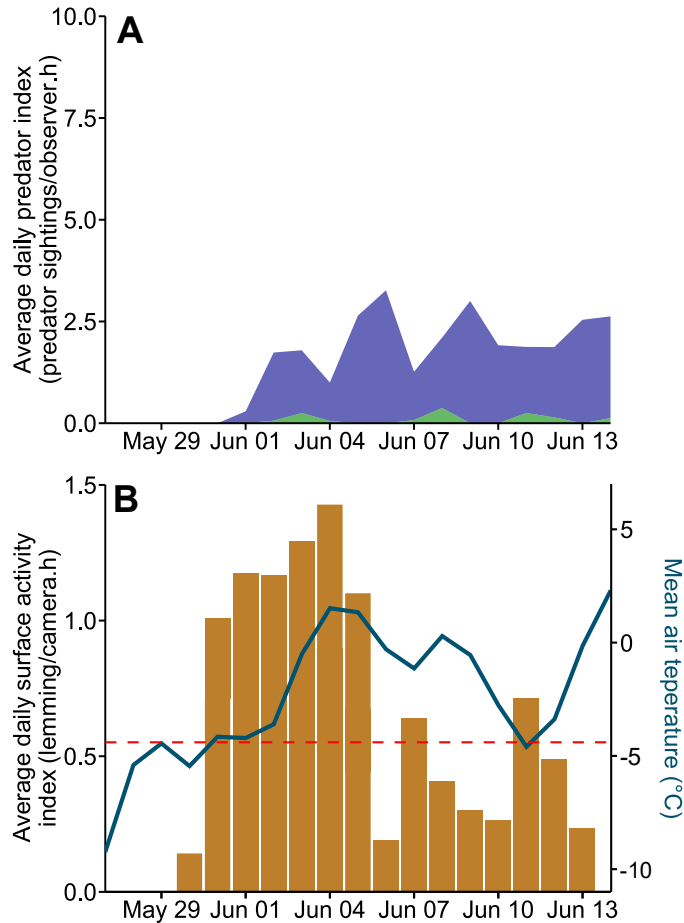




Figure S11. Average daily avian (purple) and terrestrial (green) predator index (A), from 27 May to 14 June 2023. The predator index of 2023 shows the arrival of avian migratory predators after the beginning of the study period. Daily mean ambient temperature and average daily lemming surface activity index are presented in B as reference. The dashed red line in B represents the  $-4.4^{\circ}\text{C}$  mark, where the effect of temperature on lemming surface activity plateaued.





## CONCLUSION GÉNÉRALE

Chez les espèces de petite taille vivant dans des milieux froids, les défis liés à la thermorégulation sont particulièrement élevés (McNab, 1980; Norris & Kunz, 2012). Les contraintes énergétiques imposées par ces conditions environnementales difficiles influencent le comportement des individus qui tentent d'équilibrer les coûts et bénéfices énergétiques pour répondre à leurs différents besoins (Tattersall et al., 2012; Blix, 2016). En utilisant le lemming variable comme modèle d'étude, j'ai étudié avec mes coauteurs l'effet des conditions environnementales sur l'activité des lemmings au-dessus de la neige à un moment de l'année où le jour continu et les prédateurs aviaires sont de retour après le long hiver arctique. Nos résultats appuient l'hypothèse générale selon laquelle les coûts liés à la thermorégulation peuvent conduire à l'émergence de compromis comportementaux.

Nos résultats montrent que, conformément à l'hypothèse (**H1**), les lemmings sortent à la surface de la neige afin de réduire l'énergie investie dans la thermorégulation. En effet, la probabilité d'observer des lemmings au-dessus de la neige était positivement liée à la température (**P1a**), mais négativement affectée par le couvert nuageux (**P1b**) et la vitesse du vent (**P1c**). De plus, la température opérative enregistrée à la surface était nettement supérieure à celle sous la neige (**P1d**). Ce comportement présente un avantage énergétique puisque la thermorégulation représente une dépense énergétique importante chez les petits mammifères arctiques (Chappell, 1980b; McNab, 2002). Toutefois, une fois à l'extérieur, les lemmings ne semblent pas maximiser leurs gains énergétiques en orientant leur corps par rapport au soleil ou en ajustant leur niveau d'activité en fonction du couvert nuageux (**P1e** et **P1f**). La présence de plusieurs prédateurs sur l'aire d'étude suggère que les lemmings deviennent plus vulnérables à la prédation lorsqu'ils sont à la surface de la neige, notamment en raison de leur mue printanière hâtive qui leur confère un pelage brun qui contraste avec le couvert neigeux. Ainsi, les lemmings doivent probablement jongler entre les avantages de s'exposer au soleil pour réduire leurs dépenses énergétiques allouées à la thermorégulation

et le risque d'être tué par les prédateurs, tels que les prédateurs aviaires, chassant à la surface de la neige. Les lemmings pourraient cependant atténuer le risque prédation lorsqu'ils s'exposent à la surface de la neige grâce à des comportements anti-prédation tels qu'une vigilance accrue, qui permet d'augmenter la probabilité de détecter des prédateurs (Quenette, 1990).

La présence d'eau dans l'habitat sous-nival a aussi été mentionnée comme hypothèse **(H2)** expliquant l'activité des lemmings au-dessus de la neige (Rausch, 1950; Menyushina, Comm. Pers. 2021). Il n'est pas exclu que ce phénomène puisse expliquer l'activité des lemmings sur la neige à Alert, plus tard dans la saison, lors de la fonte de la neige. Cependant, nos observations ne soutiennent pas cette prédiction **(P2)** étant donné l'absence d'eau dans le manteau neigeux lors de notre étude et puisque la fonte de la neige marquait la fin de notre suivi. Cette hypothèse **(H2)** pourrait être suffisante pour causer cette activité des lemmings en surface, mais elle n'est certainement pas nécessaire.

## **1. CONTRIBUTIONS ORIGINALES DE L'ÉTUDE**

Contrairement aux compromis impliquant le risque de prédation et l'acquisition de ressources alimentaires (Brown & Kotler, 2004; Verdolin, 2006; Creel, 2018), ceux impliquant les besoins énergétiques pour la thermorégulation sont peu étudiés, et ce bien qu'une proportion importante des dépenses énergétiques chez les mammifères soit associée à la régulation de la température corporelle (McNab, 2002). La présente étude offre un éclairage sur l'écologie comportementale du lemming variable du point de vue de la thermorégulation. Elle propose également un regard sur les compromis potentiels entre thermorégulation et risque de prédation chez une espèce centrale au réseau trophique de la toundra. Contrairement aux habitats tempérés, où le compromis entre thermorégulation et évitement des prédateurs semble généralement pencher vers la sécurité (Angilletta, 2009; Milling et al., 2017), nos observations suggèrent que, en milieu arctique, ce compromis peut se faire plutôt en faveur de la thermorégulation. En effet, en passant du temps au-dessus de

la neige, les lemmings privilégient la réduction des coûts énergétiques de la thermorégulation aux dépens de la sécurité offerte par leurs tunnels dans la neige, qui les protègent de plusieurs prédateurs (Duchesne et al., 2011; Bilodeau et al., 2013a). Nos résultats viennent donc s'ajouter à un ensemble de connaissances qui confirment, grâce à des observations comportementales, que la thermorégulation représente une contrainte majeure du budget énergétique des espèces (particulièrement celles de petite taille) vivant en milieux arctiques.

Grâce à la démocratisation de l'impression 3D qui facilite de plus en plus l'utilisation de modèles anatomiquement fidèles et faciles à produire (Watson & Francis, 2015), nous avons mesuré simultanément et à une fine résolution temporelle les températures opératives en surface et sous la neige. Ces mesures nous ont permis d'appuyer l'hypothèse de la thermorégulation. Nos résultats fournissent un aperçu de l'environnement thermique à une échelle spatiale appropriée aux lemmings. La mesure de température opérative montre que les autres variables environnementales (vent et radiation solaire) ont un impact important sur la température ressentie par les lemmings à l'échelle locale (Peterson et al., 1976) et permet d'approfondir notre compréhension du microhabitat des lemmings.

Obtenir des informations sur les lemmings lorsqu'ils sont sous la neige durant la période hivernale reste à ce jour difficile, malgré certaines innovations technologiques comme des pièges photographiques sous la neige (Pusenkova et al., 2022). Les données des caméras automatiques nous ont permis non seulement de décrire en détail les sorties à la surface des lemmings pour la première fois, mais également de donner un aperçu du comportement des lemmings lorsqu'ils sont au-dessus de la neige. Ce suivi nous a permis de récolter des informations sur l'écologie comportementale des lemmings variables à un moment de l'année où les informations disponibles sont limitées. Le suivi à l'aide de caméras à déclenchement automatique nous a également fourni des informations précieuses sur la phénologie de la mue ainsi que sur la dynamique hivernale de la population de lemmings à Alert.

De façon générale, notre étude marque une étape importante dans la compréhension du comportement d'une espèce clé de son écosystème et souligne l'impact des sorties au-dessus

du couvert neigeux sur les compromis entre la thermorégulation et le risque de prédation. En obtenant des informations précieuses sur le comportement du lemming variable dans la période qui précède la fonte de la neige, nous comprenons mieux les contraintes énergétiques, les préférences en matière d'habitat et les stratégies de survie de cette espèce. Cette compréhension accrue nous aidera à appréhender les relations prédateurs-proies et, par le fait même, la dynamique de l'ensemble de l'écosystème.

## **2. LIMITES DE L'ÉTUDE, AMÉLIORATIONS POSSIBLES ET PERSPECTIVES**

Nos observations comportementales corroborent la prémisse que l'exposition des lemmings au soleil représente un comportement risqué. En effet, lorsqu'au-dessus de la neige, les lemmings adoptent des comportements anti-prédation, tels que la vigilance et le maintien d'une proximité avec l'entrée de leur tunnel. Les comportements des lemmings suggèrent un risque de prédation bien présent à la surface de la neige. De plus, nous avons prouvé la présence de prédateurs dans l'aire d'étude lors de nos recherches. Nous n'avons toutefois pas directement mesuré l'impact des prédateurs, entre autres dû à la difficulté de mesurer le risque de prédation réel et perçu par les proies en milieu naturel, qui varie à la fois dans le temps et l'espace (Gaynor et al., 2019). Nous ne savons pas non plus comment le temps passé par les lemmings en surface influence le risque de prédation par l'hermine, une espèce qui chasse sous la neige. Les lemmings, en sortant à la surface de la neige, semblent augmenter leur vulnérabilité aux prédateurs chassant en surface tels que les prédateurs aviaires, mais pourraient réduire le risque associé aux prédateurs chassant sous la neige (Kotler et al., 1992). L'interprétation de ce compromis entre thermorégulation et risque de prédation est d'autant plus complexe que certains prédateurs tels que l'hermine, le renard et le loup peuvent chasser les lemmings qu'ils soient au-dessus ou sous la neige. Inclure une mesure quantitative du risque de prédation dans notre modèle permettrait vraisemblablement d'expliquer davantage de variation dans le moment et l'intensité de l'activité des lemmings à la surface de la neige. De plus, cela aiderait à comprendre comment les variations spatiales

et temporelles du risque de prédation influencent le comportement des lemmings. Néanmoins, nous croyons que cet ajout viendrait enrichir notre compréhension de ce compromis complexe en complétant, plutôt qu'en réduisant, l'importance des variables environnementales.

Notre étude a permis d'obtenir une compréhension générale du moment et de l'ampleur de l'activité des lemmings à la surface de la neige. Modéliser davantage de variables environnementales influençant la thermorégulation, telles que les précipitations et l'humidité à l'intérieur des tunnels de lemmings et à la surface de la neige, permettrait probablement de préciser notre compréhension de l'activité des lemmings variables au-dessus de la neige avant la fonte printanière. De plus, inclure une mesure de la visibilité extérieure à notre modèle pourrait nous renseigner sur la capacité des lemmings à détecter les prédateurs et approfondir notre compréhension du compromis entre thermorégulation et risque de prédation. En considérant l'importance du rayonnement solaire sur la régulation de la température corporelle des animaux (Norris & Kunz, 2012), nous avons également formulé plusieurs hypothèses pour expliquer les écarts avec nos prédictions sur le comportement des lemmings une fois à la surface (**P1e** et **P1f**). Plus d'informations sur l'apport énergétique du rayonnement solaire et le risque de prédation à Alert seront toutefois nécessaires pour explorer ces hypothèses. Ainsi, cela permettrait de raffiner notre compréhension des interactions entre les lemmings et son environnement.

Durant nos deux années de suivi à Alert, nous avons observé une forte abondance de lemmings. Plus d'informations sont maintenant nécessaires pour vérifier si l'activité printanière des lemmings à la surface de la neige se produit également au cours des années de faible abondance. Une réplication annuelle de notre étude pourrait ainsi révéler des informations importantes sur la structure d'âge, la phénologie de la mue ou le comportement des lemmings au cours des différentes phases de leur cycle d'abondance. Ces informations permettraient ainsi de mieux comprendre l'écologie des lemmings et leur rôle dans la dynamique de leur écosystème.





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