Rôle de l'hermine dans les cycles de lemmings du Haut-Arctique

Mémoire

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Résumé

Prédire l'abondance d'une espèce en un lieu donné représente encore aujourd'hui un défi de taille vu la diversité de facteurs à considérer et ce, à différentes échelles spatiotemporelles. En générant beaucoup de variabilité, autant dans leur abondance que dans les facteurs la régulant, les populations cycliques présentent des systèmes de choix pour étudier la dynamique des populations. Ce mémoire s'intéresse aux interactions prédateurs-proies, en examinant l'influence qu'a un prédateur spécialiste résident, l'hermine (*Mustela richardsonii*), sur les cycles de populations des lemmings du Haut-Arctique canadien (*Lemmus trimucronatus* & *Dicrostonyx groenlandicus*). Au chapitre 1, nous avons reconstitué les niveaux d'abondance de ce prédateur sur près de 30 ans grâce aux témoignages fournis par d'anciens observateurs. Selon nos résultats, les données issues des témoignages sont comparables à celles récoltées systématiquement. Au chapitre 2, en utilisant la série-temporelle d'abondance d'hermine issue du chapitre précédent, nous avons testé l'hypothèse du prédateur spécialistes (HPS) qui suppose un rôle prépondérant de ces prédateurs dans la génération des cycles de micromammifères. Comme prévu par l'HPS, nos résultats montrent que l'abondance d'hermine à l'an *t* est autant déterminée par les abondances passées (*t-1*) que présentes (*t*) de proies. De plus, des analyses saisonnières circonscrivent l'impact négatif de l'hermine sur les lemmings surtout à l'hiver, ce qui indique un rôle potentiel dans les déclins et le maintien à faible abondance des lemmings sur plus d'un an. Nos simulations soulignent aussi l'importance de l'hermine dans la création de phases de faible abondance. En somme, nos résultats montrent que l'hermine est nécessaire, bien qu'insuffisante, pour générer les cycles de 3 à 5 ans observés dans le Haut-Arctique. Ces travaux empiriques délimitent les conditions dans lesquelles les petits mustélidés pourraient influencer les cycles de populations et proposent des mécanismes permettant cette influence.

Abstract

Predicting the abundance of a species at a given location still represents a sizable challenge given the multiple factors present at different spatiotemporal scales. By generating a lot of variability in their abundance as well as in the factors regulating it, cyclic populations become prime study systems to study population dynamics. This thesis focuses on the role of predator-prey interactions by investigating the influence that a specialist resident predator, the ermine (*Mustela richardsoni*), has on the population cycles of Canadian High-Arctic lemmings (*Lemmus trimucronatus* & *Dicrostonyx groenlandicus*). In the first chapter, we reconstructed the abundance of this predator over nearly 30 years thanks to the testimonials of past observers. Our results show that testimonial-based and systematically collected data are comparable. In chapter 2, using the abundance time-serie of ermine from the previous chapter, we tested the specialist predator hypothesis (SPH) which suppose a predominant role of these predators in generating small mammal cycles. As suggested by the SPH, our result showed that ermine abundance at year *t* was determined as much by past (*t-1*) and current (*t*) prey densities. Moreover, seasonal analysis suggests the negative impact of ermines on lemmings is mostly limited to winter, indicating a potential role in the decline and the maintenance of lemmings to low abundances for more than a year. Our simulations also indicate the importance of ermines in the generation of pluriannual low abundance phases. In sum, our results suggests that ermines are necessary yet insufficient to create the 3- to 5-year cycles observed in the High-Arctic. This empirical work delimits the conditions in which small mustelids may influence population cycles and suggests mechanisms permitting such influence.

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grey area represents an estimated snow cover duration. The solid and dashed black lines respectively represent how lemming and winter nest densities are thought to vary throughout the year. Open circles indicate the density of lemmings to which the density of winter nests found in the following spring ($D_{Winter\ nest,t+1}$) should be proportional. Winter nests are sampled every year at snowmelt. During years of winter growth **(a)**, winter nest densities are used as proxies of lemming densities at snowmelt when the abandon their nests ($Nest_{abandon}$). R' over fall and late winter ($R'_{fall-late\ winter}$), and R' over spring (R'_{spring}) could be estimated separately. Alternately, in years of winter declines **(b)**, winter nest densities are used as proxies of lemming densities at the onset of the winter season when they start building their nests ($Nest_{formation}$). Seasonal population growth proxies could be estimated over fall (R'_{fall}) and over early winter and spring ($R'_{early\ winter-spring}$).

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Liste des abréviations, sigles, acronymes

CLMMs : Modèles mixtes à liens cumulés / Cumulative link mixed models

HPS/SPH : Hypothèse du prédateur spécialiste/ Specialist predator hypothesis

PCB : Circuit imprimé / Printed circuit board

À Sunny

Bip---Bip---Bip-Bip-Bip-Bip-Bip
*Oooh sh*t. [Je] ramasse mes bottes et parcours le kilomètre nous séparant du pingo à grande vitesse. Arrivé à la base, je souffle et me murmure de ne pas être déçu si rien ne s'y trouve. J'éprouve aussi une certaine crainte de procéder à une capture [d'hermine]. [En haut] j'aperçois la cage. Tranquille. Puis sa tête se tourne vers moi. […] Les perspectives de l'été changent. […] Dire que j'étais stressé se rapproche de l'euphémisme. [...] Game on.*

Extrait de mon carnet de terrain, Été 2022, Île Bylot

Remerciements

Ce mémoire est le produit certes de mon travail, mais aussi de nombreuses influences positives dont j'ai pu profiter avant, pendant, et je l'espère après l'entreprise de ce projet.

À mes parents, je vous remercie pour votre support inconditionnel tout au long de mes études / de ma vie. Bien que les opportunités de questionner mes choix furent abondantes, vous m'avez toujours encouragé à suivre les voies singulières qui m'ont menée à la recherche en écologie. Vous avez su éveiller ma curiosité (merci les Débrouillards!) et m'avez laissé jouer dans les bois assez longtemps pour que je tente d'en faire un métier. À ma sœur, merci pour les rires, le support et les incroyables souvenirs. À Esther, merci pour les belles années déjà écoulées. Tu as été présente tout du long, malgré ma difficulté à parfois ne pas parler de lemmings. Rien n'aurait été possible sans ton support, et c'est un réel plaisir d'être à tes côtés.

À mes superviseurs passés, merci pour le temps que vous m'avez accordé, pour les savoirs et les techniques que vous m'avez (du moins en partie) transmis et pour votre implication dans mon développement. Que ce soit lors de longues discussions dans un bureau, sur le terrain les mains pleines d'huile à moteur, la pelle pleine de mouches mortes ou dans un labo à tamiser des crottes, j'ai toujours eu l'impression d'avoir une bonne étoile me guidant vers les bonnes personnes.

Au Winneux Lab, que dire. En pleine pandémie, je n'aurais pu souhaiter mieux trouver comme famille d'accueil. Vous avez rendu les journées difficiles agréables et les déjà pas pires extraordinaires. Merci pour votre légèreté, votre joie de vivre et votre énergie contagieuse.

À Pierrot et à Dom, quelle team. Vous m'avez pris sous votre aile et m'avez laissé plus de liberté que je ne pouvais en demander. Je ne pourrai jamais vous remercier assez pour les opportunités que vous m'avez offertes. À vélo, sur le terrain, dans un congrès, dans un bar après un congrès, dans un bar un soir de semaine ou même en visioconférence, tout était agréable. Merci pour votre confiance messieurs.

À Marie-Christine, merci pour tout ce que tu fais. Tu rends de nombreux projets possibles et la vie à Bylot serait sûrement beaucoup plus difficile, voire impossible, sans toi. J'espère pouvoir y retourner très bientôt taquiner l'hermine que tu aimes tant.

À Gilles, merci pour ton écoute attentive, tes conseils et tes révisions sans failles. C'est un réel honneur de pouvoir travailler avec toi.

À Pringles, Sunny, Vicky et Aneth, merci d'avoir livré quelques-uns de vos secrets. Chaque instant, aussi épuisant soit-il, fût vécu dans l'émerveillement le plus complet. Désolé s'il manque de petits bouts à vos lemmings.

Aux anciens de Bylot ayant répondu à mon sondage, ceci n'aurait réellement pas été possible sans vous. Merci pour les belles rencontres, votre intérêt, et merci de m'avoir transmis vos anecdotes que terrain. Votre contribution est inestimable.

Avant-propos

Ce mémoire débute par une introduction générale abordant le contexte de l'étude. Ceci est suivi de deux articles directement liés à l'introduction et d'un troisième qui, bien que non loin du sujet principal, ne s'inscrit pas directement dans le thème de ce mémoire.

Chapitre 1 – Testimonials to reconstruct past abundances of wildlife populations

Publié dans Basic and Applied Ecology

Bolduc, D., D. Fauteux, C. A. Gagnon, G. Gauthier, J. Bêty, and P. Legagneux. 2023. Testimonials to reconstruct past abundances of wildlife populations. Basic and Applied Ecology 68:23-34. https://doi.org./10.1016/j.baae.2022.11.005

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Contribution des auteurs : DB, DF, PL et JB ont définis le projet. DB, DF, GG ont récolté les données. DB a effectué les analyses et rédigé l'article. CAG a fourni l'expertise sur les méthodes par sondage. DF, GG, JB, CAG, JB et PL ont révisé plusieurs versions de l'article.

Chapitre 2 – Seasonal role of small mustelids in rodent cycles: an empirical test of the specialist predator hypothesis in the High-Arctic

À soumettre

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Annexe 1 – Ultra-light photosensor collars to monitor Arctic lemming activity

Publié dans Animal Telemetry

Bolduc, D., D. Fauteux, É. Bharucha, J.-M. Trudeau, and P. Legagneux. 2022. Ultra-light photosensor collars to monitor Arctic lemming activity. Animal Biotelemetry 10:31. https://doi.org/10.1186/s40317-022-00302-1

Auteur principal : David Bolduc. Coauteurs : Dominique Fauteux (DF), Écric Barucha (ÉB), Jean-Marie Trudeau (JMT) et Pierre Legagneux (PL)

Contribution des auteurs : DF, PL et ÉB ont définis le projet. ÉB et JMT ont conçu les colliers. DB et DF ont récolté les données. DB a effectué les analyses et rédigé l'article. DF, ÉB et PL ont révisé plusieurs versions de l'article.

Introduction

Mesurer et prédire la densité d'une population représentent un défi de taille vu la grande diversité de dynamiques populationnelles observées, allant de cycliques régulières à chaotiques (Turchin, 2003a). Plusieurs hypothèses ont été avancées pour expliquer les variations du taux de croissance des populations, se basant soit sur des mécanismes intrinsèques, extrinsèques ou leurs combinaisons (Andersson & Erlinge 1977, Wilson et al. 1999, Turchin 2003, Sinclair et al. 2003, Inchausti & Ginzburg 2009, Odden et al. 2014, Myers & Cory 2016). Parmi les dynamiques résultantes de ces mécanismes, les cycles de population sont des cas de figure particulièrement intéressants vu leur caractère multi-annuel et leurs causes restent encore largement débattues malgré un siècle de recherche (Elton 1924, Stenseth 1999, Turchin 2003, Inchausti & Ginzburg 2009, Barraquand et al. 2014).

Principes généraux de dynamique de population

L'étude de la dynamique de population a pour objectif de quantifier les fluctuations d'abondance des populations, d'en comprendre les composantes temporelles et spatiales et d'en déterminer les mécanismes de limitation et de régulation. Les mécanismes limitants déterminent la densité à l'équilibre des populations, c'est-à-dire la densité vers laquelle tend une population dans un contexte donné (Murdoch 1994, Sinclair & Pech 1996, Krebs 2002, Turchin 2003). On peut penser à une population limitée par la qualité de l'habitat, des ressources disponibles ou son comportement de territorialité (Sinclair & Pech 1996, Krebs 2002, Turchin 2003). La limitation par le bas intervient lorsque la densité de population est limitée par le niveau trophique inférieur (i.e. abondance de nourriture), alors que la limitation par le haut représente les cas où la densité des populations est limitée par le niveau trophique supérieur (e.g. prédation, herbivorie) (Sinclair & Krebs 2002, Turchin 2003).

Les mécanismes de régulation forcent une population à retourner à une densité à l'équilibre (Murdoch 1994, Sinclair & Pech 1996). Autrement dit, un facteur régule une population lorsqu'il réduit son taux de croissance lorsque la densité augmente. La force de ces effets

densités-dépendants influencera le type de dynamique observée et déterminera en partie le taux de croissance des populations (Sinclair & Pech 1996, Turchin 2003).

Le taux de croissance réel (r) est la somme de plusieurs composantes. D'abord, le taux de croissance intrinsèque ($r_{\max}$) représente la croissance d'une population en situation idéale, lorsqu'elle n'est limitée que par ses contraintes physiologiques. Ce taux de croissance ($r_{\max}$) diffère du taux de croissance réel (r), qui lui résulte de la combinaison de $r_{\max}$ et des nombreux facteurs ayant généralement un effet négatif sur la survie, la reproduction et le recrutement (e.g. compétition intraspécifique, prédation) (Sinclair and Krebs 2002). Ces facteurs peuvent être densité-dépendants en agissant immédiatement (i.e. effets directs) ou après un certain temps (i.e. effets avec délais; Stenseth 1999) suite à la densification de la population.

Facteurs indépendants de la densité

Les facteurs indépendants de la densité peuvent influencer le taux de croissance (r). Des évènements météorologiques extrêmes (Erwin & Stasiak, 1979; Jones et al., 2017; Wuczyński & Jakubiec, 2013) ou une population de prédateurs supportée principalement par une proie alternative (Holt 1977) peuvent avoir un impact sur la population d'intérêt sans en être dépendante.

Les effets indirects de ces évènements peuvent être tout aussi importants et perturber les relations trophiques d'une communauté. Des évènements météorologiques peuvent moduler la quantité et l'accessibilité de la nourriture ou encore la susceptibilité des individus à la prédation. Les caribous (*Rangifer tarandus*) comme les campagnols (*Microtus levis*) voient la disponibilité de leur nourriture diminuer après des évènements de pluies hivernales qui figent la végétation dans la glace (Stien et al. 2012). L'épaisseur de neige peut quant à elle augmenter la susceptibilité du cerf de Virginie (*Odocoileus viriginianus*) d'être chassé par le loup gris (*Canis lupus*, Nelson and Mech 1986), réduire celle du lemming brun (*Lemmus trimucronatus*) d'être atteint par le renard arctique (*Vulpes lagopus*, Bilodeau et al., 2013) et diminuer l'efficacité avec laquelle les coyotes (*Canis latrans*) chassent le lièvre (*Lepus americanus*, Murray et al. 2011). Les évènements météorologiques sont peu prévisibles et ils sont généralement regroupés en un paramètre stochastique lors de la modélisation des

dynamiques de population. À l'inverse, les facteurs densité-dépendants sont plus prévisibles et explicitement modélisés.

Densité dépendance directe

La densité dépendance directe qualifie les facteurs dont la réponse dépend de la densité immédiate d'individus (N_t, Turchin 2003a). La compétition intra- et interspécifique en est un bon exemple (Skogland 1986, Sibly & Hone 2002, Vucetich & Peterson 2004, Jenkins et al. 2008, Krebs 2009). Les modèles de base de Lotka-Volterra consommateur-ressource montrent que ce type de densité-dépendance peut stabiliser les populations grâce à une rétroaction négative entre la densité d'individus et le taux de croissance (r), le faisant ainsi osciller autour de 0 (Rosenzweig & MacArthur 1963, Turchin 2003). Selon la réponse fonctionnelle et numérique des prédateurs (Holling 1959, 1965), la prédation peut aussi être directement dépendante de la densité de proies. Trois types de réponses des prédateurs vis-à-vis la densité de proies sont décrites par Holling (1965), le type I décrivant une réponse linéaire, le II une réponse logarithmique, où le prédateur est saturé à haute densité de proie, et le III une réponse sinusoïdale, où une certaine densité de proie est requise pour que le prédateur s'y intéresse.

Densité dépendance avec délai

Contrairement à la densité-dépendance directe, l'effet des facteurs densité-dépendants avec délai se produit en fonction de densités antérieures (e.g. N_{t-1}, Royama 1992, Stenseth 1999, Turchin 2003a). Par exemple, la réponse numérique de certains prédateurs ayant une longue période de gestation, le développement de composés défensifs chez les plantes broutées, les comportements sociaux délétères adoptés selon la densité à la naissance, les effets maternels, les agents infectieux et le parasitisme (délais de transmission) sont reconnus comme pouvant changer en fonction des densités passées (Moss et al. 1996, Gilg et al. 2003, Inchausti & Ginzburg 2009, Myers 2018). Ces facteurs peuvent déstabiliser les populations puisque des rétroactions positives entre la densité et la diminution des taux vitaux (i.e. survie et reproduction) peuvent s'installer et conduire la population très loin de sa densité à l'équilibre (Royama 1992, Stenseth 1999, Turchin 2003). Ce type d'effet a donc été jugé comme essentiel à la génération de cycles de populations en raison de son potentiel à faire chuter les populations et à les maintenir à de faibles densités pendant la

période associée au délais (Rosenzweig & MacArthur 1963, May 1976, Boonstra et al. 1998, Turchin 2003). Ces facteurs sont donc au centre de plusieurs hypothèses visant à expliquer les cycles de populations fauniques.

Tableau 0.1. Phases d'un cycle d'abondance typique

Phase	Processus	Source
Croissance	La phase de croissance se produit lorsque les populations, dont l'abondance est souvent faible, jouissent de ressources abondantes et de taux de survie et de reproduction élevés	Turchin and Batzli 2001, Blackwell et al. 2001
Pic	La population cesse de croître car les mortalités sont aussi nombreuses que les naissances. Ces mortalités, ou encore la baisse du taux de natalité sont causées par un ou plusieurs facteurs densité-dépendants.	Turchin 2003a
Déclin	Rattrapée par les facteurs densité-dépendants avec délais, la population chute drastiquement.	Krebs and Myers 1974, Martínez-Padilla et al. 2014, Fauteux et al. 2015, Myers and Cory 2016
Faible abondance	La phase de faible abondance suit le déclin et peut s'étirer sur plusieurs années. Certains facteurs intrinsèques (relations sociales intraspécifiques effets maternels), et des facteurs extrinsèques (manque de nourriture, prédation) ont été proposés comme mécanismes responsables des phases de faibles abondances. Ces facteurs densité-dépendants avec délais pourraient avoir un impact sur plusieurs années.	Hanski et al. 1991, Royama 1992, Moss et al. 1996, Boonstra et al. 1998, Turchin 2003a, Gilg et al. 2003, Inchausti and Ginzburg 2009, Myers and Cory 2016

Cyclicité dans les populations animales

Tel qu'exprimé par Krebs (1996), une population est considérée cyclique lorsque sa densité fluctue avec une périodicité pluriannuelle régulière. Les cycles sont caractérisés par plusieurs phases auxquelles sont associés des changements dans les taux vitaux de la population (voir Tableau 0.1). Certains facteurs intrinsèques, comme les comportements sociaux délétères ou les effets maternels, et extrinsèques, tels manque de nourriture ou la

prédation, ont été proposés comme mécanismes responsables des cycles et formulés en hypothèse (Hanski et al. 1991, Moss et al. 1996, Boonstra et al. 1998, Gilg et al. 2003, Inchausti & Ginzburg 2009, Myers & Cory 2016). Chacune de ces hypothèses a été suggérée par modélisation, mais certaines d'entre elles ont reçu plus d'appuis empiriques que d'autres.

Facteurs intrinsèques

Il est possible qu'une population, isolée de toute influence externe, présente des cycles de population causés par des facteurs intrinsèques. Par exemple, l'expression densité-dépendante avec délais de comportements sociaux pourrait expliquer la cyclicité des lagopèdes d'Écosse (*Lagopus lagopus scotia*), où l'agressivité des mâles envers les jeunes serait responsable des déclins (Watson et al. 1994, Moss et al. 1996). L'hypothèse des effets maternels stipule quant à elle que le taux de croissance d'une population est lié à la qualité moyenne des individus, et que celle-ci dépend de l'environnement vécu par les mères (Ginzburg & Taneyhill 1994, Ginzburg & Colyvan 2004). Celles-ci transmettraient alors non seulement leur génotype, mais aussi leur phénotype (i.e. niveau de stress) ce qui modulerait la reproduction des générations futures (Inchausti & Ginzburg 2009). Le stress subi par les mères peut émaner d'une densité de population élevée (Dantzer et al. 2013), d'un grand risque de prédation (Sheriff et al. 2009, 2015, Fauteux et al. 2018a) ou d'une combinaison de ces facteurs. Tel qu'illustré par Boonstra (2013), les effets maternels sont observés surtout chez les espèces où les conditions vécues par les mères devraient se poursuivre dans la génération suivante, comme chez le lièvre d'Amérique dont l'abondance est suivi de près par celle de son prédateur, le lynx (*Lynx canadensis*), avec un délais d'un an (O'Donoghue et al. 1997).

Facteurs extrinsèques

Bien que des cycles d'abondance puissent naître en réponse à des facteurs intrinsèques, la majorité des hypothèses font appel à des facteurs extrinsèques qui, en appelant à un niveau trophique différent, sont plus à risque de répondre avec délais. Par exemple, l'hypothèse de la surcompensation suggère qu'à haute densité, le broutement excessif ou un changement de saison entrainant une baisse de productivité végétale réduirait rapidement la qualité et/ou la quantité de nourriture. La population serait alors bien au-dessus de la capacité de charge

du milieu et chuterait drastiquement (régulation par le bas, Turchin 2003a, Barraquand et al. 2014). Il a été observé, par exemple, que les lemmings de Norvège pouvaient grandement endommager la végétation en phase de forte abondance (Oksanen & Oksanen, 1992), alors que les campagnols à dos roux de Gapper fluctueraient en abondance selon la années semencières, notamment des petits fruits (Boonstra & Krebs 2012).

Théoriquement et empiriquement, la prédation est reconnue comme un facteur limitant et régulateur des populations de proies (Rosenzweig & MacArthur 1963, Ballenberghe & Ballard 2011, Therrien et al. 2014, Fauteux et al. 2016). Elle est soupçonnée dans certaines populations de causer la phase de déclin des cycles et de maintenir les proies à de faibles abondances pendant plusieurs années (Korpimäki et al. 1991, Boonstra et al. 1998, Gilg et al. 2003). La prédation par le lynx (*Lynx canadensis*), dont la population suit celle des lièvres avec un délai de deux ans, a été montrée comme nécessaire aux cycles de 10 ans observés chez les lièvres d'Amérique du Nord (Krebs et al. 2018). Ce phénomène, soit un taux de prédation densité-dépendant avec délais, a été documenté dans plusieurs autres systèmes (Korpimäki et al. 1991, Gilg et al. 2003, Barraquand & Nielsen 2018). Ces observations, ainsi que les modèles théoriques prédateurs-proies, ont mené à la formulation et à l'étude de l'hypothèse du prédateur spécialiste.

L'hypothèse du prédateur spécialiste (HPS) stipule que la prédation serait la cause des cycles chez leurs proies (Andersson & Erlinge 1977, Hanski et al. 1991). Elle invoque la réponse numérique d'un prédateur spécialiste résident comme facteur densité-dépendant avec délai (Andersson & Erlinge 1977, Gilg et al. 2003). Les populations de proies seraient déstabilisées par la forte réponse fonctionnelle et la réponse numérique avec délais des prédateurs spécialistes, menant alors au déclin des proies et à une rétroaction positive entre la diminution de leur densité et la proportion de la population prélevé par les prédateurs spécialistes (Pearson 1966, Andersson and Erlinge 1977). Ceci peut amener la population de proies à des densités très faibles. Cette hypothèse, largement débattue, est surtout testée dans les populations cycliques de petits rongeurs (Hanski et al. 2001, Graham & Lambin 2002, Sundell et al. 2013, Mougeot et al. 2019).

Cycles de rongeurs

Dans le contexte des cycles des rongeurs, le terme « prédateur spécialiste résident » fait généralement référence à un groupe comprenant les belettes (*Mustela nivalis nivalis* et *vulgaris*) et les hermines (*Mustela erminea, M. richardsonii*, Colella et al. 2021). Ces petits mustélidés ont une capacité de mouvement limitée par rapport aux prédateurs aviaires et dépendent fortement des rongeurs, d'où leur nomination comme spécialistes résidents (Andersson et Erlinge 1977, Korpimäki et al. 1991, King et Powell 2006). Ils peuvent accéder à la plupart des terriers de leurs proies et restent actifs sous le manteau neigeux pendant l'hiver, ce qui laisse peu de refuges aux petits mammifères, à la fois dans l'espace (Simms 1979, Jędrzejewski et al. 1992, Mougeot et al. 2020) et dans le temps (MacLean et al. 1974, Fitzgerald 1977). De plus, leur efficacité à la chasse et leur tendance à accumuler les carcasses (« *surplus killing* ») pourraient leur permettre d'épuiser rapidement les populations de proies (Oksanen et al. 1985, Jedrzejewska & Jedrzejewski 1989, Jędrzejewski et al. 1992, King & Powell 2006).

Depuis le développement de l'HPS à la fin des années 70, la majorité des données empiriques qui l'appuient proviennent de la Fennoscandie où les campagnols font des cycles dont la période varie de 3 à 5 ans. En Europe tempérée, comme dans les pâturages agricoles de France et d'Espagne, dans les forêts aménagées d'Angleterre ou anciennes de Pologne, l'hypothèse a été principalement rejetée. Dans ces cas, la réponse numérique des petits mustélidés n'était pas suffisamment décalée (Jedrzejewski et al. 1995, Graham 2001, Mougeot et al. 2019) ou bien il a été démontré empiriquement (expérimentalement ou par observation) qu'ils avaient peu d'effet sur l'abondance de leurs proies (Jedrzejewski et al. 1995, Graham et Lambin 2002, Zub et al. 2008). De plus, ces études ont soutenu des processus densité-dépendants directs (Barraquand et al. 2014, Pinot et al. 2016, Sørensen et al. 2022) ou l'effet des maladies (Smith et al. 2008) comme cause des cycles de campagnols. Sur les îles Wrangel et Saint-Laurent, où les petits mustélidés sont absents, les fluctuations des petits rongeurs diffèrent des cycles de 3 à 5 ans observés dans d'autres sites nordiques, présentant respectivement des périodicités de 5 à 8 ans ou étant non cycliques (Fay et Rausch 1992, Menyushina et al. 2012). En outre, des critiques ont été émises à l'encontre des études précédentes qui soutenaient l'HPS, argumentant qu'elles étaient basées

sur des données inadéquates, des expériences trop courtes et que les paramètres de la population tels la survie n'étaient pas calculés ou rapportés (Graham et Lambin 2002, Oli 2003, Lambin et al. 2006, Lambin 2018). Bien que l'HPS ait été rejetée en tant qu'explication générale, des études récentes à grande échelle en Finlande (Sundell et al. 2013, Korpela et al. 2014) et une étude extensive au Groenland (Gilg et al. 2003) l'ont encore soutenu. Ainsi, même si les petits mustélidés ne sont pas à l'origine de tous cycles de rongeurs, ils pourraient néanmoins avoir un rôle nécessaire dans certains, notamment pour maintenir les petits mammifères à de faibles abondances pendant une période prolongée (Korpimäki et al. 1991, Boonstra et al. 1998).

Au vu de cette littérature, le rôle des petits mustélidés dans les cycles des rongeurs semble particulièrement prépondérant dans les environnements fortement saisonniers où le couvert neigeux est présent pour la majeure partie de l'année (Klemola et al. 1997, Korpimäki et Norrdahl 1998, Gilg et al. 2003, Korpela et al. 2014). Il a en effet été démontré que la saisonnalité et la durée de l'hiver favorisaient l'émergence de dynamiques cycliques (Hansson et Henttonen 1985, Stenseth et al. 1998, Andreassen et al. 2020). Deux mécanismes ont été proposés, le premier étant qu'une courte saison de reproduction estivale et de longs hivers avec des ressources réduites (par exemple, nourriture, espace, sites de nidification) conduisent à une forte densité-dépendance (Hansen et al. 1999, Saitoh et al. 2003, Korpela et al. 2013). Le deuxième mécanisme serait lié au manteau neigeux qui pourrait isoler le système rongeur-mustélidé de l'influence stabilisatrice des prédateurs généralistes (Korpimäki et Norrdahl 1989a, Oksanen et al. 2001, Bilodeau et al. 2013, Linnell et al. 2017, Lambin 2018). Ainsi, on s'attendrait à ce que dans des environnements où les hivers sont froids et enneigés, les prédateurs spécialistes jouent un rôle prédominant dans les cycles de petits rongeurs.

Cependant, l'acquisition de données empiriques sur l'abondance des rongeurs et de leurs prédateurs pendant les étés courts et les hivers rigoureux est un défi, en particulier pour les mustélidés qui sont notoirement difficiles à dénombrer (Lambin 2018). Par conséquent, l'absence de série temporelle peut expliquer le fait que de telles études sont inexistantes dans les environnements caractérisés par de longs hivers. Pour ma maîtrise, je me suis

intéressé à l'île Bylot, un système d'étude du Haut-Arctique canadien offrant une occasion unique de répondre aux questions entourant les populations cycliques de rongeurs.

Les cycles de lemmings sur l'île Bylot

Sur l'île Bylot, NU, deux espèces de rongeurs, soit le lemming brun (*Lemmus trimucronatus*; le plus abondant) et le lemming variable (*Dicrostonyx groenlandicus*) font des cycles d'abondance en synchronie sur une période de 3 à 5 ans (Gruyer et al. 2008; Bolduc et al. 2023). Ces deux espèces peuvent se reproduire dans l'espace sous-nival où elles atteignent de fortes densités caractérisant les pics de population. Grâce aux nids d'hivers que les lemmings fabriquent avec de la végétation sèche, ils réussissent à endurer le froid (Chappell 1980, Sittler 1995) et y laissent des traces de leur reproduction ou de leur prédation (Sittler 1995, Duchesne et al. 2011b).

Comme seul représentant de la famille des mustélidés à l'île Bylot, l'hermine est le seul prédateur spécialiste résident. Quoique plus généraliste au Sud (Edwards & Forbes 2003), la faible diversité de proies l'oblige à l'île Bylot à être fortement dépendante des lemmings, donc un prédateur spécialiste. De plus, bien que d'importantes dispersions post-sevrages furent enregistrées ailleurs (> 60 km, King and Powell 2006), les adultes tendent à rester sur leur territoire même si l'abondance de proie y diminue, en faisant ainsi des prédateurs résidents (King and Powell 2006). Ceci pourrait être différent dans l'Arctique où sa dispersion n'a jamais été étudiée. Sa reproduction est limitée à une portée (7-9 jeunes en moyenne, pouvant aller jusqu'à 18, King and Powell 2006) par an vu l'implantation différée des ovules 9 à 10 mois après l'accouplement (Sandell 1984). De plus, vu leur petite taille (100 à 200 g chez les adultes), les autres prédateurs, comme les renards et les rapaces, peuvent prélever une proportion importante de la population d'hermines (jusqu'à 80%, Powell 1973, Korpimäki & Norrdahl 1989a, 1989b, Lambin 2018).

Sur ce site d'étude, les évidences accumulées depuis trois décennies suggèrent que la population de lemmings est principalement régulée par le haut (prédation, Legagneux et al. 2012, Therrien et al. 2014, Fauteux et al. 2016) plutôt que par le bas (manque de nourriture, Bilodeau et al. 2014) ou de façon intrinsèque (reproduction densité-dépendante, Fauteux and Gauthier 2022). Cependant, cette prédation a été peu décortiquée à ce jour, notamment

au niveau du rôle des mustélidés pour lesquels aucune étude n'a été menée dans l'Arctique canadien.

Objectifs

L'objectif général de ce mémoire est donc de quantifier l'impact de l'hermine, un prédateur spécialiste, sur des populations cycliques de lemmings arctiques. Bien que l'abondance des lemmings soit suivie de manière systématique depuis 1993 sur l'île Bylot, celle des hermines n'est notée que de façon opportuniste depuis 2007. Mon premier objectif vise donc à reconstruire l'abondance relative des hermines au cours de la période 1993-2019. Avec ces données en main, mon projet vise ensuite à évaluer 1) la présence de cyclicité dans cette population d'hermine, 2) la réponse numérique des hermines face aux variations de densités des lemmings (avec ou sans délai), 3) l'impact des hermines sur le taux de croissance des lemmings, et la saisonnalité de cet impact et finalement 4) les conséquences qu'a l'hermine sur les cycles de lemmings.

Notre premier objectif se penche sur la cyclicité de la population d'hermine à l'île Bylot. Pour avoir une idée de son abondance à travers les années, j'ai collecté les témoignages d'observations opportunistes auprès d'anciens participants du suivi écosystémique. J'utiliserai sur ces données des analyses d'ondelettes, qui sont à même de détecter des cycles même si la périodicité varie au fil du temps. Notre hypothèse est que l'hermine devrait présenter des cycles d'une périodicité similaire à celle des lemmings (Bilodeau 2013). Ce résultat est attendu puisque les lemmings constituent la majorité du régime des hermines dans le Haut-Arctique (Gilg et al. 2006).

Notre deuxième objectif s'attaque à une supposition de l'HPS, soit que les petits mustélidés répondent avec un délai d'un an aux fluctuations d'abondance de leur proie (Hanski et al. 1991). Les séries temporelles d'abondances nous permettront de modéliser l'abondance d'hermine face aux densités présentes (t) et passées (t-1) de lemmings. Notre hypothèse est que l'abondance d'hermine devrait être influencée positivement par ces deux paramètres, tel qu'observé au Groenland (Gilg et al. 2006). Bien que l'implantation différée chez l'hermine (Sandell 1984) puisse limiter sa réponse directe, elle ne devrait pas l'empêcher.

De plus, la mise en réserve des carcasses devrait prolonger l'impact des densités des lemmings à l'an t sur l'hermine à l'an t+1.

Pour notre troisième objectif, nous tentons d'évaluer l'impact que pourrait avoir l'hermine sur le taux de croissance des lemmings ainsi que la variation de cet impact à travers les saisons. En utilisant les séries temporelles d'abondance annuelle de 1993 à 2019, d'abondance mensuelles de juin à août de 2004 à 2022 et finalement de nids d'hivers de 2007 à 2022, nous pourrons mesurer des taux croissances ou des proxys de ceux-ci à différent moment dans l'année. L'impact de l'hermine sera évalué sur ces taux de croissance, en considérant la densité-dépendance lorsque possible. Selon l'HPS, les prédateurs spécialistes seraient suffisants pour causer les déclins (Hanski et al. 1991). Comme nous observons des déclins en fin d'été, que ceux-ci semblent s'accentuer en automne (Fauteux et al. 2015) et que l'hermine reste active tout l'hiver sous le manteau neigeux, nous nous attendons à observer un impact négatif de l'hermine à travers toutes les saisons. Cet impact devrait toutefois être plus important à l'automne et à l'hiver, puisque l'hermine aura eu le temps de répondre numériquement.

Finalement, notre quatrième et dernier objectif est d'évaluer l'impact que l'hermine pourrait avoir sur les cycles de lemmings. Nous utiliserons les modèles générés par les objectifs précédents, soit celui prédisant l'abondance d'hermine (obj. 2) et le taux de croissance des lemmings (obj. 3), pour simuler des séries-temporelles en présence et en l'absence d'hermines et comparer leurs caractéristiques. Si l'hermine est nécessaire aux cycles tels qu'observés à l'île Bylot, alors les cycles des séries-temporelles de lemmings simulées en son absence devraient être différents. On s'attendrait à des cycles plus courts et à moins de phases pluriannuelles de faible abondance, comme dans les endroits où les cycles sont générés par densité-dépendance directe (Barraquand et al. 2014).

Les résultats obtenus dans ce mémoire permettent de mieux comprendre le rôle que peut jouer un prédateur spécialiste résident dans la cyclicité de sa proie. Plus précisément, nous avons maintenant une meilleure idée de la séquence temporelle, à l'échelle saisonnière,

menant aux fluctuations d'abondances, de l'impact du prédateur à chacune de ces étapes et des conditions dans lesquelles ce genre d'interactions mènent à des cycles de population.

Organisation du mémoire

Le premier chapitre évalue la robustesse de la méthode de reconstruction d'abondance relative ainsi que la cyclicité des hermines. Les témoignages d'observations opportunistes d'hermines, de lemmings et d'harfangs (*Bubo scandia*) ont été livrées par plus de 120 personnes ayant travaillé à Bylot entre 1993 et 2019 et qui ont généreusement partagé leurs souvenirs, notes de terrain ou vielles photos. Les indices d'abondances relatives issus de cette méthode ont été comparés avec les abondances standardisées. Pour évaluer la pertinence des données, certains phénomènes écologiques connus ou supposés, comme la cyclicité chez l'hermine, ont été testés. Les résultats ont été publié dans *Basic and Applied Ecology* avec l'aide de Dominique Fauteux, Pierre Legagneux, Joël Bêty, Catherine-Alexandra Gagnon et Gille Gauthier (voir Bolduc et al. 2023).

Le deuxième chapitre profite des données générées dans le premier pour s'attaquer à l'hypothèse du prédateur spécialiste. On y réalise les objectifs 2 à 4, soit d'évaluer le délai dans la réponse numérique des hermines, leur impact, ainsi que la saisonnalité de celui-ci, sur le taux de croissance des lemmings et finalement son rôle dans la cyclicité de ses proies.

En annexe, on peut trouver des travaux qui n'étaient pas initialement prévus dans ce mémoire, mais qui cadre dans l'étude des interactions prédateurs-proies impliquant les lemmings. On y évalue l'impact du port de colliers photosensibles sur le comportement et la condition corporelle des lemmings. Les résultats ont été publiés dans *Animal Biotelemetry* avec Dominique Fauteux, Pierre Legagneux, Éric Barucha et Jean-Marie Trudeau (voir Bolduc et al. 2022).

Chapitre 1 - Testimonials to reconstruct past abundances of wildlife populations

1.1 Résumé

Nous proposons ici une méthode basée sur les témoignages d'observations opportunistes pour reconstituer les abondances passées des populations n'ayant pas été suivies systématiquement. Les 205 témoignages récoltés auprès de 131 participants ont permis de dériver des indices d'abondance annuels pour trois taxons de 1991 à 2019. La validité de ces indices a été évalué en les comparant avec des indices standardisés, en calculant leur sensibilité au temps passé sur le terrain par l'observateur et en vérifiant qu'on pouvait y détecter des phénomènes écologiques connus. Nos résultats montrent que les indices issus des témoignages sont fiables. Ils nous permettent de générer la plus longue série-temporelle d'abondance relative de l'hermine dans l'Arctique canadien et d'y évaluer la cyclicité. Le fait de puiser dans la mémoire peut fournir des informations précieuses sur l'abondance passée de populations non-suivies et aider à répondre à des hypothèses qui nécessiteraient autrement des années de suivi systématique.

1.2 Abstract

Long-term monitoring of wildlife populations has greatly contributed to our current understanding of population dynamics and ecosystem functioning. Despite tireless field campaigns, however, only a fraction of the biodiversity has been monitored to date and the dynamics of potential key species have yet to be understood. Here, we propose a method based on testimonials of observations from field workers to reconstruct past abundances of unmonitored populations and fill data gaps. We contacted scientists who conducted field work at the Bylot Island field station, Nunavut, in the Canadian Arctic between 1991 and 2019 and collected 205 testimonials of past observations from 131 participants. We scored each testimonial based on its content and derived annual abundance indices for three highly fluctuating taxa, being lemmings, snowy owls and ermines. These indices were compared to standardized abundance estimates based on field sampling that were either available between 1993 and 2019 (lemmings and snowy owls) or 2007–2019 (ermines). Our results

show that abundance indices based on testimonials correlate well with those from systematic sampling and can be used to detect ecological phenomena. Moreover, we show that abundance indices were not affected by the effort of participants in the field or the delay between the observations and the collection of testimonials. Finally, we use the received testimonials to generate the longest ermine time series of relative abundance in the Canadian Arctic, spanning 29 years. Monitoring programs and research stations often have access to a pool of past participants (e.g. field workers, ecotourists) whose observations can be localized in time. As we strive to gain a deeper understanding of ecosystem functioning, tapping the memories of these people can provide valuable information on the past abundances of unmonitored populations and help answer hypotheses that would otherwise require years of systematic monitoring.

1.3 Introduction

Repeated estimates of wildlife population abundances over time provide key information on their dynamics, while developing the necessary baselines to detect anomalies and threats caused by environment- or human-induced changes (Ranta et al. 1995; Southward 1995; Powell & Steele 2012; Harvey et al. 2020). Over the years, many methods have been developed to estimate abundances using direct observations, proxies (i.e., nests, tracks or feces) or more intensive capture-mark-recapture protocols (Murray et al. 2002; Silveira et al. 2003; Fauteux et al. 2018; Amburgey et al. 2021). Each method is selected in a way to maximize precision while minimizing costs, efforts and biases (Hochachka et al. 2000; Efford 2004; Buckland et al. 2015; Fauteux et al. 2018; Camino et al. 2020). Still, most systematic monitoring methods require intense field efforts and their applicability remains limited in both time and space and applicable to only a small set of species (Efford 2004; Buckland et al. 2015), especially when the subject is rare or cryptic. Thus, compromises are unavoidable. In addition, while some species were monitored in the past due to economic or conservation priorities, others were ignored or insufficiently monitored. This poses serious challenges when studying species that are now recognized as having prominent roles in ecosystems functioning or facing threats.

Today, as we attempt to refine our understanding of the mechanisms behind population, community and ecosystem functioning (Legagneux et al. 2012; Polis & Winemiller 2013;

Mellard et al. 2021), a number of historically understudied species have become of particular interest. To address this situation, indirect and unconventional methods were developed to reconstruct past abundances of organisms. Dendrochronology, paleolimnology, sedimentary environmental DNA and historical harvest records have yielded precious insights into the past abundance of populations at multiple time scales (Elton & Nicholson 1942; Morneau & Payette 1998; Klvana et al. 2004; Burge et al. 2018; Duda et al. 2020; Kuwae et al. 2020). In some cases, decadal relative abundances have been assessed through indigenous and local ecological knowledge (Knaus et al. 1950; Ferguson et al. 1998; Anadón et al. 2009; Peñaherrera-Palma et al. 2018; Reif et al. 2021). Still, reconstruction of abundance time series can only be achieved for populations leaving marks in their environments or for species that are culturally or economically important to local users.

Here, we develop a method based on testimonials of observations to reconstruct past annual abundances and test its validity on three taxa. The species of primary interest was the ermine (*Mustela erminea*), a small and highly cryptic mustelid that is only observed in some years and thought to have a critical role in the High Arctic tundra ecosystem (Gilg et al. 2003). We were also interested in lemmings (brown, *Lemmus trimucronatus,* and collared, *Dicrostonyx groenlandicus*, lemmings) and snowy owls (*Bubo scandiacus*), both taxa being systematically monitored since the early days of the Bylot Island ecosystem monitoring. We collected testimonials of past observations from researchers, graduate students and field assistants conducting field work for the long-term ecosystem monitoring program of the Bylot Island field station, Nunavut, Canada (Gauthier et al. 2013), between 1991 and 2019. For each taxon, a score was given to each testimonial depending on the reported observations, and an annual abundance index was created by averaging scores of same-year testimonials. We then assessed the reliability of this method by comparing the testimonial-based abundance indices to abundance estimates obtained from field sampling. The overlap between methodologies was 13 years for ermines and 27 years for lemmings and snowy owls. Finally, we verified if well-known ecological phenomena, such as predator-prey interactions and cyclic population dynamics, could be detected using testimonial-based abundance indices.

1.5 Materials and methods

1.5.1 Study area

Our study area (73°08'N, 80°00'W) lies in the Qarlikturvik Valley on Bylot Island, Nunavut. The valley bottom is a mosaic of mesic tundra covered by herbs, graminoids and shrubs, and of wetlands, mostly covered by graminoids and mosses (Gauthier et al. 2011). Ermines are the only mustelid on the island and their populations are known to fluctuate in abundance in relation with lemmings, their main prey (Gilg et al. 2003, Bilodeau 2013). On Bylot Island, all rodents are either brown or collared lemmings that fluctuate in abundance according to 3- to 5-year cycles, with the brown lemming having the highest amplitude fluctuations (Gauthier et al. 2013). The snowy owl is a migratory predator specialized on lemmings and fluctuates in abundance in response to that prey (Therrien et al. 2014). In general, observing wildlife species is relatively easy in the High Arctic tundra during summer due to the absence of erect vegetation, the 24 h daylight, and the fact that several mammals and birds are curious and bold (e.g., ermines may come <10 m from people). Moreover, due to the relatively low species richness compared to temperate or tropical systems, vertebrate species identification in the field is straightforward except when distinguishing between the two lemming species at a distance.

1.5.2 Ethics statement

This research was approved by the Comité de Protection des Animaux de l'Université Laval (CPAUL; Current License for lemmings 2019-253, avian predators 2019-245) and Parks Canada (Current License SIR-2021-39399). The collection of testimonials did not require special permission as our participants are currently or were formerly employed by the Bylot Island monitoring program. Their free, prior and informed consent was confirmed at the beginning of the interview or questionnaire.

1.5.3 Selection of participants and survey method

A total of 353 potential participants composed of students, employees or researchers who took part in the ecosystem monitoring program at our study site from 1991 to 2019 was

available. Among the people enrolled for fieldwork, we contacted 259 participants who satisfied the criteria listed below, following a single stage sampling design (Creswell 2009), and eventually sent a reminder to participants that did not respond within two weeks. We asked participants to fill a questionnaire for every field season they participated in.

Attributing observations to the wrong year is a risk when collecting testimonials of past observations from participants who were involved for multiple field seasons. We assumed that participants visiting the site multiple times would find it easier to assign observations to their first field season (a memorable event due to novelty) and their last (the most recent) than to field seasons falling in between, especially if there were more than one. Thus, because we assumed that the risk of misattributing observations would increase for participants with more than three field seasons, only potential participants with one to three field seasons were initially contacted. However, if fewer than three testimonials were collected for a given year, we contacted additional participants that spent more than three field seasons until either three testimonials were collected, or all potential participants were contacted for that year.

Questionnaires were filled either directly by participants or through a structured interview on the phone or via videoconference. Self-completed questionnaires can easily reach large numbers of participants but can be of lesser quality if questions are confusing to the participant (Bryman 2016). Structured interviews with a fixed set of predetermined questions (i.e., identical to the self-completed questionnaire) can alleviate the problems caused by confusing questions due to the presence of the interviewer, but are more time-consuming (Creswell 2009; Bryman 2016). We assumed that participants involved in more than one field season would find it easier to be interviewed than to fill multiple questionnaires. Additionally, there were typically fewer participants in the years of 1991-2010 than later, increasing the importance of each testimonial in those years and making it logistically feasible to proceed by interview. All other participants who worked in the field between 2011 and 2019 for a single season received the self-completing questionnaire via email. If the questionnaire was filled incorrectly (e.g., unclear location of observations, missing information), we contacted the participant for an interview. A figure summing our selection of participants and survey method is available in supplementary materials.

1.5.4 Testimonials

We built a 14 questions, closed format (i.e., with a predetermined set of answers) questionnaire on Microsoft Forms to collect testimonials of opportunistic observations of ermines, lemmings and snowy owls between 1991 and 2019 at our study site (Table 1.S1). Brown and collared lemmings were pooled as "lemmings" as they are hard to distinguish at a distance. The questionnaire was pre-tested by four experienced ecologists who have in-depth knowledge of the study area and wildlife species. Questions were directed towards whether the participants observed one, several or no individuals of the above-mentioned species and at which frequency. Considering the studied species, their high amplitude fluctuation of abundance and their ease of detection, we considered that no academic or professional training in wildlife biology was needed to properly answer the questionnaire. Answers were collated into scores that represent a hierarchical level of abundance (Table 1.1). For ermines, the scores reflected four different levels of abundance: no ermine < one individual < many sightings of lone individuals < presence of at least one family. For lemmings, questions were directed towards distinguishing low, intermediate and high abundance years (i.e., 3 possible scores). Because snowy owls typically nest at our site only when lemmings are highly abundant (Therrien et al. 2014), we used binary scores. We averaged testimonial scores across participants for a given species and year providing an annual relative abundance index. These abundance indices differ from the ones derived from systematic or standardized protocols in several ways: they were not obtained by the same observers (i.e., there were many more people providing testimonials than people participating in the systematic sampling) and were not always covering the same time scale during the summer (i.e. lemming trapping and owl nest searching were done at specific periods whereas testimonials were based on the whole field season). Such indices were only calculated for the Qarlikturvik Valley, where most of our participants spent their time. Testimonials that originate from other regions of Bylot Island were not considered.

We estimated the sensitivity of the testimonial-based annual abundance indices (i.e., averaged scores) to an additional testimonial. To do so, we randomly sampled an additional testimonial from all available testimonials, across all years, combined it to the real testimonials and calculated a new abundance index. A 95% confidence interval was built by

repeating this process 5000 times (i.e., sampling and calculating the average score). This bootstrapped confidence interval is a simple representation of the sensitivity of each annual index to the recorded values and considers the possibility that years with scores of 0 might be false negatives (i.e., the species of interest was present but not detected).

Table 1.1. Types of observations reported in the questionnaires and associated scores.

Species	Testimonial answer	Score
Ermine	None were seen	0
	One sighting of a lone individual	1
	Multiple sightings of lone individuals	2
	At least one family group sighting	3
Lemmings	None were seen	0
	Some were seen, but rarely	1
	They were often seen	2
Snow owl	None were seen	0
	Nesting snowy owls were seen	1

Two additional sources of data were collected. First, to estimate the impact of time spent in the field on testimonial scores, each testimonial obtained from 2003 to 2019 was associated with the number of days spent in the field by the observer. This information was only available for the period 2003-2019. Secondly, some participants supported their observations of ermine with direct evidence from notebooks (i.e., they had written down their observations at the time) and/or dated photographs. These were recorded as proof of observations allowing us to ground-truth part of the received testimonials (see Statistical analyses). Since lemmings and snowy owls were systematically monitored for most of the period over which testimonials were collected, this additional information was only recorded for ermines.

1.5.5 Systematic sampling

To assess the reliability of testimonial-based abundance indices, we compared them with abundance estimates obtained from more systematic field sampling for either a subset (i.e.,

ermine) or the whole time series (i.e., lemmings and snowy owls). Although a minority of participants trapped lemmings or searched for snowy owl nests during their field work (respectively two and one person per year), questions were directed towards what their general impression of abundance was, not what they had trapped or surveyed, which helped mitigate interdependency between the testimonials and systematic indices.

For the ermine, standardized estimates of relative abundance were available from 2007 to 2019 based on incidental observations recorded daily in the field throughout the summer. Past studies reported that systematic recording of incidental field observations provided reliable estimates of relative abundance, especially in species with high-amplitude population fluctuations (Hochachka et al. 2000; Fauteux et al. 2018). Since 2007, a protocol was set to collect incidental wildlife observations on a daily basis from all field workers on Bylot Island along with the observation effort calculated as the number of hours spent in the field by each person. Although this method has not been tested specifically for ermines, it provided the most comprehensive dataset available for this species covering the whole summer (i.e., ~1 June until 20 August). The relative abundance of ermines during the summer was derived from the sum of opportunistic observations recorded (i.e., number of observed individuals) divided by total field effort (person-hours).

Summer densities of lemmings were estimated with trapping surveys from 1993 to 2019 in the Qarlikturvik Valley. Two methods were used: snap-trapping (1993-2016) and live-trapping (2004-2019). Abundance estimates obtained with snap-trapping were converted into densities based on the high correlation between snap- and live-trap estimates during the overlapping period (2004-2016) (see Fauteux et al. 2018 for methodological details). Densities of both collared and brown lemmings were summed to obtain a single estimate per year. Only the density estimates from the wetland habitat were used as this habitat was continuously monitored from 1993 through 2019.

For snowy owls, nest densities (nest/km^2) were available from 1993 to 2019 either on an area of 52 (1993-2000) or 104 km^2 (whole Qarlikturvik Valkley 2001-2019). Owl nests were found by spotting owls flying off a nest at a distance or harassing people intruding into their territory during systematic searches of suitable nesting areas such as ridges along hills or along river embankments (Seyer et al. 2020).

1.5.6 Statistical analyses

1.5.7 Field effort and proof of observations

We investigated if the number of days spent in the field in a given year by participants influenced their testimonial scores. To do so, we used cumulative link mixed models (clmms; R package "ordinal", Christensen & Brockhoff, 2013). These models estimate if the probability that an observation falls in a certain ordered category (i.e. score) is influenced by external variables (e.g., Gagnon et al., 2020). We built the following model with year and participant as intercept random effects : $Score \sim Number\ of\ days + (1|Year) + (1|Participant)$; and compared its AICc score to a null model : $Score \sim 1 + (1|Year) + (1|Participant)$. We considered that if the ΔAICc between the models was < 2, then the number of days in the field had low influence on a testimonial score (Arnold 2010).

We also attempted to ground-truth ermine observations with proof of observations when available, such as dated pictures or field book notes. Thus, we calculated two metrics: the proportion of years for which ermines had been reported by testimonials and at least one proof of observation exists, and the proportion of testimonials that provide such proofs. A high proportion of ground-truthed observations provided high confidence in the testimonials since no standardized sampling data existed on ermines for most of the 1991-2019 period.

1.5.8 Comparison between testimonial-based and systematic sampling abundance indices

We investigated if testimonial-based and systematic sampling abundance indices correlated positively using Spearman ranks correlation. Significant correlation coefficients (ρ) of ≥0.7 were considered as high. We computed a bootstrapped 95% CI on the correlation coefficient to assess significance.

Additionally, for lemmings and snowy owls, we tested if the time since the reported observations had an effect on the correlation score of testimonial-based and systematic sampling time series. To do so, we computed the Spearman correlation scores across the

time series in sliding windows of 9 years (i.e. a third of the time series) by 1-year increment. We built three generalized linear models (family Gamma, link = log), each with a single covariate, to investigate which one best explained the Spearman correlation scores. The covariates were the delay in years between field observations and completion of the questionnaire (represented by the year in the middle of the window), the average number of testimonials per year in the considered window, or the intercept (i.e. null model). All fixed effects were in interaction with the term species, as both lemmings and snowy owl data were used. We then proceeded with a model selection based on AICc. We considered that the model with the lowest AICc score and a ΔAICc < 2 would indicate which parameter had the stronger effect on the Spearman correlation scores (Arnold 2010), i.e., on the relationship between testimonial-based and systematic sampling-based estimates of population sizes.

1.5.9 Ecological relevance

To be of any use in deciphering ecosystems dynamics, testimonial-based abundance time series should be able to account for ecological processes. We verified if well-known ecological phenomena, either already documented at our study site or elsewhere, could be detected with the testimonial-based time series. First, we attempted to detect the known predator-prey relations between snowy owls and lemmings (Therrien et al. 2014) by testing the Spearman correlation coefficient between their respective testimonial time series. Abundance of snowy owls is known to be positively related to lemming density in the Arctic (Gilg et al. 2006; Therrien et al. 2014).

Secondly, the population dynamics of lemmings and ermines were analyzed by testing for the presence of cycles in testimonial-based abundance time series. For lemmings, we compared those results with the ones obtained using systematically estimated densities. Lemming populations are known to fluctuate according to 3- to 5-year cycles, and ermines tend to do the same in the Arctic (Sittler 1995; Gilg et al. 2003; Gruyer et al. 2008; Bilodeau 2013). Clear, unnoisy cycles can be easily detected with autocorrelation coefficients or autoregressive models, but ecological time series influenced by stochasticity often violate assumptions of these methods (Cazelles et al. 2008; Menyushina et al. 2012).

Wavelet analyses are designed to handle such time series that may be affected by stochasticity and vary in periodicity over time (Cazelles et al. 2008). Ermines and lemming time series were detrended with local Loess polynomial regression to ensure stationarity. We used a 10 year detrending window to encompass at least two cycles.

To determine the robustness of the results from the wavelet analyses, we used the same methodology on 500 testimonial-based time series that were previously generated by bootstrapping abundance indices with testimonials randomly sampled from all testimonials (see Testimonials section). For each iteration, we extracted the power average (i.e. the strength of detection for a given periodicity) and its significance compared to white noise at $\alpha < 0.05$ and $\alpha < 0.1$. All wavelet analyses, as well as the resulting periodicity, were fitted to our data with the R package "WaveletComp" (Roesch & Schmidbauer 2018).

1.6 Results

1.6.1 Testimonials

Overall, among the 259 contacted people, 131 participants either answered the questionnaire or were interviewed. Collected answers from both methods for a single field season and participant are hereafter called a testimonial (Fig. 1.1; Table 1.2). A total of 205 testimonials were collected with half of them obtained from interviews, the other half from self-completed questionnaires. We obtained multiple testimonials from 46 participants and participants spent an average of 1.38 (mode of 1.0) field seasons at the study area. One participant, who was involved for 10 field seasons, was exceptionally interviewed to increase sample size in the first year of the project (1991). Participants reported 70 observations of ermines, 126 of lemmings and 87 of snowy owls in total. Testimonials allowed the reconstitution of relative abundances time series in all taxa for the whole study period (Fig. 1.2). As expected, relative abundance showed large interannual variations, ranging 0-2.9 for ermines, 0-2 for lemmings and 0-1 for snowy owls.

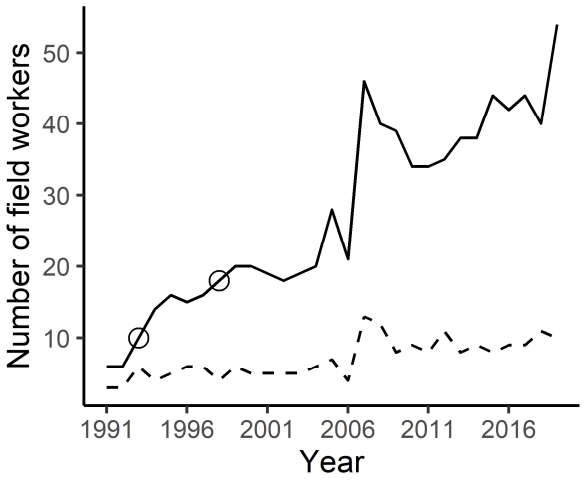

Fig. 1.1. Number of field workers present annually at the Bylot Island research station (solid line) and number of participants to our questionnaire (dashed line) per year. Empty dots in the solid line in 1993 and 1998 are years when the total number of people who were present at the field station is unknown.

Table 1.2. Summary of the information reported in the testimonials reported for the Qarlikturvik Valley, Bylot Island, NU. A testimonial includes the observations of a participant for a single year.

Criteria	Statistics
Number of participants	131
Number of testimonials	205
Number of testimonials reporting sightings of lemmings	126
Number of testimonials reporting sightings of snowy owls	87
Number of testimonials reporting sightings of ermines	70
Proportion of ermine sightings supported by photographs or field book notes	0.44
Mean, mode and maximum number of seasons spent at the study area per participant.	1.38, 1, 10
Proportion of testimonials issued from interviews	0.5
Mean, minimum and maximum number of testimonials per year	7.1 [3,13]

1.6.2 Field effort

We found little evidence that the number of days spent at the study area influenced the testimonial score for all three species as null models were either preferred or showed a ΔAICc < 2 compared to the model including time (Table 1.3). The term Participant was dropped from all models as comparison between the full model and models without either Participant or Year as random effects showed that only Year was a significant factor. The *p*-values of the LRT tests between full models and those without Participant were respectively 0.98, 0.99 and 0.90 for the ermine, lemmings and snowy owl models.

1.6.3 Comparison between testimonial-based and systematic sampling abundance indices

For all taxa, testimonial-based and systematic or standardized sampling abundance indices were significantly correlated, highly for ermines and lemmings, and to a lesser extent for snowy owls (Table 1.4, Fig. 1.2). For the standardized monitoring of ermine, total field effort spent recording incidental observations ranged from 680 to 3712 observer-hours per year, and the total number of ermine sightings annually ranged from 0 to 34. It is worth noting that 82% of the years when an ermine observation was reported in testimonials, at least one proof (dated photograph or field book notes) was provided by a participant (Fig. 1.2). The time since the reported observations and the average number of testimonials per year were strongly negatively correlated (ρ = -0.96). Our model selection suggests that the average number of testimonials is the main determinant of the Spearman correlation score but that the effect of time cannot be excluded (Table 1.5).

1.6.4 Ecological relevance

Testimonial-based abundance time series of snowy owls and lemmings were significantly correlated, although slightly less than between time series obtained from systematic sampling (i.e. nest and trapping densities, Table 1.4). Wavelet analyses based on testimonial-based abundance time series suggest that the ermine population of Bylot Island was cyclic over the study period (Fig. 1.3). The average periodicity detected in the time series neglecting uncertainty at $\alpha < 0.05$ was 2.9 years (CI 95% [2.7; 3.0]). However, analysis of bootstrapped time series, which considered the 95% CI of the scores, suggests a

slightly longer periodicity around 3.3 years (CI 95% [2.6; 4.8]). Significant periodicity was also detected in lemming time series based on both testimonial-based abundance (average periodicity of 3.3 years, CI 95% [2.0; 3.85) or systematically sampled densities (average periodicity of 3.8 years, CI 95% [3.6; 4.0]).

Table 1.3. Model selection testing the effect of the number of days spent at the study area (Time) on the testimonial scores for ermines, lemmings, and snowy owls. K = number of parameters, LL = Log-likelihood, ΔAICc = the difference between the current model and the one with the lowest AICc value, AICcwt = AICc weight. Models followed by an * were selected on the basis that they had the lowest number of parameters and a ΔAICc <2.

Species	Model	K	LL	ΔAICc	AICcWt
Ermine	Null*	4	-105.57	0	0.73
	Time	5	-105.48	1.97	0.27
Lemmings	Time	4	-73.63	0	0.62
	Null*	3	-75.21	1.00	0.38
Snowy owl	Null*	2	-38.19	0	0.73
	Time	3	-38.14	2.00	0.27

Table 1.4. Spearman rank correlations between testimonial-based and systematic sampling abundance time series. Correlation coefficients (ρ) and their 95% bootstrapped confidence interval (C.I.) are presented. Coefficients in bold are significant (i.e., 95% C.I. does not include zero).

	Ermine testimonial	Ermine opportunistic observations	Lemming testimonial	Snowy owl testimonial	Lemming density
Ermine opportunistic observations	**0.84 [0.56, 0.95]**				
Lemming testimonial	**0.50 [0.13, 0.78]**	0.43 [-0.14, 0.84]			
Snowy owls testimonial	-0.21 [-0.19, 0.60]	0.13 [-0.58,0.69]	**0.53 [0.19, 0.77]**		
Lemming density	0.29 [-0.09, 0.61]	0.31 [-0.28, 0.782]	**0.83 [0.63, 0.94]**	**0.47 [0.10, 77]**	
Snowy owl nest density	0.14 [-0.22, 0.51]	0.21 [-0.42, 0.79]	**0.65 [0.35, 0.85]**	**0.69 [0.49, 0.85]**	**0.69 [0.40, 0.88]**

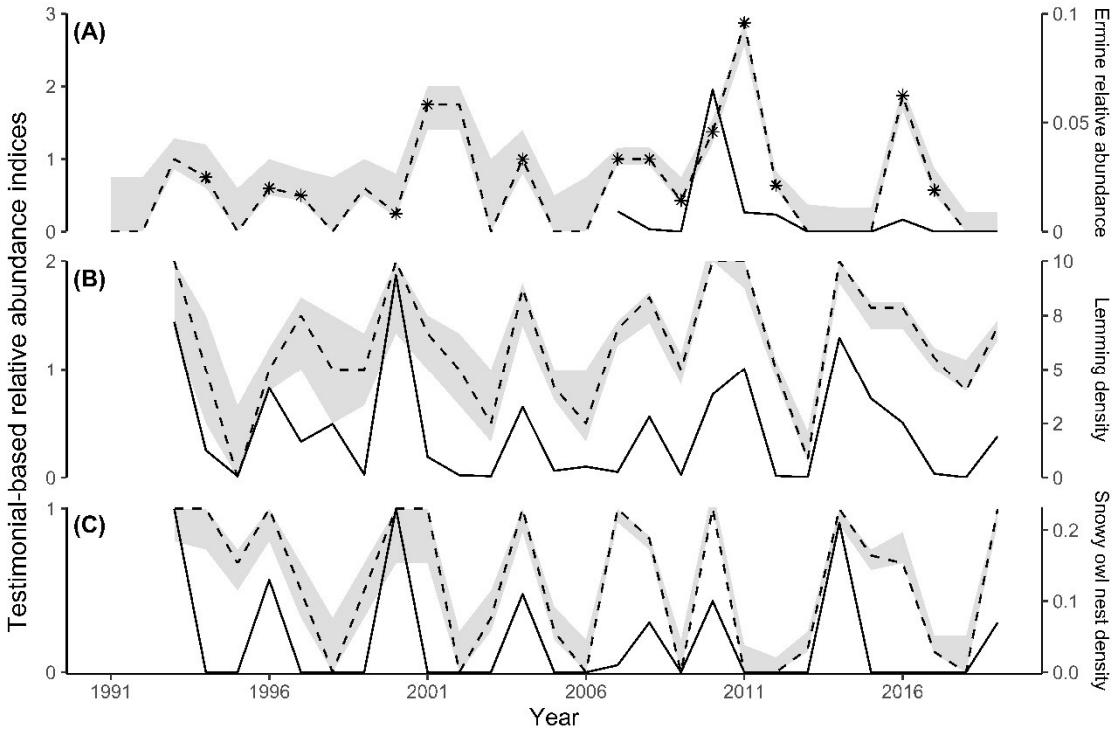

Fig. 1.2. Annual abundance estimates based on testimonials (dashed line) and systematic sampling (solid line) of three sympatric taxa on Bylot Island, Nunavut, Canada. The 95% confidence intervals (grey ribbon) of annual indices are calculated with an additional random testimonial sampled from all testimonials (see methods for details). **(A)** Ermine**.** Asterisks represent years where at least one proof (i.e. dated photograph or field book notes) of observation was reported. Abundance is estimated by dividing the number of opportunistic observations recorded by annual field effort. **(B)** Lemmings. Density is measured as individuals/ha (densities of both brown and collared lemmings were summed). **(C)** Snowy owls. Density is measured as the number of active nests per km^2.

Table 1.5. Model selection of parameters impacting the Spearman correlation coefficient between testimonial-based and systematic sampling abundance estimates based on 9-years sliding time-window subsets of the original time series (27 years). Lemmings and snowy owls are considered. Parameters are the delay between field observations and the completion of the questionnaire (Delay), the average number of annual testimonials during the time window (ANT), and the species. K = number of parameters, LL = Log-likelihood, ΔAICc = the difference between the current model and the one with the lowest AICc value, AICcwt = AICc weight. Models followed by an * were selected on the basis that they had a ΔAICc < 2 with the second-best model.

Model	K	LL	ΔAICc	AICcWt
ANT×Species *	5	52.02	0	0.93
Delay×Species	5	49.48	5.08	0.07
Intercept×Species	2	28.83	38.74	0

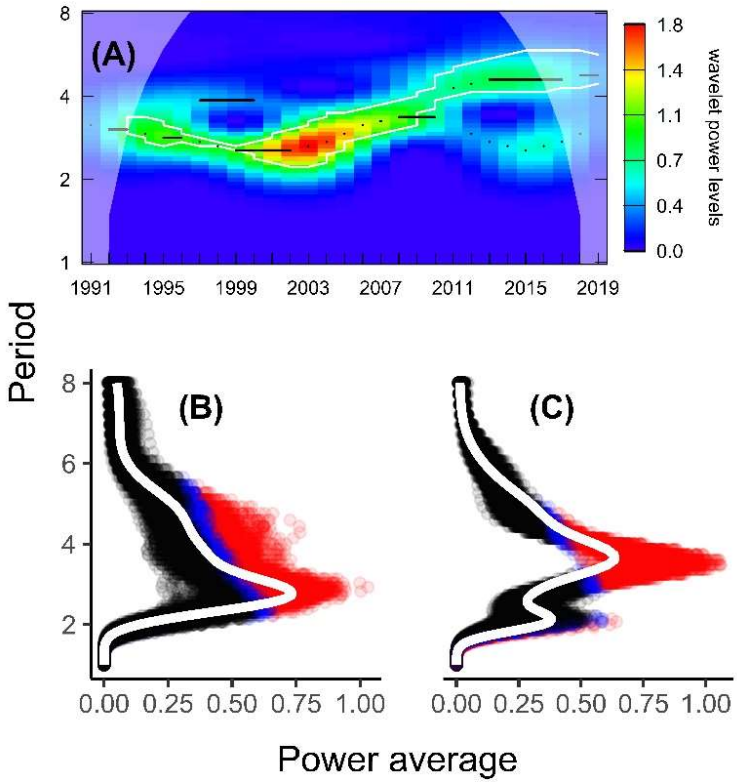

Fig. 1.3. Wavelet analysis results of the relative abundance of ermines and lemmings at Bylot Island, Nunavut, Canada, based on testimonial. **(A)** Wavelet power spectrum of the relative abundance of ermines. Colors indicate the wavelets power level, black lines or dots are the detected periods and the white line delimits the area where the cyclic pattern is significant. The pale-coloured area on the edges of the power spectrum is outside the cone of influence. **(B) Ermine** and **(C) Lemming:** Power average of each period for 500 simulated testimonial-based time series. Blue dots represent periods that differ significantly from white noise at $\alpha < 0.1$ and red dots at $\alpha < 0.05$. Black dots are not significantly different ($p > 0.1$). White line represents the observed power averages in **(B)** the original ermine testimonial-based time series and **(C)** the lemming density time series.

1.7 Discussion

Our results showed that the relative population abundance of highly fluctuating arctic small mammals and snowy owls can be reconstructed over almost three decades from testimonials of field workers. Specifically, we have shown that abundance indices generated from our testimonial-based method were 1) not affected by the field effort of participants (number of days spent in the field), but mainly related to the number of testimonials obtained, 2) highly correlated to abundances estimated with systematic or standardized sampling, and 3) insightful to characterize the population dynamics of species and predator-prey relationships. These claims were supported in three different taxa, for which the overlap between systematic sampling and testimonial-based time series varied between 13 and 27 years. This suggests that we can confidently reconstruct the abundance of ermines over a 29-year period, which is more than twice the length of the abundance time series derived from standardized sampling for this cryptic and potential key predator of the High Arctic tundra. Our method differs from other methods based on interviews of land users (i.e., indigenous and local ecological knowledge) seeking to reconstruct past abundances (Knaus et al. 1950; Ferguson et al. 1998; Anadón et al. 2009; Peñaherrera-Palma et al. 2018; Reif et al. 2021) by its aim to create annual abundance indices. It appears as a promising avenue to reconstruct abundance time series of species recently considered in ecological monitoring projects where field workers can provide testimonials of past observations. It may be particularly useful to reconstruct past abundances of highly fluctuating species, such as those with outbreak dynamics.

1.7.1 Reliability of testimonials, ecological relevance and limitations

Abundance indices based on testimonials may have great potential, but they have inherent caveats calling for caution when interpreting them. The field effort, which can vary tremendously between participants, could affect the number of reported sightings (Hochachka et al. 2000) and ultimately the abundance scores associated to testimonials. Yet, in all cases, we have found no link between time spent at the study area (i.e., field effort) and the score associated with a testimonial. However, such result does not dismiss the lack of precision of scores when effort is low. Our result can be explained by our use of abundance categories instead of an exact number of sightings, as observations of

participants with different field efforts can easily fall into the same category. In fact, considering the landscape at our study site (flat, treeless tundra) and the behavior of the concerned taxa, the answers to the questionnaire should be obvious to any observer who spent some time in the field during a given year. Moreover, participants who have been in the field for a shorter period (e.g., one week) overlapped with those staying for longer periods (e.g., several weeks), and thus could share information about their observations while in the field, again reducing the potential impact of field effort.

Interestingly, the correlation coefficients of testimonial-based and systematic abundance indices observed here (i.e. > 0.7) are of the same magnitude than those reported by Fauteux et al. (2018) and Hochachka et al. (2000), who, respectively, compared standardized incidental observations to lemmings live-trapping densities (r = 0.90) and to common raven (*Corvus corax,* r = 0.60), coyote (*Canis latrans,* r = 0.65) and spruce grouse (*Falcipennis canadensis,* r = 0.80) abundances based on systematic nest searching and transects. Hence, although testimonial-based and systematic or standardized abundance indices may have different origins (i.e. different observers, protocols) and cover different spatial or temporal scales, both can be proxies of the abundance of a given species.

Correlations between abundance indices from testimonials and from systematic or standardized sampling were higher for ermines and lemmings than for snowy owls, possibly due to the higher number of testimonial scoring possibilities (respectively 4, 3 and 2), which could have allowed a better categorization of true abundance. Differences between the systematic sampling protocols of snowy owls and the behavior of our participants can also explain this result. Our systematic monitoring protocols only records breeding pairs observed within a specific area, while testimonials from participants could also have included non-breeding individuals or pairs observed outside the systematically sampled area.

Our results suggest that the correlation scores between testimonial-based and systematic sampling abundance indices were best explained by the average number of testimonials, and less so by the delay between the observations and the questionnaire. Although we cannot completely rule out the effect of time on memories, the high proportion of

participants who had access to dated pictures or notebooks likely limited errors in testimonials. Reif et al. (2021) showed that older ornithologists, with their memories and field notes, were able to assess the trends of 75% of the 209 bird populations monitored in the Czech Republic Atlas from 1960 to 2010. Moreover, studies have shown that memories associated with strong emotions, both positive and negative, are clearer for a longer period than memories without emotion (Tyng et al. 2017). This could have had a positive effect on the accuracy of testimonials as most, if not all, participants had strong interest in charismatic arctic wildlife like snowy owls and ermines and, to a lesser extent, lemmings. Thus, even if collected decades after the events, testimonials, and the abundance indices they generate, can be valuable (Reif et al. 2021).

In addition to informing on past abundance, our method can also be used to investigate ecological phenomena. Testimonial-based abundance indices were able to decipher the dependency of snowy owls on lemmings as well as the cyclic dynamics of lemmings and ermines, phenomena observed at our study sites (Gruyer et al. 2008; Bilodeau 2013; Therrien et al. 2014) and elsewhere (Johnson et al. 2000; Gilg et al. 2006) with systematic sampling. Thus, even when lacking the precision brought by rigorous systematic sampling, testimonial-based abundance time series appears successful in detecting ecological phenomena such as predator-prey interactions and population dynamics of species with high amplitude fluctuations of abundance.

1.7.2 Applications

Research projects where the observations by participants can be relatively precise spatially and temporally can benefit from a testimonial-based approach. Long-term research projects, research stations with regular field workers or national parks often have access to a large population of potential participants (e.g., seasonal workers, ecotourists). The low cost of this approach can be particularly helpful for research questions where the cost of standard sampling techniques is prohibitive, but where potential observers are numerous.

The testimonial-based approach can be complementary to systematic sampling and fills some of its deficiencies. Systematic sampling often yields precise estimates but requires significant effort, both in time and budget, and is valid at a limited spatial or temporal scale

(Anadón et al. 2009). Observations from field workers or land users, on the other hand, are harder to locate but can properly describe abundance variation on a large spatial scale with relatively little effort (Peñaherrera-Palma et al. 2018; Braga-Pereira et al. 2021). They can inform us on long-term populational trends even if estimates are neither quantitative nor as precise as systematic sampling measurements (Ferguson et al. 1998; Anadón et al. 2009; Peñaherrera-Palma et al. 2018). Moreover, to avoid the bias associated with creating an annual abundance index from averaged arbitrarily given scores, cumulative-link mixed models (Christensen & Brockhoff 2013) can be used to model the probability of a testimonial to fall in an ordered category.

1.7.3 Limits and potential improvements

Our experience with the testimonial-based approach, as well as insights from social sciences and the literature on indigenous and local knowledge, point towards some key aspects to consider if this method is to be used successfully in wildlife ecology. First, the target participant population must be knowledgeable about the species of interest (Anadón et al., 2009; Camino et al., 2020; Gagnon & Berteaux, 2009; Peñaherrera-Palma et al., 2018). Participants need to be able to properly identify species. In our case, we had a relatively large population of knowledgeable participants (field workers) capable of identifying the limited number of species present at the study site and locating them in time. Yet, even under these favorable conditions, within-year testimonial scores differed between participants. The experience of participants in animal identification may be more critical in systems with more biodiversity. As a solution, collecting as many testimonials as possible without increasing the risk of attributing them to the wrong year should make testimonial-based abundance indices more reliable, as suggested by our analysis. However, as observed here, time series based on testimonials from a sufficient number of participants may rarely exceed 30 years due to the increased difficulty of contacting the earliest participants.

Secondly, questions asked to participants need to be precise and able to produce different set of answers that can be ordered in terms of relative abundance (i.e., Table 1.1). An ordinal scale allows the attribution of scores to answers or to use cumulative-link mixed

models if the abundance is to be modelled. Species-specific questions concerning observable proxies of abundance is a key element.

1.7.4 Conclusion

Our testimonial-based approach successfully reconstructed past relative abundances of three Arctic terrestrial taxa and generated the longest ermine time series for the Canadian Arctic. Our results, along with the increasing body of literature on local and traditional ecological knowledge (Anadón et al., 2009; Braga-Pereira et al., 2021; Camino et al., 2020; Ferguson et al., 1998; Gagnon et al., 2020; Peñaherrera-Palma et al., 2018), substantiate the usefulness of testimonials in research and conservation. While one must recognize the limitations of this method, it can unlock the necessary data to address difficult ecological questions in ecosystems where traces of past abundances are left in the memory of knowledgeable field workers or land users. Further research should focus on calibrating testimonial-based relative abundance indices with systematic sampling data and thus widen the scope of questions for which this type of information can be used.

1.8 Conflict of Interest

We declare no conflict of interest.

1.9 Authorship statement:

David Bolduc: Conceptualization, Methodology, Data Acquisition, Data Analysis, Writing – Original Draft and revisions; **Dominique Fauteux**: Conceptualization, Methodology, Data Acquisition, Writing – Review & Editing; **Catherine A. Gagnon**: Methodology, Writing – Review & Editing; **Gilles Gauthier**: Data Acquisition, Writing – Review & Editing; **Joël Bêty**: Conceptualization, Data Acquisition, Writing – Review & Editing; **Pierre Legagneux**: Conceptualization, Methodology, Writing – Review & Editing.

1.10 Acknowledgement

We sincerely thank all participants to our questionnaire for their time and enthusiasm, M.-C. Cadieux for her help in contacting past fieldworkers and Dominique Berteaux for reviewing the initial questionnaire.

1.11 Funding

This work was supported by the Sentinelle Nord program from the Canada First Research Excellence Fund, ArcticNet [grant number PP12] and the National Science and Engineering Research Council [grant number RGPIN-2019-05185].

1.12 Data accessibility statement

All data used in this manuscript will be made available in open access upon request or publication on NordicanaD.

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1.14 Supplementary materials

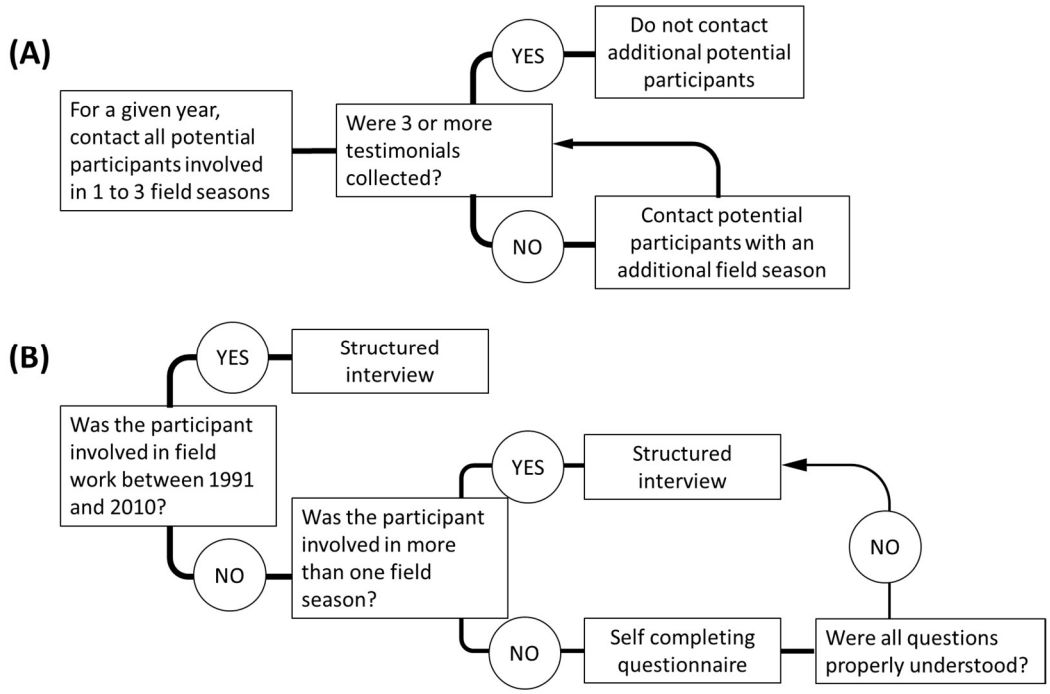

Fig. 1.S1. Schematic description of the **(A)** participant selection and **(B)** survey method for the collection of testimonials of opportunistic observations from scientists who conducted field work at the Bylot Island field station, Nunavut, Canada.

Table 1.S1. Questionnaire sent to participants

	Question	Type	Answer example or choice
1	All testimonials are precious. Would you accept to discuss your observations with us?	Confirmation	1-Yes 2-No
2	Which year were you on Bylot Island?	Time information	ex: 2011
3	What was your main tasks during your stay on Bylot Island?	Participant information	ex: I was a field assistant working on lemmings.
4	During your stay, have	Fauna	1-Yes, I remember seeing ermines.

	you seen ermines?	observations, Ermines	2-No, I remember not seeing ermines. 3-I don't remember.
5	During your stay, do you remember if your colleagues had seen ermines?	Fauna observations, Ermines	1-Yes, I remember that ermines were seen. 2- No, I remember that no ermines were seen. 3- I don't remember.
6	If you saw ermines, how often did you observe them?	Fauna observations, Ermines	1-Once in the whole summer. 2-More than once during the summer. 3-I don't remember.
7	If you saw ermines, were they solitary individuals or families?	Fauna observations, Ermines	1-I remember seeing, or hearing that somebody else had seen, a family. 2-I remember seeing, or hearing that somebody else had seen, a solitary individual. 3-I don't remember.
8	If you saw ermines, give all locations where you or someone else sighted them.	Fauna observations, Ermines	Qarlikturvik Valley (Camp 1, Black mountains); Camp 2; Camp 3; Goose Point; Dufour Point; Others; I don't know.
9	If you have answered "Others" to question 8 please precise.	Fauna observations, Ermines	"I have in my notebook an ermine at XYZ GPS location"
10	During your stay on Bylot Island, do you remember if yourself or others have seen lemmings?	Fauna observations Lemmings	1-Yes, I remember seeing lemmings. 2-No, I don't remember seeing lemmings. 3-I don't know.
	If you saw lemmings, can you describe their relative abundance? (ex:	Fauna observations, Lemmings	"I saw none", "I saw one every now and then", "I saw a lemming every day, there were plenty".

11	"They were everywhere", "I saw few", "I think we were in a peak")		
12	During your stay on Bylot Island, do you remember if yourself or others have seen nesting snowy owls?	Fauna observations, Snowy owls	1-Yes, I remember that snowy owls were nesting this year. 2-No, I remember that snowy owls were not nesting this year. 3-I don't know
13	Did you take pictures of ermines during your stay on Bylot Island?	Confirmation	1-Yes 2-No 3-I don't know
14	Additional comments or observations.	Confirmation	" I saw ermines twice in 2001. Once here and once there"

Chapitre 2 - Seasonal role of small mustelids in rodent cycles: an empirical test of the specialist predator hypothesis in the High-Arctic

2.1 Résumé

Malgré un durable intérêt sur la question, le rôle des petits mustélidés dans les cycles de micromammifères reste toujours incompris. Ici, nous testons l'hypothèse du prédateur spécialiste (HPS), qui suggère un rôle prépondérant des petits mustélidés dans la génération des cycles d'abondance, avec des données à long-terme sur l'abondance d'hermine (*Mustela richardsonii*) et de ses proies, les lemmings (*Dicrostonyx greonlandiscus* & *Lemmus trimucronatus*) à l'île Bylot, NU. Nos résultats montrent que l'abondance d'hermine était influencée autant par les abondances présentes (*t*) que passées (*t-1*) de lemmings, faisant des hermines une source potentielle de densité-dépendance avec délais, tel que prévu par L'HPS, et ce durant l'hiver. Nos simulations ainsi que l'analyse saisonnière de l'impact de l'hermine suggèrent qu'elle prolongerait la phase de faible abondance et pourrait retarder le rétablissement des populations de lemmings, menant ainsi à des cycles de 3 à 5 ans.

2.2 Abstract

Despite long-lasting interest, the exact mechanisms behind population cycles remain elusive. An ongoing debate concerns the specialist predator hypothesis (SPH), which suggests a that small mustelid predation is necessary to generate rodent cycles. Specifically, the SPH predicts that the predator should respond numerically to the abundance of its prey with a delay of approximately one year, leading to delayed density-dependence in the dynamics of the prey population. Yet, the interactions between these elusive predators and their prey are difficult to monitor, especially in the snowy environments where small mustelids may have a predominant role. Here, we analyze the numerical response of small mustelids, the seasonality of their interactions with rodents and their impact on population cycles using long-term seasonal data on ermines and cyclic lemmings at a High Arctic site.

To address the SPH, we modelled the numerical response of ermines from past and current summer densities of prey and used path analyses to infer the origin of the delayed density-dependence in lemmings. The seasonality of their interactions was assessed using seasonal proxies of lemming population growth rate, obtained from the combination of summer densities and winter nest counts. We finally compared the cyclic properties of simulated lemming populations, generated in the presence or absence of ermines, with those of the observed population to grasp the impact of this small mustelid on population cycles.

Our results show that the numerical response of ermines to lemming fluctuations was delayed by one year and could mediate the delayed density-dependence in lemming growth rates. The impact of ermines was small but circumscribed to winter, a critical period when shifts in cycle phases occur and direct density-dependence seems relaxed. Our simulations suggest that ermines are not necessary to cycles *per se*, hence rejecting the SPH as an explanation to all cycles, but rather could promote low abundance phases, delay the recovery of lemming populations and lead to cycles of ca 3 to 5 years. Finally, our study corroborates the idea that declines are best explained by direct density-dependence and that small mustelids delayed response induce the low phase and lead to ≥3-year periodicities.

2.3 Introduction

The causes of population cycles have been debated since their first description to the scientific community (Elton 1924). Early models and empirical studies concluded that, for populations to cycle, their growth had to be affected by regulating factors that depended on past population densities, hereafter named delayed density-dependent factors (May 1976, Stenseth 1999). Maternal effects, social interactions, food limitation and predation were all hypothesized to induce such delayed density-dependence (Krebs et al. 1973; Andersson & Erlinge 1977; Ginzburg & Taneyhill 1994; Ergon et al. 2001; Turchin & Batzli 2001; Stenseth et al. 2002). As time is necessary to convert prey into offspring, predators that specialized on a prey species and showed little emigration capacities were quickly recognized as potential drivers of population cycles (Rosenzweig & MacArthur 1963). The role of such predators in the prey population dynamics was formulated as the specialist predator hypothesis (SPH). It states that to destabilize the prey population and induce cycles, resident specialist predators must respond numerically to the prey abundance with a

delay, have sufficient numerical and functional responses to regulate the prey population and have little possibility for prey switching or emigration (Andersson & Erlinge 1977; Korpimäki & Krebs 1996; Hanski et al. 2001).

In the context of rodent cycles, the term "specialist resident predator" usually refers to small mustelids, a group including weasels and ermines (*Mustela spp.*). In northern environments, they show an almost exclusive reliance on rodents as both groups remain active under the snowpack (Andersson & Erlinge 1977; Korpimäki et al. 1991; King & Powell 2006). The year-round presence of small mustelids and their capacity to enter most burrows of rodents leaves their prey little spatial and seasonal refuges (MacLean et al. 1974; Fitzgerald 1977; Simms 1979; Jędrzejewski et al. 1992; Mougeot et al. 2020). Moreover, their prey-caching behavior, which results in the killing of more individual prey than necessary for their daily survival (i.e., surplus killing), could enable them to rapidly deplete prey populations (Oksanen et al. 1985; Jędrzejewska & Jędrzejewski 1989; Jędrzejewski et al. 1992; King & Powell 2006). On the other hand, the term "generalist predators" (sensu Andersson & Erlinge (1977)) englobes predators that rapidly respond to changes in a prey population, either functionally with prey switching, like resident generalist predators, or numerically through migration and aggregation, like nomadic specialists. Such direct responses are thought to stabilize the prey dynamics (Andersson & Erlinge 1977; Korpimäki 1993; Hanski et al. 2001).

The SPH drew support from the analyses of long time-series of vole abundance in Fennoscandia (Hanski et al. 1991; Klemola et al. 1997; Korpimäki & Norrdahl 1998) and more recently from intensive studies in Finland (Sundell et al. 2013; Korpela et al. 2014) and Greenland (Gilg et al. 2006). However, studies in temperate Europe, which ranged from primeval forests to agricultural pastures, largely rejected the SPH, either because the numerical response of small mustelids was not delayed enough (Jedrzejewski et al. 1995; Graham 2001; Mougeot et al. 2019) or because they were shown empirically to have little impact on their prey (Jedrzejewski et al. 1995; Graham & Lambin 2002; Zub et al. 2008). This northern-temperate discrepancy could be explained by differences in seasonality as the long-term presence of snow, which isolates the rodent and mustelids from other predators, has been shown to promote cycles (Hanski et al. 2001; Norrdahl & Korpimäki 2002;

Stenseth et al. 2002). In northern systems where mustelids are absent, small rodents often fluctuate differently than the classic 3 to 5-yr cycles, either exhibiting longer cycle periodicity of 5 to 8 years or no periodicity at all (Fay & Rausch 1992; Menyushina et al. 2012). Furthermore, criticism emerged regarding previous studies that supported the SPH, arguing that they were based on inadequate data, short experiments and that population parameters (e.g., survival) were not calculated or reported properly (Graham and Lambin 2002, Oli 2003, Lambin et al. 2006, Lambin 2018). Even though the SPH has been rejected as a general explanation of cycles, small mustelids could still have a necessary role in maintaining small mammals at low abundances for an extended period (Korpimäki et al. 1991; Boonstra et al. 1998).

The SPH should ideally be tested with seasonal, long-term and synchronous empirical data on both rodents and mustelids. However, acquiring empirical data of population abundance throughout the year is challenging, especially for mustelids that are notoriously difficult to monitor. Hence, due to logistical constraints, such studies are extremely rare in environments characterized by long winters (Kleiven 2022) during which the snowpack could isolate the rodent-mustelid system from the stabilizing influence of generalist predators (Korpimäki & Norrdahl 1989a; Oksanen et al. 2001).

Here, we used a long-term environmental monitoring program conducted in the High-Arctic (Bylot Island, Nunavut, Canada) to evaluate the SPH and investigate the potential role of small mustelids (ermines, *Mustela richardsonii*) in the seasonal population dynamics of cyclic brown and collared lemmings (*Lemmus trimucronatus* & *Dicrostonyx groenlandicus*). First, we tested a key prediction of the SPH, that small mustelids respond numerically with a delay of one year to fluctuations of abundance of their prey. Even though we expected a limited direct response of ermines due to their restrictive reproductive physiology (Sandell 1984), surplus killing and food caching (Jedrzejewska & Jedrzejewski 1989) should enable them to survive at moderate abundance even after rodent prey reach low abundances. Hence, current prey densities are likely to impact ermine reproduction, survival and ultimately their abundance, whereas past prey densities might still influence its abundance through food-caching.

Secondly, we aim to seasonally assess the impact of ermine abundance on lemming population growth rates. On Bylot Island, lemming declines are mostly observed during fall. The growth, which does not happen every year, occurs in winter as they can reach high abundances through subnivean reproduction (Duchesne et al. 2011; Fauteux et al. 2015). If ermines are to drive lemming cycles, their impact should be strongest during fall and winter, indicating their role in decimating the lemming population or limiting its subnivean growth. Their impact during summer is thought to be limited as pups are not weaned (King & Powell 2006), intraguild predators constrains the activity of small mustelids (Zub et al. 2008) and lemmings are at their maximal reproductive capacities (Bilodeau 2013; Pitelka & Batzli 2018).

Finally, we used estimates of ermine abundance and lemming growth rates to produce predator and prey zero growth isoclines and assess the potential role of ermines in generating the observed 3 to 5-year lemming cycles (Gauthier et al. 2013). If specialist predators are sufficient to bring the prey population into a decline, then the prey isocline should extend over the range of observed densities. Moreover, if ermines are necessary to the observed cycles, then cycles characteristics (periodicities, proportion of years in the low phase) of lemming populations simulated without ermines should differ from those of the observed data. For example, periodicities and low phases could be shorter as observed in some vole populations in Europe (Barraquand et al. 2014) or longer as observed on Wrangle Island in Russia where ermines are absent (Menyushina et al. 2012).

2.4 Material and Methods

2.4.1 Study area

Our study area (73°08'N, 80°00'W) is located in the Qarlikturvik Valley on Bylot Island, Nunavut, Canada. The valley bottom is a mosaic of wetlands, characterized by ice-wedge polygons and mostly covered by graminoids and mosses, and of mesic tundra covered by herbs, graminoids and prostrate shrubs (Gauthier et al. 2011). The wet and mesic tundra comprise approximately of 14% and 76% of our study area, respectively. The remaining 10% is covered by the riparian habitat made of linear depressions carved by streams running through mesic tundra. The riparian habitat is particularly important for Arctic small

mammals in winter because they are conducive of heavy snow accumulation and provide the most insulated habitat against the extreme cold temperatures. Brown and collared lemmings are the only rodents present and both species fluctuate in abundance according to 3 to 5-years cycles (Gruyer et al. 2008; Bolduc et al. 2023). Brown lemmings have high amplitude cycles with >100-fold between peaks and lows whereas collared lemmings have low amplitude fluctuations. The ermine is the only mustelid on the island and their abundance is correlated with that of lemmings (Bolduc et al. 2023). The other resident predators are arctic foxes (*Vulpes lagopus*) and, when lemming density is high, nomadic snowy owls (*Bubo scandiacus*) and migratory rough-legged hawks (*Buteo lagopus*) and long-tailed jaegers (*Stercorarius longicaudus*) often nest there (Therrien et al. 2014).

2.4.2 Lemming abundance

Summer abundances of each lemming species were estimated in the two main habitats (wetland and mesic) with trapping data collected from 1993 to 2022. Snap-trapping (720 trap-nights/habitat) was conducted in late-July or early-August from 1993 to 2016 and live-trapping (11-ha grid/habitat, 432 trap-nights/grid/session) was conducted in mid-June ($D_{June,t}$), mid-July ($D_{July,t}$), and mid-August ($D_{August,t}$) from 2004 to 2022, except in 2020 and the two first session of 2021 due to COVID-19. Snap-trapping estimates were converted in annual population densities ($D_{Annual,t}$) based on the correlation between snap-trap indices and the mean of $D_{July,t}$ and $D_{August,t}$ live-trap estimates during the overlapping period (2004-2016) (see Fauteux et al. (2018) for methodological details). For years when live-trapping was conducted $D_{Annual,t}$ was equal to $D_{July,t}$. As we were interested in the lemming density over the study area, densities of both lemming species were summed and weighed based on the proportion of wetland (14%) and mesic habitats (86%, as it comprised the unmonitored riparian habitat) present in the study area to create a single estimate per year (Fig. 2.1).

2.4.3 Ermine relative abundance

There was no systematic survey of ermine abundances before 2007. Hence, we used ermine relative abundances estimated from testimonials of opportunistic observations made by fieldworkers on Bylot Island from 1993 to 2019 (205 fieldworker-year). Fieldworkers were

asked to remember their observations of ermines during summer (early June to late August) and their account was translated on an ordinal scale (0 = no ermine sightings, 1 = one ermine sighting, 2 = multiple sightings of lone ermines, and 3 = sighting of an ermine family). The average of these yearly scores provided an ermine relative abundance index (hereafter $Ermine_t$ for year *t,* Fig. 2.1) was strongly correlated with the short time series of relative abundance available from systematic survey (details in Bolduc et al. 2023). The same method was applied for the 2022 field season.

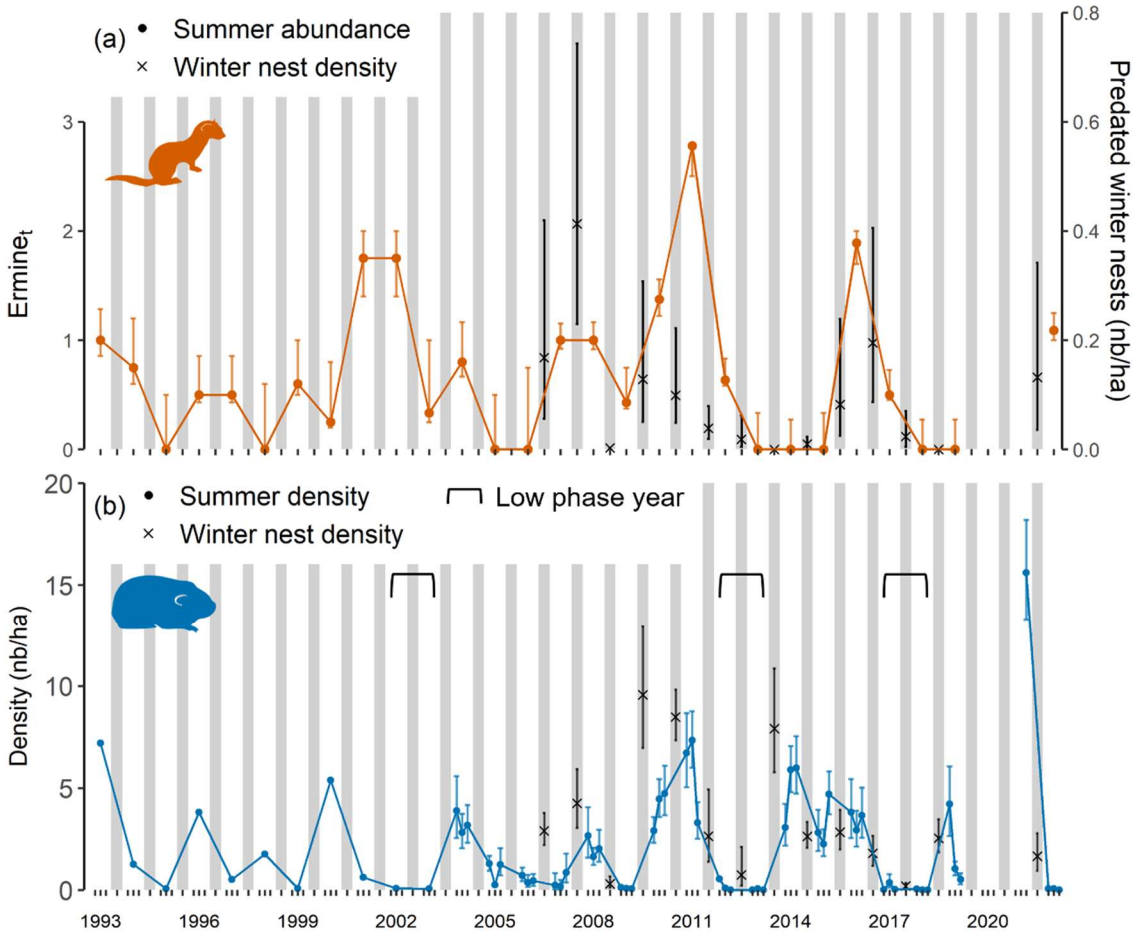

Figure 2.1. Seasonal time-series of ermine and lemming abundances on Bylot Island (Nunavut, Canada). Shaded area represents winter. a) Ermine relative abundance index (solid line, orange dots) in summer and density of lemming winter nests with signs of ermine predation (black crosses) and their 95% CI. b) Habitat-weighted summer lemming density (solid line, blue dots) and density of all winter nests (grey crosses) with their 95% CI when available. On the x-axis, ticks within summers align with the 15th of June, of July

and of August. Low phase years are grouped under braces. The phase was defined as years of < 0.5 ind/ha preceded and followed by a decline. If a given year fitted this description, the following year was included in the low phase.

2.4.4 Winter nest monitoring

From 2007 to 2022, lemming winter nests were sampled at snowmelt by walking 30 to 74 ~500 m permanent transects in mesic, wetland and riparian habitats. Detected nests were dissected and destroyed to avoid counting the following year. For each nest, distance from the transect and presence of signs of predation (e.g. lemming body parts such as paws, skulls, skin, stomachs, abundant hairs, etc.) was noted. Nest densities were estimated by distance sampling (Buckland et al. 2015) separately for each habitat. The rare nests at more than 30 meters from the transect were removed from the analyses (i.e., data truncation). Detection probabilities were modelled across years, allowing realistic detection function even in low abundance years, which are data deficient. The half-normal function was used for the mesic habitat whereas hazard-rate was used in wetland and riparian habitats. A yearly density estimates per nest category, either with predation ($D_{pred.\ winter\ nests,t+1}$) or of all nest ($D_{winter\ nests,t+1}$), was obtained by summing the densities from mesic, wetlands, and riparian habitats and weighed proportionally to their respective cover in our study area (76%, 14%, and 10%). Nest are considered at time *t+1* as factors affecting their presence are in time *t*.

2.4.5 Lemming population growth rates

To assess the seasonality of the impact of ermines on lemmings, interannual and seasonal growth rates of the lemming population were calculated. To do so, a constant equivalent to half of the lowest lemming density measured during our study (0.0235 ind/ha) was added to all lemming densities to allow log transformation. The interannual growth rate (year *t* and *t*+1) was calculated as :

$$R_{interan.} = \ln\left(D_{Annual,t+1}/D_{Annual,t}\right) \quad (1)$$

From 2004 to 2022, we also calculated the summer growth rate of year *t* as

$$R_{summer} = \ln\left(D_{August,t}/D_{June,t}\right) \quad (2)$$

and the fall-spring growth rate between year *t* and *t*+1 as

$$R_{fall-spring} = \ln\left(D_{June,t+1}/D_{August,t}\right) \quad (3)$$

Because growth rates are calculated on periods of different lengths, R values were transformed into instantaneous growth rates using $R_{daily} = R^{Span^{-1}}$, where *Span* is the number of days separating live-trapping sessions. *Span* was of 365 days for $R_{interan.}$, 56 ± 5 days for $R_{summer,}$and of 307 ± 3 for $R_{fall-sprin}$.

We made two assumptions regarding lemming populations over the nine months covered by $R_{fall-spring}$. First, we assumed that density of winter nests at snowmelt reflected the maximal density reached by lemmings over the winter. Even if lemmings may die or disperse during the winter, their nests will remain (Bilodeau et al. 2013) and potentially be used by other individuals (Duchesne et al. 2011). Secondly, we assumed that the lemming population trajectory (growth or decline) did not change over the winter, which seems common at least in Norwegian lemming (*Lemmus lemmus*, Kleiven 2022). Consequently, we assumed that if the lemming population was declining between fall *t* and spring *t*+1, the nest density at snowmelt should be proportional to the density of lemmings at nest formation (i.e., early winter of year t). Alternately, if the population is growing, it should be proportional to the density of lemmings at nest abandonment (late winter of year t+1, Fig. 2.2). Reasons regarding why the first year of the survey was excluded are given in Supplementary Material 1.

These assumptions enabled us to estimate four different proxies of seasonal population growths (R') at key points in time: R'_{fall} (Eq. 4) and $R'_{early\ winter-spring}$ (Eq. 5) in years of winter decline (based on $R_{fall-spring}$), and $R'_{fall-late\ winter}$ (Eq. 6) and R'_{spring} (Eq. 7) in years of winter growth (see Fig. 2.2).

$$R'_{fall} = \frac{D_{Winter\ nests,t+1}}{D_{August,t}};\ if\ R_{interan} \leq 0 \quad (4)$$

$$R'_{early\ winter-spring} = \frac{D_{June,t+1}}{D_{Winter\ nests,t+1}}; if\ R_{interan} \leq 0 \quad (5)$$

$$R'_{fall-late\ winter} = \frac{D_{Winter\ nests,t+1}}{D_{August,t}}; if\ R_{interan} > 0 \quad (6)$$

$$R'_{spring} = \frac{D_{June,t+1}}{D_{Winter\ nests,t+1}}; if\ R_{interan} > 0 \quad (7)$$

When growth rate was null, as it sometimes happened between years of very low abundance, we considered the population as declining.

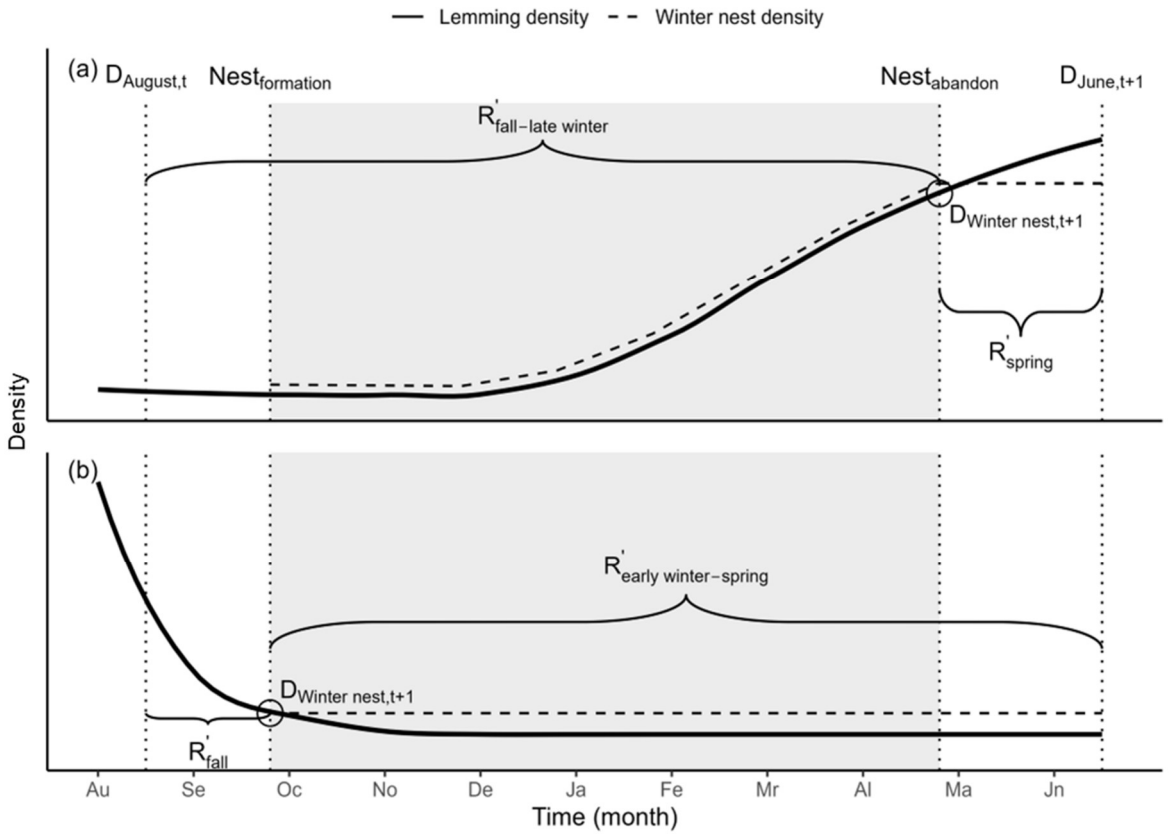

Figure 2.2. Graphical representation of how proxies of growth rates (R'; i.e., growth rates estimated from a mix of winter nest and live-trapping data) were estimated for years of winter growth (a) and declines (b). Dates are relative and can change among years. The grey area represents an estimated snow cover duration. The solid and dashed black lines respectively represent how lemming and winter nest densities are thought to vary

throughout the year. Open circles indicate the density of lemmings to which the density of winter nests found in the following spring ($D_{Winter\ nest,t+1}$) should be proportional. Winter nests are sampled every year at snowmelt. During years of winter growth **(a)**, winter nest densities are used as proxies of lemming densities at snowmelt when the abandon their nests ($Nest_{abandon}$). R' over fall and late winter ($R'_{fall-late\ winter}$), and R' over spring (R'_{spring}) could be estimated separately. Alternately, in years of winter declines **(b)**, winter nest densities are used as proxies of lemming densities at the onset of the winter season when they start building their nests ($Nest_{formation}$). Seasonal population growth proxies could be estimated over fall (R'_{fall}) and over early winter and spring ($R'_{early\ winter-spring}$).

2.4.6 Statistical analysis

2.4.7 Numerical response of ermines to lemming densities

We examined how ermines ($Ermine_t$) responded to current (t) and past (t-1) lemming densities as well as their own past abundances using quasibinomials generalized linear models which are suited to handled bounded data like the ermine abundance index (Gómez–Déniz et al. 2020). $Ermine_t$ was divided by three to be rescaled between 0 and 1 and models were weighted by the number of testimonials used to derive each relative abundance estimate. After confirming the absence of collinearity between covariates (covariance inflation factor < 3) and scaling them, competing hypotheses were:

$$Ermine_t \sim \ln(D_{Anual,t}) \quad (8)$$

$$Ermine_t \sim \ln(D_{Anual,t-1}) \quad (9)$$

$$Ermine_t \sim \ln(D_{Annual,t}) + \ln(D_{Annual,t-1}) \quad (10)$$

$$Ermine_t \sim Ermine_{t-1} + \ln(D_{Annual,t}) + \ln(D_{Annual,t-1}) \quad (11)$$

$$Ermine_t \sim Ermine_{t-1} + \ln(D_{Annual,t}) \quad (12)$$

These models were evaluated against a null model using model selection based on the second order quasi-Akaike's criterion (QAICc). Models with a ΔQAICc >2 were not considered. Coefficients of parameters present in models with ΔQAICc ≤ 2 were model-averaged.

2.4.8 Impact of ermines on lemming growth rate

To assess the impact of ermines on lemming growth rates, two indices of ermine abundance and one index of activity were separately used as covariates. We used the summer abundance $Ermine_t$, the density of lemming winter nests predated ($D_{pred.winter\ nests,t+1}$) as an index of ermine winter density, and the winter predation ratio ($PR = D_{pred.\ winter\ nests,t+1}/D_{winter\ nests,t+1}$) as the predation pressure of ermines on lemmings in winter. As any ratio, PR could have been problematic and verifications were made in Supplementary Materials 2.

We modelled the instantaneous growth rates Rs as a function of their respective initial lemming density ($D_{i,t}$, i being either June, August or Annual; see Eq. 1-3), to assess density-dependence, and $Ermine_t$. $R_{fall-sprin}$ was also modelled as a function of $D_{pred.winter\ nests,t+1}$ and PR as these indices could reflect ermine abundance during this period. These two models were weighted by the number of winter nest transects sampled (30 to 74). Model details are given in Table 2.2. For R' values (growth proxies, Eq. 4 to 7), ermine-related covariates were considered if it reflected ermine abundance or activity during or before the considered growth rate proxy. Moreover, depending on the R', initial lemming density was either $D_{August,t}$ or the density of lemming winter nest found in the following spring ($D_{winter\ nests,t+1}$). Even though sample size is restrictive (n = 5 or 8), we evaluated the impact of density-dependence and an ermine-related covariate simultaneously to correct for correlations between covariates. Model details are given in Table 2.3 and the original data is presented in Supplementary Material 3 for density-dependence and $Ermine_t$.

2.4.9 Delayed density-dependence in lemmings

We examined if past densities of lemmings ($D_{Annual,t-1}$) could influence their annual growth rate ($R_{interan}$) directly when ermine abundance ($Ermine_t$) was considered. We tested this hypothesis by building a path analysis (Shipley 2009) from models predicting $Ermine_t$ (Table 2.1 (M1)) and $R_{interan}$ (Table 2.2 (M1)) which used data from 1993 to 2019. The n is 26 as for 1993 past lemming densities are not available. Independence between $R_{interan}$ and $D_{Annual,t-1}$, hence the presence of delayed-density dependence generated by another factor than ermine abundance, was assessed at $\alpha < 0.05$ using Shipley's d-sep test (Shipley 2009). A schematic representation of this analysis is presented in the results (Fig 2.5).

2.4.10 Potential control of lemmings by ermines

Regulation of lemmings by ermines was assessed in two different ways. First, we determined ermine and lemming zero growth isoclines based on our empirical data. Second, we simulated lemming abundance time-series under different scenarios, 1- without stochasticity, 2- with stochasticity, and 3- with stochasticity and without ermines. From these simulated and observed lemming time series, we extracted the periodicity of cycles using wavelet analysis, the proportion of years in pluriannual low phase and the frequency distribution of annual lemming densities. Simulated time-series were considered different from the observed one if the original value was not contained in the 95% CI of periodicities and of proportion of years in the low phase. Densities were compared according to a t-test. Details of the whole procedure are given in Supplementary Materials 4.

2.5 Results

2.5.1 Numerical response of ermines to lemming densities

The best model explaining ermine abundance included lemming density at time t and t-1 ($D_{Annual,t}$ and $D_{Annual,t-1}$) as predictors but a competing model included $Ermine_{t-1}$ with both lemming densities covariates or $D_{Annual,t-1}$ in isolation (Table 2.1 (M1-M4)). Both current and past lemming densities had a positive influence of similar size on ermine abundance (Fig. 2.3) suggesting equally strong direct and delayed density-dependent numerical responses of ermines (model-averaged scaled β, $\ln(D_{Annual,t}) = 0.66$ [0.04;

1.27]; ln ($D_{Annual,t-1}$) = 0.56 [0.02; 1.10]). $Ermine_t$ seemed to be positively influenced by its past abundance but the effect was imprecise (model averaged scaled β of $Ermine_{t-1}$ = 0.41 [-0.15; 0.98]). Hence, further analyses (path analysis and simulations) will only use the model including lemming density at time t and t-1 (Table 2.1 (M1)).

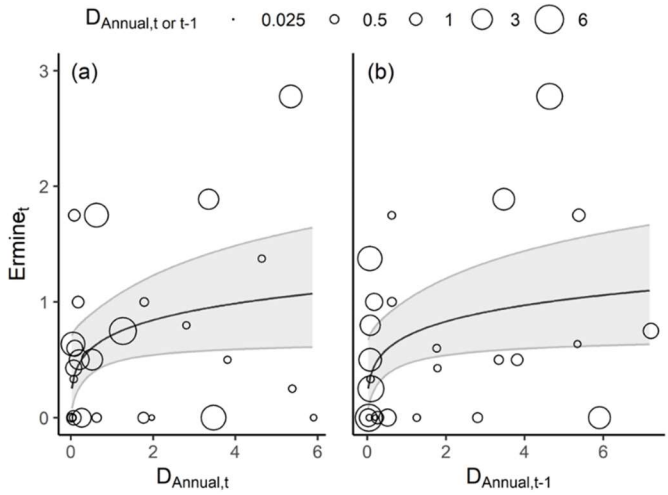

Figure 2.3. Relationship between the ermine abundance index and (a) current ($ln(D_{Annual,t})$) and (b) previous ($ln(D_{Annual,t-1})$) lemming densities on Bylot Island (Nunavut, Canada). Dot size is proportional to (a) $D_{Annual,t-1}$ and (b) $D_{Annual,t}$. Gray shaded areas represent 95% CI. Predictions were obtained from top-ranked model in Table 2.1 and multiplied by 3 to fit the actual ermine abundance index which is bounded between 0 and 3.

Table 2.1. Model selection testing the effect of current and past July lemming densities on ermine abundance index.

Model		K	QLL	ΔQAICc	QAICcWt
M1	$D_{Annual,t}, D_{Annual,t-1}$	4	-22.15	0.00	0.35
M2	$D_{Annual,t}, D_{Annual,t-1}, Ermine_{t-1}$	5	-21.41	1.61	0.50
M3	$D_{Annual,t-1}$	3	-24.41	1.69	0.65
M4	$D_{Annual,t}, Ermine_{t-1}$	4	-23.02	1.74	0.79
M5	$D_{Annual,t}$	3	-24.69	2.26	0.91
M6	Null	2	-26.15	2.60	1.00

Note: Generalized linear models with quasibinomial distribution were used. K = number of parameters, QLL = Quasi Log-likelihood, ΔQAICc = difference between the model and the one with the lowest QAICc value, QAICcWt = QAICc weight. Models with a ΔQAICc < 2, the least number of parameters and only significant parameters were selected and are followed by a *.

2.5.2 Seasonal impact of ermines on lemming growth rate

Interannual and fall to spring growth rates were negatively related to summer ermine abundance ($Ermine_t$), proportion of winter nests predated (PR, Fig. 2.5) and current lemming density ($D_{i,t}$, Table 2.2, M1, M2, M4 and M6)) but not to density of winter nests predated by ermines ($D_{pred.winter\ nests,t+1}$, Table 2.2, M5). However, 95% confidence intervals of the effect of $Ermine_t$ overlapped 0 for interannual growth rates in the short time-series (2004-2019) and $R_{fall-spring}$. None of the covariates influenced lemming summer growth rate (Fig. 2.4, Table 2.2, M3). As for the seasonal growth proxies (R'), the three indices of ermine abundance or predation generally had a similar influence (Table 2.3). During years of winter decline, R'_{fall} was negatively affected by density-dependence but not by ermine-related covariates whose 95% CI largely overlapped 0. For the early winter-spring period ($R'_{early\ winter-spring}$), the effect of density-dependence was either null or positive and the growth rate was negatively related to all ermine-related covariates yet the 95% CI of $\ln(PR)$ included 0. In years of winter growth, $R'_{fall-lat\ \ winter}$ density-dependence was either null or negative and the growth rate was negatively related to all ermine-related covariates. Finally, during spring, R'_{spring} was only affected negatively by density-dependence, ermines having null effects (Fig. 2.4, Table 2.3).

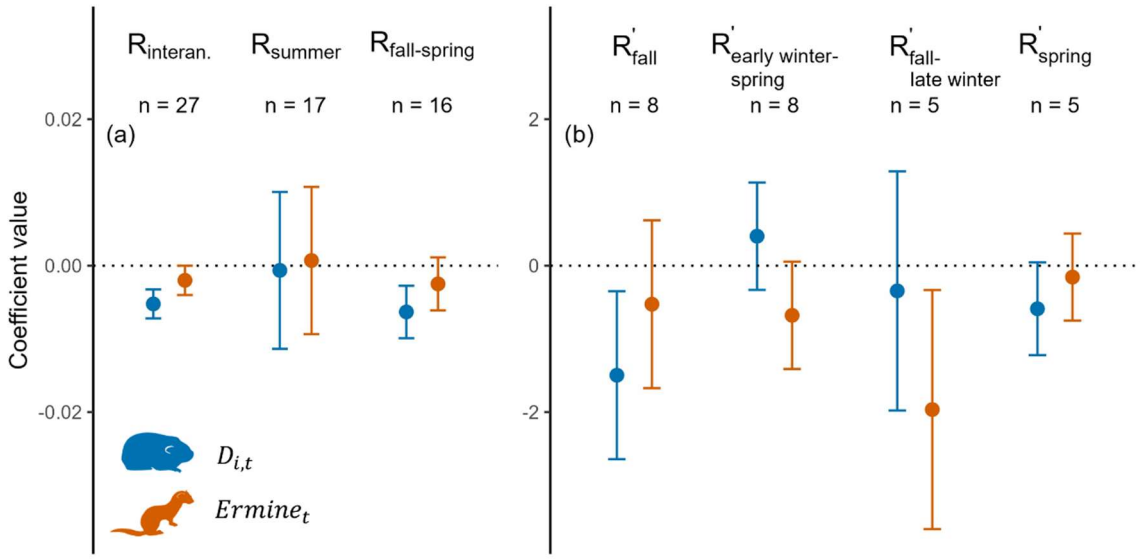

Figure 2.4. Seasonal influence of ermines and density-dependence on lemming population growth rates (a; R) or its proxies (b, R') between current time t and $t+i$ on Bylot Island, NU, Canada. Covariates are current lemming density ($D_{i,t}$) and ermine abundance ($Ermine_t$). Error bars represent 95% CI and the number of observations in each model (n) is given. See model details in Table 2.2 & 2.3. **(a)** Coefficient values are scaled and comparable between seasons since Rs are instantaneous growth rates. **(b)** Because of the unmeasured duration of periods associated with seasonal proxies (R'), coefficients are not comparable between seasons but are scaled and comparable within seasons.

2.5.3 Delayed density-dependence in lemmings

The path analysis revealed that the delayed density-dependence in the lemming population growth rate could be mediated by $Ermine_t$ (Fig. 2.5). However, other factors could mediate delayed density-dependence as the independence test (d-sep test) between $D_{Annual,t-1}$ and $R_{interan.}$ returned a *p-value* of 0.10 and the overall model, a Fisher's C of 4.64. This rather poor fit indicates that covariates are missing or are too unprecise.

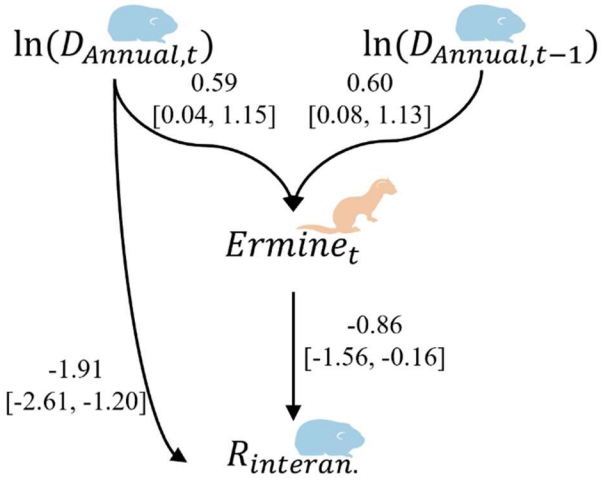

Figure 2.5. Standardized path coefficients illustrating direct and delayed density-dependence effect ($ln(D_{Annual,t})$ and $ln(D_{Annual,t-1})$) on annual lemming growth rate ($R_{interan}$) in presence of ermines ($Ermine_t$) on Bylot Island (Nunavut, Canada) for the period 1993-2019. Bold numbers are standardized beta coefficients with 95% CI in brackets. Black lines are significant paths and grey dashed line nonsignificant paths (parameters deemed independent by Shipley's d-sep test at $\alpha < 0.05$). Fisher's C = 4.64.

2.5.4 Impact of ermines on lemming cycles

The ermine zero growth isocline extended over all observed lemming densities and rapidly reached a plateau, whereas the one of lemmings covered between 0.06 to 1.05 ind/ha (Fig. 2.6). Isoclines crossed when $Ermine_t$ was at 0.62 and $D_{Annual,t}$ was at 0.57 ind/ha. The

deterministic simulation quickly reached an equilibrium exactly where the isoclines crossed (Fig. 2.6). Hence, comparing characteristics of this simulation to the original data is of little interest.

Both stochastic simulations gave rise to cycles (2.1 to 4.5-years with ermines, 2.4 to 3.3-years without ermines, 3.6 to 4.4-years in the observed time-series, Fig. 2.7). Similarly, low phases were present in both stochastic simulations. The proportion of years fitting the low phase definition was of 0.22 in the observed data, a proportion included by the 95% CI of the simulation with ermines 0.14 [0.00, 0.41] but not the simulation without 0.05 [0,0.19] Fig. 2.7). Lemming densities in the observed time series differed significantly from the simulations without ermines (p = 0.02) but not when ermines were present (p = 0.73, Fig. 2.7).

Table 2.2. List of generalized linear models investigating direct-density dependence and the impact of ermines on lemming interannual and seasonal growth rates (R)

Models		n	Density-dependence Coeff & 95% CI	Impact of ermines Coeff & 95% CI
M1	$R_{interan.}^{93-19} \sim Ermine_t + \ln(D_{Annual,t})$	27	-5.2 [-7.2, -3.3]	-2.0 [-4.0, 0.0]
M2	$R_{interan.}^{04-19} \sim Ermine_t + \ln(D_{Annual,t})$	15	-4.7 [-7.9, -1.6]	-2.4 [-5.6, 0.8]
M3	$R_{summer} \sim Ermine_t + \ln(D_{June,t})$	17	-0.6 [-11.3, 10.0]	0.7 [-9.4, 10.7]
M4	$R_{fall-spring} \sim Ermine_t + \ln(D_{August,t})$	16	-6.6 [-10.8, -2.4]	-2.7 [-7.0, 1.5]
M5	$R_{fall-spring} \sim D_{pred.winter\ nests,t+1} + \ln(D_{August,t})$	13	-7.8 [-12.0, -3.6]	-0.5 [-5.5, 4.6]
M6	$R_{fall-spring} \sim \ln(PR) + \ln(D_{August,t})$	13	-6.3 [-9.4, -3.4]	-5.0 [-8.1, -1.8]

Note: $D_{i,t}$ is the density of lemmings at a given trapping session, *i* being either June, August or Annual. $Ermine_t$ is the relative abundance of ermines during the summer (scaled between 0 and 1), whereas $D_{pred.\ winter\ nests,t+1}$ is the density of lemming winter nests predated by ermines. PR is the predation ratio, calculated as the proportion of winter nests with signs of ermine predation. The number of observations (n) is given for each model and they all had a gaussian distribution with a ln link function. Coefficients must be multiplied by 10^{-3}.

Table 2.3. List of generalized linear models investigating direct-density dependence and the impact of ermines on lemming seasonal growth rate proxies (R')

Growth rate proxy	Model ID	Density-dependence		Ermine effect	
		Covariate	Coefficient & 95% CI	Covariate	Coefficient & 95% CI
R'_{fall}	M1	$D_{August,t}$	-1.5 [-2.6, -0.3]	$Ermine_t$	-0.5 [-1.7, 0.6]
	M2	$D_{August,t}$	-1.3 [2.6, 0.0]	$D_{pred.\ winter\ nests,t+1}$	-0.6 [-1.9, 0.8]
	M3	$D_{August,t}$	-1.7, [-2.9, -0.4]	ln (PR)	0.4 [-0.8, 1.7]
$R'_{early\ winte\ spring}$	M4	$D_{winter\ nests,t+1}$	0.4 [-0.3, 1.1]	$Ermine_t$	-0.7 [-1.4, 0.1]
	M5	$D_{winter\ nests,t+1}$	0.9 [0.1, 1,73]	$D_{pred.\ winter\ nests,t+1}$	-1.5 [-2.3, -0.7]
	M6	$D_{winter\ nests,t+1}$	0.3 [-0.6, 1.3]	ln (PR)	-0.5 [-1.5, 0.5]
$R'_{fall-late\ winter}$	M7	$D_{August,t}$	-0.3 [-2.0, 1.3]	$Ermine_t$	-2.0 [-3.6, -0.3]
	M8	$D_{August,t}$	-1.9 [-2.4, -1.3]	$D_{pred.\ winter\ nests,t+1}$	-1.3 [-1.8, -0.7]
	M9	$D_{August,t}$	-1.7 [-2.7, -0.7]	ln (PR)	-1.1 [-2.0, -0.1]
R'_{spring}	M10	$D_{winter\ nests,t+1}$	-0.6 [-1.2, 0.0]	$Ermine_t$	-0.2 [-0.8, 0.4]
	M11	$D_{winter\ nests,t+1}$	-0.6 [-0.9, -0.2]	$D_{pred.\ winter\ nests,t+1}$	-0.2 [-0.6, 0.1]
	M12	$D_{winter\ nests,t+1}$	-0.5 [-1.0, -0.1]	ln (PR)	-0.2 [-0.6, 0.2]

Note: $D_{August,t}$ is the density of lemmings at the mid-August trapping session and $D_{winter\ nests,t+1}$ is the density of lemming winter nest found in June of the following year. $Ermine_t$ is the relative abundance of ermines during the summer, whereas $D_{pred.\ winter\ nests,t+1}$ is the density of lemming winter nests predated by ermines. PR is the predation ratio, calculated as the proportion of winter nests with signs of ermine predation. Models M1-M6 were based on 8 observations and M7-M12 on 5. All models had a Gamma distribution and with a ln link except for M10-12 which had a gaussian distribution.

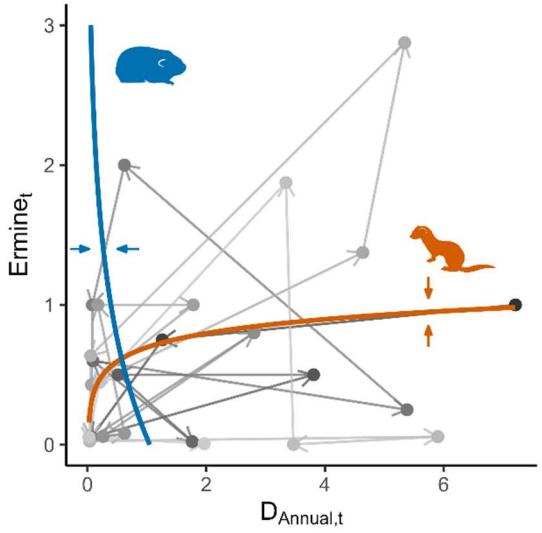

Figure 2.6. Zero-growth isoclines of ermines (orange line) and lemmings (blue line) on Bylot Island (Nunavut, Canada) derived from empirical data. Colored arrows are the predicted direction of change in abundance relative to the isoclines. Dots represent original data with grey arrows representing the direction and the magnitude of change between t and t+1.

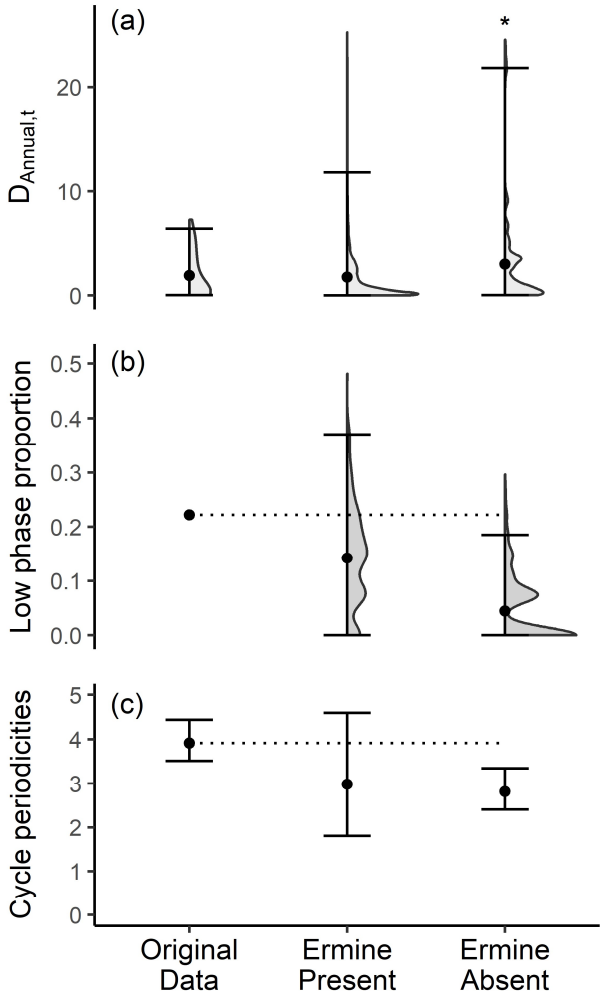

Figure 2.7. Comparison of the observed time series and stochastic simulations of lemming populations with or without ermines. **(a)** Frequency distribution, mean and 95% CI of lemming densities in July $D_{Annual,t}$. Asterisks denote simulations significantly different from the original data. **(b)** Frequency distribution, mean and 95% CI of the proportion of years when lemmings were considered in their low phase. **(c)** Average of dominant periodicities with 95% CI detected using wavelet analyses. Dotted line is the mean in the original data.

2.6 Discussion

Even though ermine predation alone seems insufficient to generate High-Arctic lemming cycles, our empirical study generally supports the specialist predator hypothesis (SPH) as a possible explanation of this phenomenon. Indeed, ermine abundance was determined as

much by the previous than by the current summer lemming densities. Our path analysis showed that the reliance of ermines on past lemming densities could mediate the delayed density-dependence observed in the lemming population interannual growth rate. Moreover, the limited negative impact of ermines seemed restricted to winter, a crucial season associated with the drastic growths seen in this lemming population (Fauteux et al. 2015). On the other hand, the effect of ermines on lemming growth rate was less than half that of direct density-dependence, indicating that ermines are not the sole responsible for causing lemming declines. Our empirically-based isoclines and simulations highlighted the significant role of ermines in limiting lemming maximal population densities, in maintaining the abundance of their rodent prey to low levels for more than a year and in allowing cycles of longer periodicities (>3 years). Hence, despite a limited and temporally circumscribed impact on lemming population growth rates, ermines act at a critical moment and can therefore change the overall population dynamics of their prey.

2.6.1 Direct and delayed numerical response of ermines

As predicted by the SPH, we found that the partially delayed numerical response of ermines could mediate the delayed density-dependence observed in this High-Arctic cyclic population of lemmings, even though other factors might be in play. That ermines could respond directly, at the annual scale, to their prey abundance fluctuation is not surprising : to our knowledge, this was reported by all studies conducting seasonally synchronous monitoring of small mustelids and their rodent preys (Jedrzejewski et al. 1995; Graham 2001; Gilg et al. 2006; Mougeot et al. 2019). However, delayed responses of a year were only detected in northern locations such as in Fennoscandia (Korpimäki et al. 1991; Sundell et al. 2013) and Greenland (Gilg et al. 2006). Such a dichotomy in the observed numerical response of small mustelids argues for a strong effect of latitude on mustelid-rodent interaction (Hansson & Henttonen 1985). In fact, no or relatively short (< 8 months) delays were detected in temperate Europe (Poland; Jedrzejewski et al. 1995, England; Graham 2001, Spain; Mougeot et al. 2019). Such north-south dichotomy could be explained by the unfavorable conditions small mustelids meet at lower latitudes, such as higher densities of generalist predators (Lambin et al. 2000; Hanski et al. 2001) and a reduced or absent protection from the snowpack (Powell 1973; Korpimäki & Norrdahl 1989a; Linnell et al.

2017). Other mechanisms could favor small mustelids delayed response in northern locations. Colder temperatures found at higher latitudes may promote the effectiveness of carcass caching, as observed for the food-caching Eurasian Pygmy Owl (*Glaucidium passerinum*), and allow the continued presence of small mustelids following periods of peak abundance (Oksanen et al. 1985; Jędrzejewska & Jędrzejewski 1989). Direct observations of the foraging activity of radio-collared ermines during a summer of very low lemming density on Bylot Island (0.07 ind/ha) supports this hypothesis : 68% of carried food items (n = 19, includes small passerines and lemmings) and 86% of carried lemmings (n = 15) were retrieved from caches as suggested by their either frozen or partially decayed state (11.6 h of observation, n = 4 ermines, Bolduc et al. *unpublished*).

2.6.2 Seasonally varying regulation

The regulation faced by lemming populations varied greatly between seasons, being absent during summer and most significant in the fall to spring period. The lack of regulation during summer, both from ermines and direct density-dependence, is quite interesting as lemmings sometimes decline during this season at our study site. It suggests that lemming reproduction at that time more than compensates for the toll taken by ermines and the directly density-dependent component of other predators activity (Gilg et al. 2006; Therrien et al. 2014). The lack of impact from ermines is not unexpected as their predation rate had been estimated to be half the daily growth of lemmings (1.2% vs. 2.2% per day, Bilodeau 2013, Therrien et al. 2014). Their comparatively slow numerical response likely prevents them from catching up, unlike the faster-reproducing least weasels which were found to reduce summer growth rates of voles in Fennoscandia (Korpela et al. 2014). Moreover, as shown with their zero-growth isoclines, ermines quickly reach their maximal abundance and become limited by factors other than prey abundance, like territoriality or intraguild predation (Korpimäki & Norrdahl 1989b; King & Powell 2006; Gotelli 2008). What exactly causes the late-summer declines at our site remains an open question but is unlikely to be related to ermine abundance or direct density-dependence.

Regulation mostly occurred between the end of summer and the next spring; a period that has been associated with declines in many small rodent populations including this one (Fauteux et al. 2015; Pinot et al. 2016; Krebs et al. 2023). Here, direct density-dependence

had twice the impact of ermine abundance on population growth rate. Moreover, the lemming zero-growth isocline indicated that above 1.05 ind/ha ermines alone could not induce a decline. These results suggest that long delays of over 9 months in density-dependence are unnecessary to cause the late-summer and fall declines observed in this population (Fauteux et al. 2015). Indeed, lemmings are thought to reduce their reproductive activities at the onset of fall (Pitelka & Batzli 2018) and a short delay in the numerous predators functional and numerical response could potentially induce a drastic decline (Korpimäki 1993; Gilg et al. 2006; Korpela et al. 2014; Therrien et al. 2014; Fauteux et al. 2016). The idea that declines are mostly directly density-dependent is in line with the modelling work of Barraquand et al. (2014, 2022) and could explain the presence of short cycles in Spain, France and Poland (Zub et al. 2012; Barraquand et al. 2014; Mougeot et al. 2019). Other hypotheses regarding the cause of these drastic declines, such as lack of food due to overgrazing (Legagneux et al. 2012; Bilodeau et al. 2014) or negative density-dependent reproduction (Fauteux et al. 2015; Fauteux & Gauthier 2022) have found no support on Bylot Island.

Although uncertain due to our small sample size, the seasonal analyses on growth rate proxies revealed interesting trends: that negative density-dependence is relaxed when the snow cover is present, only to be replace by a negative impact of ermines. If, as currently thought, the negative density-dependence comes from the rapid numerical and functional responses of avian predators and arctic foxes, then the arrival of a protective snow cover and the departure of avian predators should remove this negative effect as observed. Insights from this study system even suggest a positive effect of lemming density on their winter reproduction (Poirier et al, *unpublished*). As for the impact of ermines during winter, it could be explained by three key factors. First, ermines are largely relaxed from intraguild predation and they can safely move and hunt under the snowpack (Zub et al. 2008). Second, lemmings and small mustelids do not hibernate and rely partly on snow depth to limit thermoregulatory costs (Chappell 1980; Zub et al. 2009; Duchesne et al. 2011). Hence lemmings face a difficult trade-off between thermoregulation and risk of predation as places they should favor, like deep snow with warm subnivean space (Poirier et al, 2023), are also places where ermines are likely to be found (Bilodeau et al. 2013). Third, intense winter reproduction is required for lemmings to reach high abundances (Reid & Krebs

1996; Fauteux et al. 2015) but ermines may interfere with recruitment through either lethal or non-lethal effects. Lethal effect alone are unlikely as small mustelids usually reduce their activity (King & Powell 2006; Zub et al. 2009; Sundell et al. 2013) and increase their reliance on cached carcasses when temperature drops (Jedrzejewska & Jedrzejewski 1989). They may rather interfere with the intrinsic growth rate of lemmings as females seems to suffer heavier predation from small mustelids than males during winter (MacLean et al. 1974; Sittler 1995; Schmidt et al. 2021). Such vulnerability of females could drastically reduce recruitment and further explain why in the following low-density summers, males are three times more abundant on Bylot Island (Fauteux and Gauthier 2022). Other mechanisms potentially explaining winter declines, like inversed density-dependent reproduction (Pinot et al. 2016), are not thought to be significant on Bylot Island (Fauteux and Gauthier 2022).

2.6.3 Low abundance phases

Phases of low abundance are thought to emerge mostly from delayed density-dependence (Boonstra et al. 1998), which, as the path analysis showed, could be mediated here by the ermines partially delayed numerical response. The lemmings zero-growth isoclines also suggest that, in the High-Arctic, ermine abundance may be decisive in maintaining lemmings at low densities once they have reached such levels (i.e., between 0.06 and 1.05 ind/ha). As discussed above, such regulation may be possible through biased impact on the vulnerable wintering females which are crucial for population growth (Klemola et al. 1997; Fauteux & Gauthier 2022). This same isocline also underlines the extremely low densities that lemmings must reach to escape ermine regulation. Indeed, when densities drop below 0.06 lemmings/ha during summer, most ermines probably starve or leave the system, allowing the lemming population to grow again, sometimes 100-fold compared to the previous summer (Fauteux et al. 2015). Such a low refugial density highlights the potential role of metapopulation dynamics because lemmings may become locally extinct. Although the observed behavior of the population does not fully fit with the predictions of the isoclines, possibly due to the role of the other intrinsic and extrinsic factors, it is striking to see such a simple model built with data from a single season perform so well.

Our stochastic simulations also suggest that ermines play an important role in maintaining lemmings at low abundance for more than a year. By doing so, they allow cycles of longer periodicities (3-5 years) like those observed on Bylot Island. However, ermines were not necessary to generate cycles *per se* as ~3-yr cycles were found in the ermine-less simulations. This aligns with the models of Gilg et al. (2006) and Barraquand et al. (2022) on lemmings and of Korpela et al. (2014) on voles considering that they all stated that predation by small mustelids alone was insufficient. It also matches the periodicity of vole cycles observed in temperate regions where the SPH is usually rejected (Zub et al. 2012; Mougeot et al. 2019). Taken together, the simulations results do not support the SPH considering that lemming cycles may occur without ermines. However, they indicate that cycles of 4 or 5 years, as most often seen on Bylot Island and in other northern regions, are unlikely to occur without small mustelids.

2.6.5 Limitations

Our results fall well within the expectations of small mustelid and rodent interactions in a northern ecosystem. However, the ermine-related data we used is indirect and it is worth underlying how it may have affected our results. The delayed response of ermines, derived from the testimonials of opportunistic observations, could be an artifact if these predators increased their activity, and thus their detectability, when prey abundances were low (Klemola et al. 1999, Graham 2002). Whether they do so or not remains unclear (Sundell et al. 2013), but our method may have circumvented this by promoting the detection of direct rather than delayed response of ermine to lemming densities. As reported by the participants of our survey (Bolduc et al. 2023), ermine families, the highest observation category in our methodology, were often observed in years of peak lemming abundance. Hence, the delayed response of ermines is unlikely to be a methodological artifact. Also, we attempted to decipher the seasonal variations in the relationship between ermines and lemmings by using both the summer relative abundance of ermines and the signs of predation they left in winter nests. Even though the different models mostly indicated a negative impact during winter, (i.e. the moment between nest formation and abandonment), we did not find a negative relationship between lemming fall-to-spring growth and the absolute number of predated nests ($D_{pred.winter\ nests}$) when taking density dependence into

account. As $D_{pred.winter\ nests}$ correlates with $D_{winter\ nests}$, which itself is indicative of the realized growth during winter, it is after all not surprising that no negative effects were found. We currently know very little about the predation of winter nests by ermines, how it may vary with prey density and in the end if it is a reliable abundance index on its own. Hence results emerging from the use of such data must be considered carefully. Finally, we have pooled the two species of lemmings present on Bylot Island. In doing so, we might have oversimplified their interactions with small mustelids. Indeed, they were shown to suffer differential predation from avian predators (Therrien et al. 2014). The joint analysis of their cyclicity potentially overlooked some asynchrony between these species (Valcourt 2022). Nonetheless, collared lemmings always remained at low densities and brown lemmings were >10x more abundant during peak years over the course of our study. Since we are not aware of any evidence of prey preference, we assumed that ermines would respond to the overall large amplitude cyclic dynamics that was almost exclusively driven by brown lemmings.

2.6.6 Conclusion

Our results suggest that the role of ermines in generating the observed lemming population cycles is limited, but necessary. The partially delayed numerical response of ermines to lemming fluctuations could mediate delayed-density dependence, induce prolonged phases of low abundance and lead to longer population cycles (3-5 years). However, we found that direct density-dependence, likely due to the rapid functional and numerical response of other predators (Legagneux et al. 2012; Therrien et al. 2014; Fauteux et al. 2016), was the main driver of lemming population growth. The impact of ermines on lemming growth rate was half that of direct density-dependence, but it was circumscribed to winter, a period critical to lemming growth where negative density-dependence seemed relaxed. Indeed, the seasonal variations of both negative density-dependence and the impact of ermines highlight the need to consider multiple biotic (e.g., intraguild predation, seasonally varying prey reproductive capacities) and abiotic factors (i.e. subnivean refuges, thermoregulatory needs) that change radically between summer and winter.

Our simulations of lemming populations contradict the predictions of the SPH, that small mustelids predation is necessary to rodent cycles as ~3 years cycles were observed in ermine-less simulations. Rather, they underline that small mustelids are necessary to the longer cycles of 3-5 years with pluriannual phases of low abundance characteristic of rodent populations from Arctic and boreal ecosystems, hence providing support for the SPH in this particular case only.

Our study reinforces the hypothesis that top-down regulation is a likely mechanism driving rodent cycles observed in the High-Arctic (Gilg et al. 2006, Legagneux et al. 2012, Therrien et al. 2014, Fauteux et al. 2016) and Fennoscandia (Korpela et al. 2014). Predator-exclusion experiments conducted in the Arctic increased the amplitudes of lemming cycles and slowed the declines, but they all failed to prevent the low abundance phase (Reid et al. 1995; Wilson et al. 1999; Fauteux et al. 2016). They also all failed to exclude ermines and weasels. Here, we provide compelling evidence that these small mustelids had the capacity of causing the low phases in these experiments. Finally, our study supports the hypothesis that small mustelids are necessary to the 3 to 5-yr cycles of northern small rodents, but that the isolation of the mustelid-rodent system, either under the snow (Hansson & Henttonen 1985; Hanski et al. 2001) or by the emigration of predators, may be a condition to be met. Further investigations should focus on the possible mechanisms by which small mustelids may affect their rodent prey and on the influence of climatic variables on the mustelid-rodent systems.

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2.8 Supplementary materials

2.8.1 Supplementary material 1 - Winter nests of 2006-2007

The interannual population growth of winter 2006-2007 indicated a decline despite intermediate winter nest densities, which violates a key assumption of this analysis. It was also the first year of winter nest sampling and potential errors when separating recent nests vs. those ≥2 years old may have led to overestimated winter nest densities (Sittler 1995). Hence analyses were conducted both with and without the data from winter 2006-2007 to assess the influence of a particular year. The interpretation of coefficients did not change except for the effect of PR on R'_{fall} which became negative (β = -0.6 [-2.4, 0.14] instead of 0.4 [-0.8, 1.7], Table S1).

Table S1. List of generalized linear models investigating direct-density dependence and the impact of ermines on lemming seasonal growth rate proxies (R') using data from 2006 to 2022

Growth rate proxy	Model ID	Density-dependence		Ermine effect	
		Covariate	Coefficient & 95% CI	Covariate	Coefficient & 95% CI
R'_{fall}	M1	$D_{August,t}$	-1.5 [-2.2, -0.7]	$Ermine_t$	-0.4 [-1.2, 0.4]
	M2	$D_{August,t}$	-1.4 [-2.1, -0.74]	$D_{pred.\ winter\ nests,t+1}$	-0.3 [-1.0, 0.35]
	M3	$D_{August,t}$	-1.7 [-2.4, -0.9]	ln (PR)	**-0.6 [-2.4, 0.14]**
$R'_{early\ winter-spring}$	M4	$D_{winter\ nests,t+1}$	0.4 [-0.3, 1.0]	$Ermine_t$	-0.6 [-1.3, 0.1]
	M5	$D_{winter\ nests,t+1}$	0.9 [0.1, 1,7]	$D_{pred.\ winter\ nests,t+1}$	-1.3 [-2.1, -0.5]
	M6	$D_{winter\ nests,t+1}$	0.3 [-0.6, 1.2]	ln (PR)	-0.5 [-1.4, 0.4]

Note: $D_{August,t}$ is the density of lemmings at the mid-August trapping session and $D_{winter\ nests,t+1}$ is the density of lemming winter nest found in June of the following year. $Ermine_t$ is the relative abundance of ermines during the summer, whereas $D_{pred.\ winter\ nests,t+1}$ is the density of lemming winter nests predated by ermines. PR is the predation ratio, calculated as the proportion of winter nests with signs of ermine predation. Models M1-M6 were based on 9 observations and M7-M12 on 5. All models had a Gamma distribution and with a ln link. In bold are the coefficient which suggest an interpretation different from the original results where data from 2006 is omitted. Model results of $R'_{fall-late\ winter}$ and R'_{spring} are not shown as they only use data from growth years and 2006 was a decline. Hence their results did not change.

2.8.2 Supplementary material 2 - Verifying the impact of predation ratio

As any ratios, PR has caveats. $D_{winter\ nests,t+1}$ is strongly and positively correlated with the winter growth rate $R_{fall-spring}$ (Krebs et al. 2012; Fauteux et al. 2015). Hence, most parameters divided by $D_{winter\ nests,t+1}$ should have a negative relationship with $R_{fall-spring}$. To evaluate if our results were the product of chance alone, we simulated PRs 5000 times by shuffling the $D_{pred.winter\ nests,t+1}$ to random years and recalculated PR with the $D_{winter\ nests,t+1}$ of the respective year. For every simulation, we ran the original model

$$R_{fall-spring} \sim \ln(D_{August,t}) + \ln(PR) \qquad (B1)$$

and saved the coefficient of PR. We then compared the original coefficient to the distribution of simulated ones. While the original coefficient was of -0.0050 [-0.0081, -0.0018], the simulated one was of -0.0025 [-0.0056, 0.0013] indicating a small effect of PR.

2.8.3 Supplementary Material 3 - Data used in the seasonal proxies (R') analysis

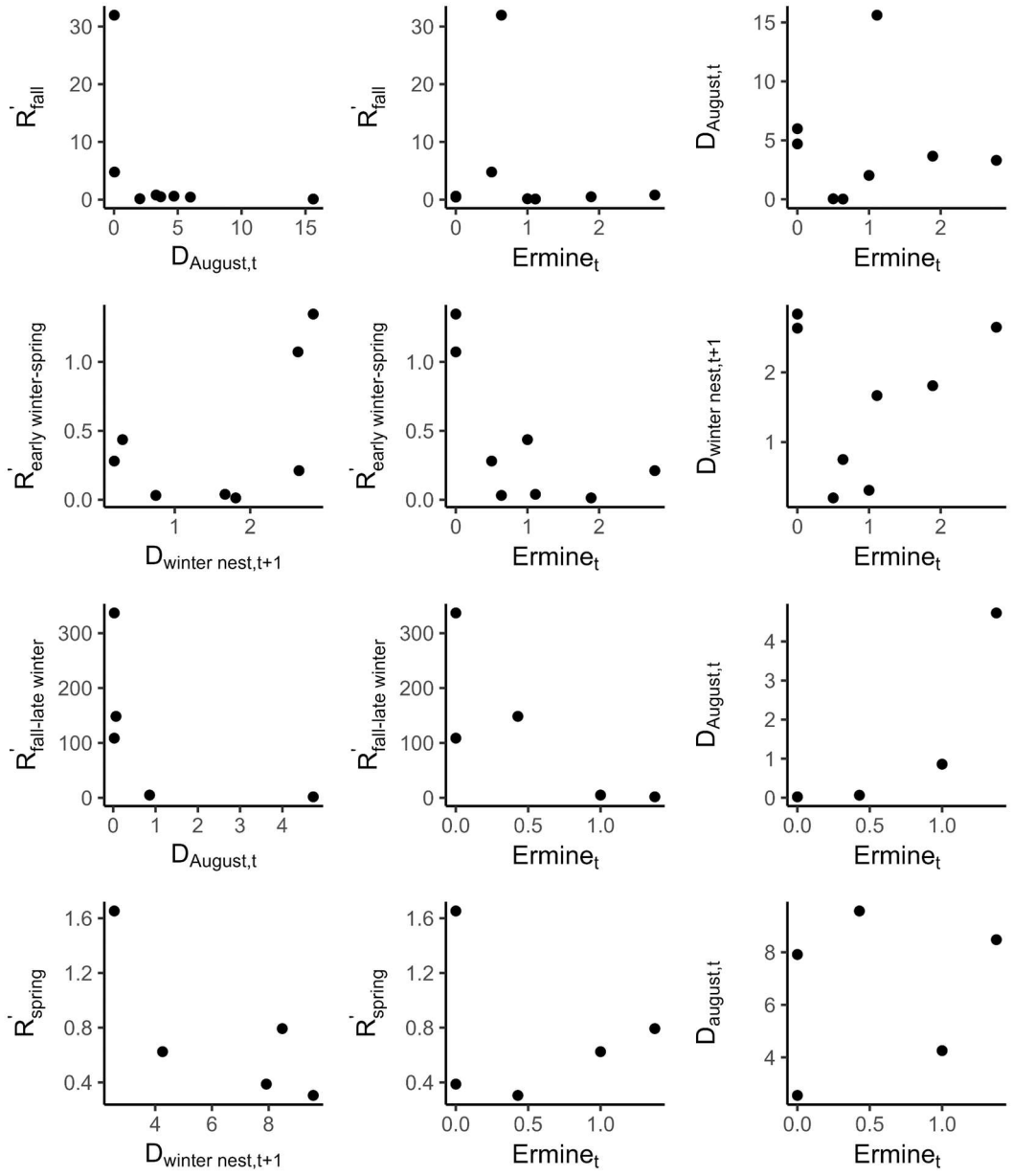

Fig. S3. Data used in the seasonal analysis of lemming growth rate proxies on Bylot Island, NU, Canada. R' are the growth rate proxies for a given period shown in subscript. $Ermine_t$ is the relative abundance of ermines during summer, $D_{winter\ nests,t+1}$ is the density of lemming winter nests found in the following spring and $D_{August,t}$ is the density of lemming estimated with live-trapping at mid-August.

2.8.3 Supplementary Material 4 - Methods to simulate abundance time-series

To determine the potential of ermines to regulate the lemming population, we proceeded in three steps. First, we determined ermine and lemming zero growth isoclines. The ermine isocline was drawn by resolving

$$Ermine_{t+1} - Ermine_t \sim Ermine_t + \ln(D_{August,t}) \quad (S4.1)$$

to find the combination of parameters where the difference between $Ermine_{t+1}$ and $Ermine_t$= 0. The same procedure was used for the lemming isocline using the previously described model (Table 2.2 (M1)) so that the lemming growth rate was equal to 0.

$$R_{interan.} \sim Ermine_t + \ln(D_{August,t}) \quad (S4.2)$$

We did not calculate ermine growth rates because $Ermine_t$ was bound between 0 and 3. Second, we used the model predicting interannual lemming growth rate, $R_{interan.}^{93-19}$ (see results, Table 2.2 (M1)) and the most parsimonious model predicting annual ermine abundance, $Ermine_t$ (see results, Table 2.1 (M1)) to simulate lemming density and ermine abundance time-series. We first found values of annual lemming density, $D_{July,t+1}$, by multiplying $D_{July,t}$ by the predicted values of $R_{interan.}^{93-19}$ Then, as our best model indicated that ermine abundance was dependent on lemming abundance in current and previous years, $Ermine_t \sim \ln(D_{July,t}) + \ln(D_{July,t-1})$ (see results, Table 2.1), moving one time step ahead gives $Ermine_{t+1} \sim \ln(D_{July,t+1}) + \ln(D_{July,t})$. We simulated both populations over 15,000 time steps (or years) under three scenarios: a fully deterministic one where no stochasticity is included, one with stochasticity (residuals of both models were randomly added to predictions) and a final one where stochasticity is present but ermines are absent ($Ermine_t = 0$).

Finally, we extracted from simulated and original lemming population time series the periodicity of significantly detected cycles ($\alpha < 0.05$), the presence of low phases (i.e. extended periods of very low and constant densities, Boonstra et al. 1998), and the frequency distribution of annual lemming densities. The presence of cycles and their periods was assessed using wavelet analyses with the R package WaveletComp (Roesch & Schmidbauer 2018). We searched for cycles of periods from 1 to 8 years by scanning each time-series 1000 times and compared the results to white noise to assess significance at $\alpha < 0.05$. Box-Cox and KPSS tests were made on all time-series to ensure constant variance and

stationarity. The 95% confidence intervals (CI) of the significantly supported periods were calculated and time series with non-overlapping 95% CI were considered different. To compare the proportion of years in the low phase between the simulated and observed time series, we cut the simulated time series of 15000 years into consecutive bout of 27 years (length of the observed time series) before metrics were calculated. The first 27-year bout of simulated time series was not used as it could be influenced by starting values. A year was considered in the low phase if $D_{July,t}$ < 0.50 ind/ha and $R_{interan.}$and $R_{interan.,t-1} \leq 0$ (e.g., a low-density value both preceded and followed by a declining or stable growth rate). Years of low densities (< 0.50 ind/ha) following a year identified as a low phase was also considered as such. The threshold of 0.50 ind/ha is very conservative as at our study site, densities observed in the low phases were all < 0.1 ind/ha. The proportion of years in the low phase in the observed time series was considered different to a simulated one if its value fell outside the 95% CI of the latter. Finally, the mean of simulated annual densities ($D_{July,t}$) was compared to the observed one with t-test and significance level was set at $\alpha <$ 0.05.

Box-Cox and KPSS tests revealed that the $\ln(D_{July,t})$ values of simulated time series had constant variance and were stationary, hence suitable to wavelet analyses. It was not the case for the observed time series, whose $D_{July,t}$ had to be detrended using a local Loess polynomial regression on a 12-year window before reaching constant variance. This difference in reaching constant variance is due to the presence of densities much higher (>8 ind/ha) in simulated time series than the one observed in the field between 1993 and 2019.

Conclusion

Élucider les causes des cycles de population représente encore aujourd'hui un Saint-Graal pour la communauté scientifique. L'importance accordée à ce phénomène émerge de la grande influence qu'ont ces populations sur leurs écosystèmes respectifs et des avancées théoriques en dynamique des populations possibles par leur étude. Dans l'optique d'un monde en changement rapide, les causes de ces cycles doivent impérativement être comprises si l'on veut en protéger les fonctions écosystémiques. Puisque les cycles de lemmings sont essentiels au fonctionnement de l'écosystème arctique canadien, où ils

permettent la reproduction d'une variété de rapaces et de mammifères terrestres, l'objectif général de mon mémoire était de mieux comprendre le rôle qu'a l'hermine au sein de ce phénomène.

Remonter dans le temps, un témoignage à la fois

Comme il est notoirement difficile de faire le suivi des hermines (King & Powell 2006, Lambin 2018) et que de longues séries-temporelles sont nécessaires à l'étude des cycles, mon premier objectif était de reconstituer l'abondance relative de ce petit mustélidé à l'île Bylot de 1993 à 2019. Pour ce faire, un court questionnaire a été envoyé à plus d'une centaine de gens ayant participé aux travaux de terrain sur l'île. Nous visions principalement les personnes n'ayant pas fait plus de 3 étés de terrain pour diminuer les risques d'erreur, c'est-à-dire qu'une observation soit associée à la mauvaise année. On leur demandait de se remémorer, pour une année précise, les observations qu'ils avaient faites d'hermine, de lemmings et d'harfangs. Chaque témoignage se voyait attribuer un score par espèce selon les réponses fournies. Ainsi, pour une année donnée, l'indice d'abondance relative d'une espèce correspondait à la moyenne des scores des témoignages fournis pour cette même année.

Cette méthode étant inhabituelle, nous avons dû nous assurer que les indices d'abondance relative générés étaient fiables. C'est à cette étape qu'interviennent les données récoltées sur les harfangs et les lemmings, qui ont été suivis systématiquement sur toute la période 1993-2019. De fortes corrélations avec les données d'abondance disponibles, une absence d'effet du temps passé sur le terrain par l'observateur et la possibilité de détecter des phénomènes écologiques connus nous ont donné confiance envers les données issues des témoignages.

En plus de fournir des données pour le reste de ce mémoire, le développement de cette méthode représente une fin en soi. En effet, elle pourrait être utilisées dans d'autres systèmes bénéficiant d'une large population d'utilisateurs ayant une certaine connaissance de la faune. Cette approche est particulièrement intéressante là où le coût des techniques d'échantillonnages systématiques est prohibitif mais où les observateurs sont nombreux. Par ailleurs, ce type de méthode peut être complémentaire aux suivis systématiques et

combler certaines lacunes. Bien que plus précis, les suivis systématiques ont souvent une étendue spatiale et temporelle limitée (Anadón et al. 2009) vu leurs coûts élevés et leurs efforts important. Les observations opportunistes, d'un autre côté, sont moins précises mais peuvent décrire correctement les variations d'abondance de certaines espèces à grande échelle avec relativement peu d'effort (Ferguson et al. 1998, Anadón et al. 2009, Peñaherrera-Palma et al. 2018). La méthode que nous proposons se démarque des autres approches d'estimation d'abondance basées sur les entrevues (Knaus et al. 1950, Ferguson et al. 1998, Anadón et al. 2009, Peñaherrera-Palma et al. 2018, Reif et al. 2021) par sa capacité à générer un indice par année.

Toutefois, certains points clés sont à considérés pour utiliser cette méthode avec succès : les participants doivent avoir une certaine connaissance sur les espèces d'intérêts (Anadón et al. 2009, Gagnon & Berteaux 2009, Peñaherrera-Palma et al. 2018, Camino et al. 2020) et les questions doivent être précises et capable de produire différentes réponses pouvant être ordinée en termes d'abondance relative.

Ce travail a permis de montrer qu'il était possible de faire appel aux souvenirs d'observation opportunistes pour obtenir rapidement des données sur plusieurs décennies. Nos travaux, en plus de la grandissante littérature sur le savoir écologique local et traditionnel (Ferguson et al. 1998, Anadón et al. 2009, Peñaherrera-Palma et al. 2018, Camino et al. 2020, Gagnon et al. 2020), soulignent l'utilité de tels témoignages en recherche écologique. Bien qu'il faille souligner les limites de cette méthode, elle permet d'obtenir les données à long-terme nécessaire pour poser des questions écologiques complexes dans les systèmes visités par des observateurs au penchant naturaliste.

Décortiquer le rôle de l'hermine

Dans le chapitre 2, nous avons tiré un maximum d'information des bases de données disponibles pour mieux cerner le rôle de l'hermine dans les cycles de lemmings. La première étape visait à tester une prémisse clé de l'hypothèse du prédateur spécialiste (HPS), à savoir si la réponse numérique du prédateur accusait un retard d'environ un an par rapport aux fluctuations d'abondances de sa proie. Nos résultats montrent bien que l'abondance d'hermine est déterminée en partie par les densités passées de lemmings,

comme prévu par l'HPS. De plus, la réponse numérique de l'hermine semble suffisante pour expliquer la densité-dépendance avec délais présente dans la population de lemming.

Il ne suffit toutefois pas qu'un prédateur réponde avec délais pour générer des cycles d'abondance. L'abondance du prédateur doit aussi avoir un impact négatif sur le taux de croissance de la population de proies. Pour les lemmings de l'île Bylot, il est clair que l'hermine a un impact négatif sur leur taux de croissance, et nos résultats suggèrent que cet impact serait limité à l'hiver. Enfin, selon l'HPS, le prédateur spécialiste est nécessaire à l'apparition de cycles et leur présence devrait induire des phases de faible abondance chez leur proie. Grâce à nos populations de lemmings simulées stochastiquement avec et sans hermines, on constate que l'hermine allonge la périodicité des cycles (jusqu'à 5 ans) et que ceux-ci comportent plus de phases de faible abondance. Par contre, contrairement aux prédictions de l'HPS, les populations de lemmings simulées en l'absence d'hermine présentaient tout de même des cycles d'environ 3 ans. Ceci indique que les petits mustélidés ne seraient pas nécessaires à la formation de cycles *per se* et que l'HPS ne permet donc pas d'expliquer tous les cycles de petits mammifères, bien qu'elle s'applique aux cycles plus long (3-5 ans) observés dans les régions nordiques (Gilg et al. 2006, Korpela et al. 2014).

Ces conclusions nous permettent d'ajouter un morceau important dans la littérature sur les cycles de populations, particulièrement en ce qui concerne le rôle des prédateurs spécialistes. En effet, ceux-ci ne semblent pas nécessaires aux cycles observés en Europe tempérée (Jedrzejewski et al. 1995, Graham 2001, Zub et al. 2008, Mougeot et al. 2019). D'un autre côté. l'HPS n'a pas pu être rejetée en Fennoscandie (Hanski et al. 1991, Korpimäki et al. 1991, Sundell et al. 2013, Korpela et al. 2014) et au Groenland (Gilg et al. 2006). Notre étude renforce donc l'idée qu'en milieu nordique, caractérisé par une forte saisonnalité, une communauté de prédateurs aviaires très mobile et des abondances relativement faibles de rongeurs, les petits mustélidés seraient nécessaires aux cycles à plus long périodicité (3-5 ans) tels qu'observés. Plus précisément, ces éléments permettraient d'isoler le système mustélidé-rongeur durant l'hiver et réduiraient l'abondance de prédateurs intraguildes durant les années de déclin ou de faible abondance, favorisant ainsi le maintien de la population de mustélidé. Tel que suggéré par les isoclines de croissance

nulle, les rongeurs doivent atteindre des densités relativement faibles pour être régulés par les petits mustélidés. De plus, des abondances relativement faibles de rongeurs seraient nécessaire à la régulation par les petits mustélidés. À de plus fortes abondances, le recrutement devrait largement surpasser la mortalité induite par ces prédateurs dont la réponse numérique est limitée par leur territorialité et leur propre prédation (Korpimäki and Norrdahl 1989b, Lambin 2018).

Limites de l'étude et perspectives

La force de ce mémoire, d'avoir réussi à récolter des données sur plusieurs décennies en l'espace de quelques mois, est aussi son talon d'Achille. Bien que nos résultats soient robustes, notre méthode par les témoignages ne permet pas de bien mesurer l'amplitude des variations d'abondance de l'hermine. Les témoignages ne contiennent pas non plus d'informations permettant d'élucider les mécanismes de variations d'abondance, comme le régime, l'utilisation de l'espace ou la mortalité des hermines. Qui plus est, l'absence de suivi direct des individus nous prive de l'histoire naturelle de cette espèce.

Avoir des données d'abondance de lemmings et d'hermine sur une aussi longue période est un exploit en soi. Par contre, ceci ne se reflète pas statistiquement, nos modèles étant basés au maximum sur 27 points de données, ce qui reste peu. Il n'y a aussi aucune réplication spatiale, bien que nos résultats corroborent ce qui a été fait ailleurs (Gilg et al. 2006, Korpela et al. 2014, Barraquand et al. 2022). La taille d'échantillon est surtout problématique pour l'analyse saisonnière de l'impact de l'hermine sur le taux de croissance des lemmings. Ici, les modèles ne se basent que sur 5 ou 8 années. Cette même analyse est basée sur des prémisses qui, bien que logiques, ne sont pas testables. Ces résultats doivent donc être interprétés avec prudence.

Ceci mène par contre à d'intéressantes questions sur les méthodes nécessaires pour recueillir des données libres de telles contraintes. Tel que déjà enclenché par Prof. Gilles Gauthier à l'Université Laval et poursuivi par Dominique Fauteux, des boîtiers simples munis de caméras automatiques permettront un suivi continu et direct de la population de lemmings comme d'hermine. Une fois joints à des modèles appropriés (Augustine et al. 2018, Nakashima et al. 2021) il devrait être possible d'avoir des estimations de densité à

travers toutes les saisons. Sur l'île Bylot, l'été 2022 nous aura montré qu'il était possible de faire un suivi direct d'individus, moyennant certains efforts. Je joins donc Bilodeau (2013) dans sa conclusion : « Augmenter le nombre d'observations comportementales et de suivis télémétriques sur l'hermine […] pendant toutes les phases du cycle des lemmings apparaît essentiel pour évaluer son rôle. Ceci est réalisable, mais demandera toutefois des efforts considérables sur le terrain ». Ce genre de suivi nous informera sur des paramètres largement invoqués dans ce mémoire mais qui, à toutes fins pratiques, non pas étés mesurés. Je parle ici du taux de mortalité infligé aux hermines par les autres prédateurs (prédation intraguilde), du succès de chasse par l'hermine ainsi que la proportion des proies mise en réserve. Le développement de colliers-microphones (Couchoux et al. 2015, Studd et al. 2021), où l'on pourrait entendre les attaques ainsi que la consommation des proies, serait un pas intéressant dans ce monde invisible. La proportion de proies cachées deviendrait calculable, car le nombre de proies tuées – le nombre consommées = nombre cachées. Les étapes à venir concernent donc un suivi en continu de l'abondance des populations et le suivi fin des prédateurs comme l'hermine.

Conclusion

Ces travaux ont un impact à plusieurs échelles. Pour le suivi écosystémique de l'île Bylot, ce mémoire a permis de créer une longue série-temporelle d'un prédateur clé. Celle-ci est déjà réutilisée par des collègues. Les travaux effectués à l'été 2022 ont aussi permis de développer une méthode de suivi d'hermines, mais de façon directe et intensive. L'utilisation de caméras-trappes pour cibler les endroits où l'hermine est présente réduit drastiquement l'effort de trappage.

À l'échelle de l'Arctique, nos travaux lèvent le voile sur une interaction au cœur des fluctuations d'abondance qui le rythme. Le chapitre 2 suggère que l'hermine est nécessaire aux cycles caractérisés par des périodes de 3 à 5 ans et des phases de faible abondance. Nous avons décortiqué la dynamique de ce prédateur méconnu, liée aux densités passées et présentes de lemmings, ainsi que son rôle, observable seulement en hiver.

En ce qui a trait à l'étude des cycles de population, ce test additionnel de l'hypothèse du prédateur spécialiste fait avancer notre compréhension des mécanismes menant à ce

phénomène. Nos résultats indiquent que la densité-dépendance avec délais peut être médiée par la réponse partiellement retardée des prédateurs spécialistes et que ceux-ci sont responsables des phases de faible abondance. De plus, nous joignons les conclusions de Barraquand et al. (2014, 2022) en montrant que les déclins sont majoritairement causés par de la densité-dépendance qui, à l'échelle annuelle, est directe. Dans notre cas, tout indique que cette composante de la densité-dépendance serait liée aux autres prédateurs du système dont la réponse numérique serait plus rapide (Therrien et al. 2014, Fauteux et al. 2016, Fauteux & Gauthier 2022).

Pour la communauté scientifique, nous laissons une méthode qui pourrait être utile aux nombreux suivis à long-termes disséminés à travers le globe. Ces suivis ont grandement contribué à notre compréhension du monde naturel et de nombreuses questions sont apparues depuis leur établissement. Il est donc fort probable que les protocoles instaurés au départ ne permettent pas de répondre aux nouvelles questions. Notre méthode offre une façon de retourner dans le temps pour acquérir des données d'hier qui, bien que peu précises, permettent de répondre aux questions d'aujourd'hui.

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Annexe 1 - Ultra-light photosensor collars to monitor Arctic lemming activity

A1.1 Résumé

Dans l'Arctique, l'utilisation des terriers est critique pour la survie des lemmings considérant le haut risque de prédation durant l'été. Ce comportement est toutefois difficile à étudier vu la petite taille (< 90 g) des lemmings et la faible possibilité de bien détecter leurs allées et venues. Nous avons donc développé des colliers photosensibles de 1.59g pour enregistrer les transitions entre l'intérieur (sans lumière) et l'extérieur (avec lumière) du terrier. Les colliers ainsi que leur impact sur leur porteur ont été évalués en captivité comme sur le terrain. Les porteurs n'ont pas perdu de masse à cause du collier et n'étaient pas moins recapturés que leurs pairs non équipés. Les données issues des colliers montrent des patrons d'activités clairement définis d'alternance entre l'intérieur et l'extérieur des terriers. Cette technologie, grâce à l'ensoleillement continu de l'été arctique, pourra permettre l'enregistrement passif de l'activité d'un petit mammifère clé pour cet écosystème.

A1.2 Abstract

Background: Studying the anti-predatory behavior of mammals represents an important challenge, especially for fossorial small mammals that hide in burrows. In the Arctic, such behaviors are critical to the survival of lemmings considering that predation risks are high every summer. Because detailed information about how lemmings use burrows as hideouts is still lacking, we developed a 1.59 g photosensitive collar to record any event of a small mammal moving between a dark area (e.g., burrow) and a bright area (e.g., outside the burrow). Tests of how collars affected lemming behavior were conducted in captivity in Cambridge Bay, Nunavut, Canada in November 2019 and field tests were conducted on Bylot Island, Nunavut, Canada in August 2021.

Results: The device was made of two chemical batteries and a printed circuit board (PCB) equipped with a photosensor and a real-time clock that recorded amplitude transient thresholds of light (lux) continuously. In accordance with ethical use of such devices, we verified that no abnormal loss of body mass was observed in captive or free-ranging lemmings, and no difference in recapture rates were observed between those with and without a collar, though we could not test this for periods longer than 108h. Measurements of light intensities revealed consistent patterns with high lux levels at midday and lowest during the night. Lemmings showed clearly defined behavioral patterns alternating between periods outside and inside burrows. Despite 24h daylight in the middle of the summer, August nighttime (i.e., 23:00 to 04:00) lux levels were insufficient for amplitude transient thresholds to be reached.

Conclusion: By taking advantage of the long periods of daylight in the Arctic, such technology is very promising as it sets new bases for passive recording of behavioral parameters and builds on the prospect of further miniaturization of batteries and PCBs.

Keywords: Light sensor; modern ethology; *Lemmus trimucronatus*; *Dicrostonyx hudsonius*; *Dicrostonyx groenlandicus*; subterranean; predator refugia

A1.3 Background

Lemmings are small burrowing rodents that are considered as keystone species in the Arctic tundra ecosystem. They represent the main prey of many avian and mammalian predators and are well known for their 3- to 5-year high amplitude abundance cycles that have substantial impact on the local vertebrate diversity (Ims & Fuglei 2005; Schmidt et al. 2008; Gilg et al. 2009; Schmidt et al. 2012; Gauthier et al. 2013). Identifying the causal factors of these cycles epitomize one of the oldest ecological questions (Ehrich et al. 2020), and several hypotheses have been proposed such as regulation by food, predators or intrinsic factors, such as stress (Elton 1924). Recent studies conducted in the High Arctic, provide compelling evidence that predators are an important factor behind this century-old enigma (Gilg et al. 2003; Inchausti & Ginzburg 2009; Legagneux et al. 2012; Fauteux et al. 2016). However, little is known about potential behavioral strategies that lemmings employ to face such heavy predation that peaks in summer during the presence of migratory predators.

A key aspect in predator-prey interactions is how predation shapes the use of refuges by herbivores such as burrows, and vice versa (Brown 1992). Many fossorial herbivores like lemmings rely partly on roots in their diet (Fauteux et al. 2017), which allows them to browse in the safety of burrows. However, roots rarely consist of a sufficient food source especially in the summer characterized with numerous fine roots that are poorly nutritive (Bardgett et al. 2005; Lubbe et al. 2021), and herbivores must make compromises between predator avoidance and food acquisition. Searching for mates and natal and breeding dispersal also force herbivores to move outside burrows (Banks et al. 1975). Such behaviors can vary among individuals, especially between mate-searching polygamous males and nursing females, whose survival have different impacts on population growth. Unfortunately, lemming behavior is difficult to monitor through conventional methods, such as direct observations, because they use extensive networks of runways and tunnels to move around and are easy to lose sight of.

To better understand daily routines of lemmings during summer when they are highly exposed to both avian and mammalian predation (Gilg et al. 2003; Therrien et al. 2014), we

developed a new miniature photosensitive collar of 1.59 g that continuously records all transitions between dark and bright environments. We first assessed the physiological response of lemmings to these collars measured as body mass variations in captive and free-ranging lemmings over 24-72h, and if lemmings with or without collars had different recapture rates, reflecting potential short-term impact on survival or behavior. The collar was designed to i) work under Arctic summer conditions for a fossorial small mammal (i.e., temperatures range from -5°C to +20°C, high humidity and dirt), ii) be resistant to tearing by claws, iii) record light transitions continuously for >2 weeks and iv) be reusable on other individuals when battery levels allow it. The recorded transitions between bright and dark environments would provide a reliable proxy of a lemming moving out of its burrow to open tundra, and vice versa, yielding information on the use of refuges. This device was developed considering the 24h daylight during summer in the High-Arctic that creates ideal conditions for highly contrasting light intensities, which facilitates detection of transitions by the collars.

A1.4 Methods

A1.4.1 Development of the printed circuit board (PCB), reading hardware and software

A PCB was designed to hold the required components and compose the circuit mechanisms of the collar. Because the PCB was intended to be installed on a collar, it had to be flexible. This was achieved by first forming a 4-layer PCB circuit board fabricated with polyimide substrates. Although the final flexibility was somewhat limited by the rigid components installed on board, we reserved ‘keepout’ areas without components to allow specific bends that would fit with the round shape of the collar.

The device was centred around a microcontroller, Texas Instruments MSP430FR2355, a real-time clock (RTC) AB0815 from Abracon with a quartz crystal reference, and an ambient light sensor LTR-308 ALS Lite-On corporation. Light intensities measured by the optic sensor were proportional to ambient light (luxes). The custom-made PCB with all components weighs 282 mg. When the two lightweight chemical batteries (330 mg each; Energizer® Zinc Air [Zn/O2]) were fixed on the PCB, the total mass was 942 mg. The

board dimensions were 27.9 x 5.3 mm and the PCB was a flex board with a thickness of 200 µm. The RTC upkeeps the time and date while sustained by diminutive currents in the µA range. In addition, the microprocessor, a part of the microcontroller, also remained in a dormant mode to reduce battery consumption. General architecture design is given in Fig. A1.1A.

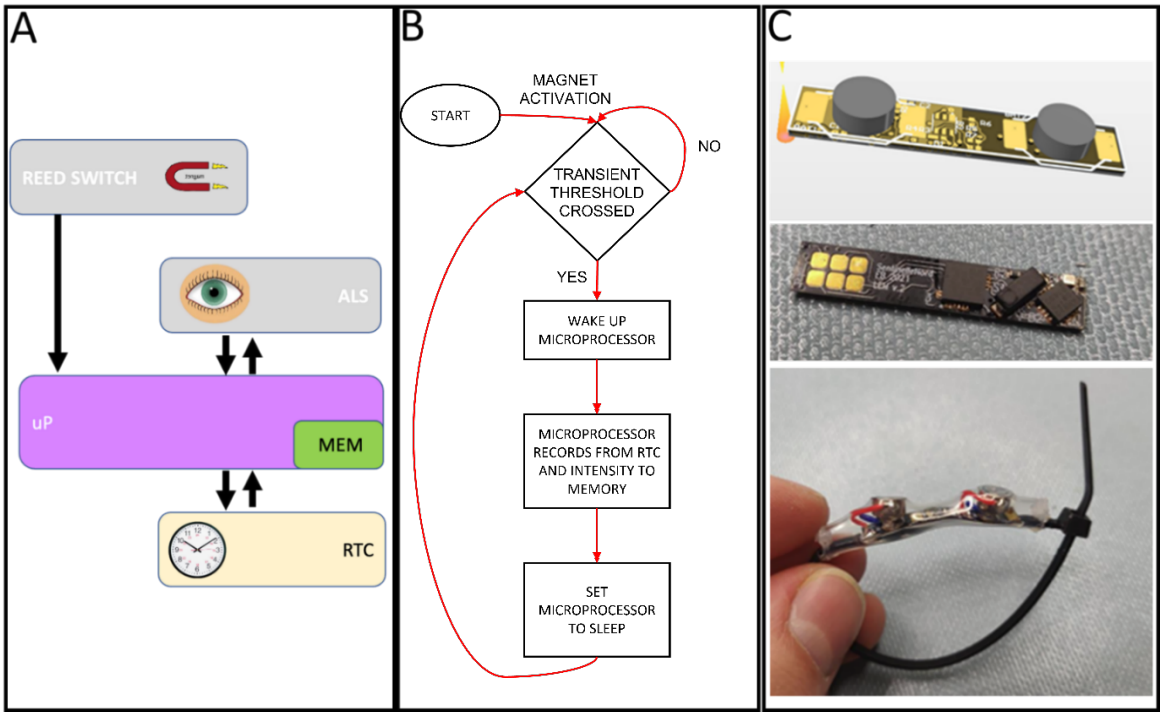

Fig. A1.1. In **A**, architecture of the instrumented lemming collar. The principal components are: the microprocessor (uP), with an ferroelectric memory (MEM); the ambient light sensor (ALS); the Real Time Clock (RTC) and a triggerable magnetic reed switch use to activate the device. In **B**, algorithm of the light-sensitive collar. Intensity changes lead to analysis by the microprocessor only in situations when light level thresholds determined a priori are crossed. In **C**, 3-D model (top), PCB assembly (center) and final device prototype (bottom).

Exits and entries from the burrow were detected and monitored by keeping track of ambient light transitions. Abrupt changes in light intensity create an interrupt signal that triggers further analysis by the microcontroller. After each light transition (e.g., from dark to light) and if the new state is maintained for at least 4 seconds, the transient amplitude (i.e., light

intensity right after crossing a transient threshold), real time (from 00:00 to 23:59), and date of the event is stored in random access memory (RAM). Fleeting events that occurred within 4 seconds are ignored because they are generally assumed to be noise events such as passing under an object or in a small, illuminated portion of a tunnel. Very slow transitions are also ignored because they can be too easily triggered from changing weather (e.g., overcast vs. sunny, day to night or passing clouds, see algorithm in Fig. A1.1B). Fig. A1.1C presents the external structure and shape of the PCB and completed collar.

When a change in light intensity crosses the amplitude transient threshold levels, the system logs the real-time clock data and transfers SRAM buffered data to the 32 kB ferroelectric permanent memory. To avoid high power consumption from the permanent memory, it is only actuated when such transitions that last >4 seconds occurs. A miniature magnetic switch mounted on the PCB bestows the possibility of in field activation with a simple 3 magnet swipes performed within 10 seconds. The redundancy affords the prevention of false activations and battery economy by avoiding actuation of the system prior to its final installed deployment time. The microcontrollers were programmed with a custom host firmware. This configuration allows parameter modification in the module via a RS-232 to USB terminal interface and a simple terminal software on a personal computer.

A1.4.2 Assembling the collar

To assemble the collar, the PCB was first slid into a transparent 2 cm heat shrink sleeve. A tie wrap was then slid under the PCB inside the heat shrink sleeve. Only then was the shrink heated with a heat gun, which fixed the PCB on the tie wrap. To keep away any water or humidity from the PCB, both ends of the reduced heat shrink were filled with acetic acid-free silicon without touching the PCB itself. Due to the heat shrink sleeve covering the ambient light sensor, light intensities that are recorded do not represent direct sunlight, but the transparency of the sleeve allowed a reliable proxy.

A1.4.3 Impact of collars on lemmings in captivity

Adult brown lemmings have a minimum weight of ~30 g, whereas collared lemmings start at ~40 g (Gruyer et al. 2010; Fauteux et al. 2015). The mass of the collar (1.59 g) was ≤5% of the body mass of adult lemmings (Table A1.1). Keeping tracking devices below a 5%

threshold is recommended (Murray & Fuller 2000), but could still negatively impact behaviors and vital rates (see O'Mara et al. (2014) for a review; (Hamley & Falls 1975; Berteaux et al. 1996; Moorhouse & Macdonald 2005). We evaluated how collars impacted lemmings by comparing body mass changes, a proxy of body condition, and recapture rates, a proxy of survival or behavioral alteration, between lemmings with and without collars. In November 2019, 4 brown lemmings (*Lemmus trimucronatus*) and 2 collared lemmings (*Dicrostonyx groenlandicus*) were held in captivity in Cambridge Bay, Nunavut, Canada. They were provided ad libitum food and water before and during the experiments. For more details about how the lemmings were live-trapped in the field, for the housing conditions and care given to the captive lemmings, see Poirier et al. (2021).

Table A1.1. Mass (mg) of each component of the photosensitive collar

Element	Mass
Tie-wrap	280
Printed circuit board	282
Heat-shrink sleeve	330
Caulking	34
Two Zinc Air batteries	660
Total	1586

The experiment consisted of all lemmings being monitored daily without a collar for several days (lemmings were monitored since August 2019 after their initial capture (Poirier et al. 2021), and then equipped with a 1.5 g dummy collar between 24h and 108h (i.e., a tie wrap with a mass fixed by a heat shrink). Each individual was kept under observation for the first 15 minutes and then checked every 2 hours for the first 8 hours, then every 12 hours, to ensure the collars were not causing drastic changes in behavior (e.g., constantly scratching or trying to take off the collar) or choking. The body mass of each lemming was monitored with an electronic scale (±0.01 g) every day to every week before the collar was installed on it. Once the collar was fit on the lemming, the body mass

was measured every day. To determine if collars had an impact on the body conditions of lemmings, we compared the daily mass change of equipped lemmings to their daily mass change before they had the collars on. Two different (non-overlapping) pre-experimental periods of 12 or 8 days were chosen as controls, because lemmings either continuously gained or had a stable mass during these periods (Fig. A1.2A). We performed a one-sided t-test, weighting for the duration of the monitoring in each period, to test the hypothesis that equipped individuals had a lesser daily mass gain than when unequipped.

A1.4.4 Impact of collars on lemmings in the field

We deployed light-sensitive collars on small mammals in three locations of the Canadian Arctic where populations are monitored every year and assessed the impact of collars on body condition and recapture probability. Rodents fitted with collars were brown lemmings (n = 5 & 36) and northern collared lemmings (*Dicrostonyx hudsonius*, n = 11 & 0) in respectively in Cambridge Bay and Bylot Island, Nunavut, whereas Ungava collared lemmings (n = 6), an Eastern meadow vole (*Microtus pennsylvanicus*) and a Northern Bog Lemming (*Synaptomys borealis*) were fitted with a collar in Salluit, Quebec. All rodents were monitored at these sites with live-trapping and capture-mark-recapture methods as part of multi-annual surveys. At all sites, trapping grids made of 96 to 144 live-trapping stations, each station being separated by 30 m, and arranged according to a cartesian plane were used (Bylot Island: 3 grids; Cambridge Bay: 4 grids Salluit: 2 grids). Longworth and Little Critter traps were used at all these sites. Capture-mark-recapture methods consisted of opening and baiting traps followed by visits of traps every 12 hours until 6 visits were completed. All lemmings captured were marked with a PIT- or ear-tag, weighed and sexed. During live-trapping, adult lemmings with a minimum body mass of 34 g (to ensure that collars accounted ≤5% of the total body mass) were fitted with collars. The total number of collars deployed at each site differed due to low lemming densities in both Cambridge Bay and Salluit (<1 ha^{-1}), while lemming densities were high on Bylot Island (15 ha^{-1}; unpublished data). All manipulations were approved by the Animal Care Committees of the Canadian Museum of Nature (2018.02.001) and Université Laval (2019-253, VRR-18-050), Parks Canada (SIR-2021-39399), Department of Environment of Nunavut (WL2019-

038), Kitikmeot Inuit Association (KTX119N006), and Ministère des Forêts, de la Faune et des Parcs du Québec (SEG 2021-05-31-125-10-S-F).

Recapture probabilities of individuals with and without collars were calculated for each trapping grid. Here, recapture probabilities were calculated as the total number of recaptures across all individuals divided by the total number of captures (i.e. sum of first captures and recaptures). To test if recapture probabilities of equipped individuals were lower than those of unequipped individuals, we used a one-sided t-test with weighted observations to account for the number of deployed collars per grid. This was done to reduce the influence of grids with low sample size on the statistical test.

Using exclusively the data of Bylot Island, where a peak lemming abundance yielded many more captures than at the other sites, we also evaluated the difference in daily mass change between equipped and unequipped lemmings. The relative daily mass changes and 95% confidence intervals (CI) of each group were weighted for the time between captures. We used a one-sided t-test weighted for the time between captures to evaluate if daily mass changes of equipped individuals were lesser than those of equipped individuals.

A1.5 Result and Discussion

The miniature photosensitive collars that we developed provided detailed information about daily routines of lemmings in natural conditions during the Arctic summer and were found to have no impact on body mass or recapture rates after being equipped for as long as 2.5 days in the field and 4.5 in captivity days (Fig. A1.2A). While on the field, we were able to extract data from 13 of the 26 retrieved collars.

A1.5.1 Impact of collars on lemmings in captivity

For the test in captivity, the one-sided t-test showed that equipped lemmings had daily mass changes that were similar to those observed in pre-equipped periods 1 ($p = 0.39$) or 2 ($p = 0.94$) (Fig. A1.2B). Thus, the dummy collars had negligible or null effect on daily mass change.

A1.5.2 Impact of collars on lemmings in the field

We found no negative effect of the collars on daily mass change of brown lemmings on Bylot Island based on the weighted one-sided t-test (p-value = 0.21; Fig. A1.2C). Similarly, a weighted one-sided t-test showed that the recapture probabilities of equipped individuals were not lower than those of unequipped individuals (p-value = 0.62), even if recapture probabilities varied across sites (Table A1.2).

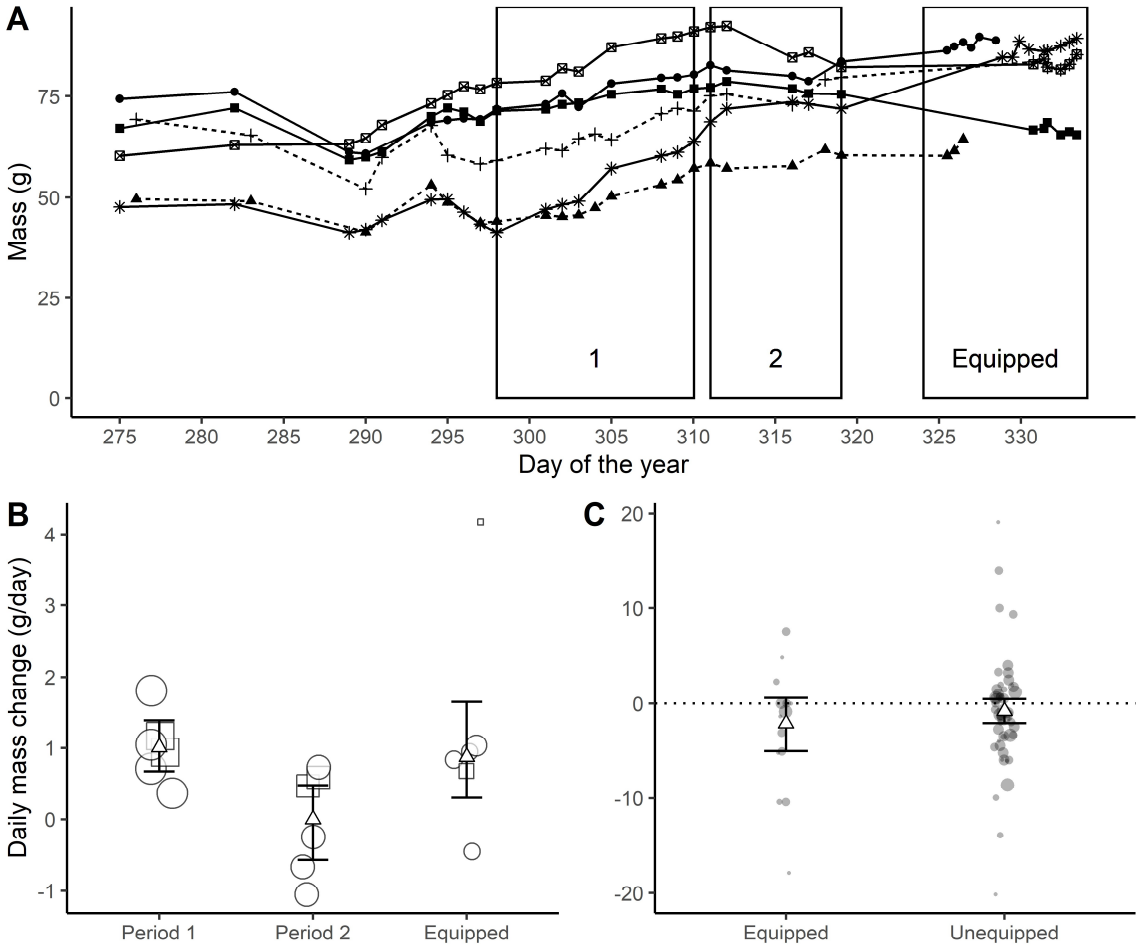

Figure A1.2. Impact of a photosensitive collar on the daily mass change of captive and wild lemmings. **A) & B)** The masses of six captive lemmings were monitored across 58 days in Cambridge Bay, NU, Canada. Period 1 and 2 are periods when lemmings are not equipped with a 1.5 g dummy collar, contrary to the Equipped period. In each period, daily

mass gain was calculated. **A)** Body mass of 4 captive brown (full lines) and 2 collared (dotted lines) lemmings. Rectangles delimit different periods. Symbols represent different individuals. **B)** Daily mass changes of captive lemmings with 95% CI. The white triangle represents the weighted mean in each period, and squares and circles represent respectively brown and collared lemmings. Point size is proportional to the number of days the daily mass change is based on. **C)** Field observations of daily mass changes of equipped and unequipped brown lemmings with their 95% CI in the Bylot Island, NU, Canada. White triangles are the weighted mean. Point size is proportional to the number of days the daily mass change is based on, here the time between captures).

Overall, our results are in line with those of previous studies conducted on the impact of radio collars on small rodents that weigh ≤5% of the body mass of the host (Berteaux et al. 1996; Korpimäki et al. 1996). Indeed, our study confirms negligible, if any, negative impacts on the body mass of lemmings over time and no noticeable change in behavior. Moreover, we further included an analysis of recapture rates, which both considers potential changes in survival and behavior (e.g. trap-shyness), and yielded no difference caused by the collar. No injury or rash was found on the necks of lemmings after collars were removed, which suggests that the material used for the collar (i.e. tie wrap and heat shrink) ensured a certain level of comfort. However, the short wearing time (4.5 days in captivity and 2.5 in the wild) prevents us from assessing potential long-term impacts of the collars. We could not conduct the same tests in the field with the other small rodent species, which calls for further assessments. However, most of the literature cited in this article showing weak or no effect of ultra-light collars on small mammals were conducted on voles. Thus, similar results as those observed here for lemmings should apply to other Arctic small rodents that weigh >30 g.

Table A1.2. Sample size (N) and recapture probabilities of unequipped and equipped small rodents with a photosensitive collar (R) in each live-trapping grid of the Canadian Arctic: Bylot Island (NU), Cambridge Bay (NU) and Salluit (QC). Recapture probabilities are the odds of recapturing a newly released individual. Recapture probability averages are weighted for the number of captures for unequipped individuals, or deployed collars for equipped individuals in the grid. Coordinates of each trapping grid are presented in degree decimal with the WGS84 geodetic system.

Location	Trapping grid (coordinates*)	$N_{unequipped}$	$R_{unequipped}$	$N_{equipped}$	$R_{equipped}$
Salluit	C (62.22°N, 75.62°W)	16	0.56	5	0.60
	L (62.17°N, 75.68°W)	9	0.44	3	0.33
Cambridge Bay	LPH (69.12°N, 105.42°W)	20	0.50	2	0.50
	LPM (69.11°N, 105.42°W)	30	0.33	8	0.13
	OTH (69.10°N, 104.93°W)	4	0.25	3	0.00
	OTM (69.11°N, 104.95°W)	20	0.55	3	0.67
Bylot Island	LG1 (73.16°N, 79.94°W)	183	0.33	10	0.30
	LG2 (73.15°N, 79.97°W)	202	0.47	15	0.47
	LX (73.15°N, 79.94°W)	171	0.35	11	0.73
Weighted average *R*			0.40		0.43

A1.5.3 Light-sensitive collars to detect circadian rhythms in cryptic species

Light-sensitive collars recorded multiple transitions throughout the days (mean 89.73 per day, range [14, 430]), indicating regular movements inside and outside burrows (Fig. A1.3). For all collars deployed on lemmings, 95% of transitions were recorded between 5 AM and 22 PM. The absence of transition recorded during the night could either be the result of lemmings staying underground during that period, or that the amplitude in changes of light intensities was too low to be detected by the collars. Although the optical sensor can respond to low light intensities (0.01 lux) the minimum trigger thresholds were likely set too high (i.e. 120-240 lux) preventing the recording of transitions in low-light conditions. A potential solution to this problem may be to reduce such threshold to a value

close to 0. Indeed, 0 lux were often observed during daytime and were associated with lemmings being in their burrows. Alternatively, different thresholds could be programmed for daytime and nighttime.

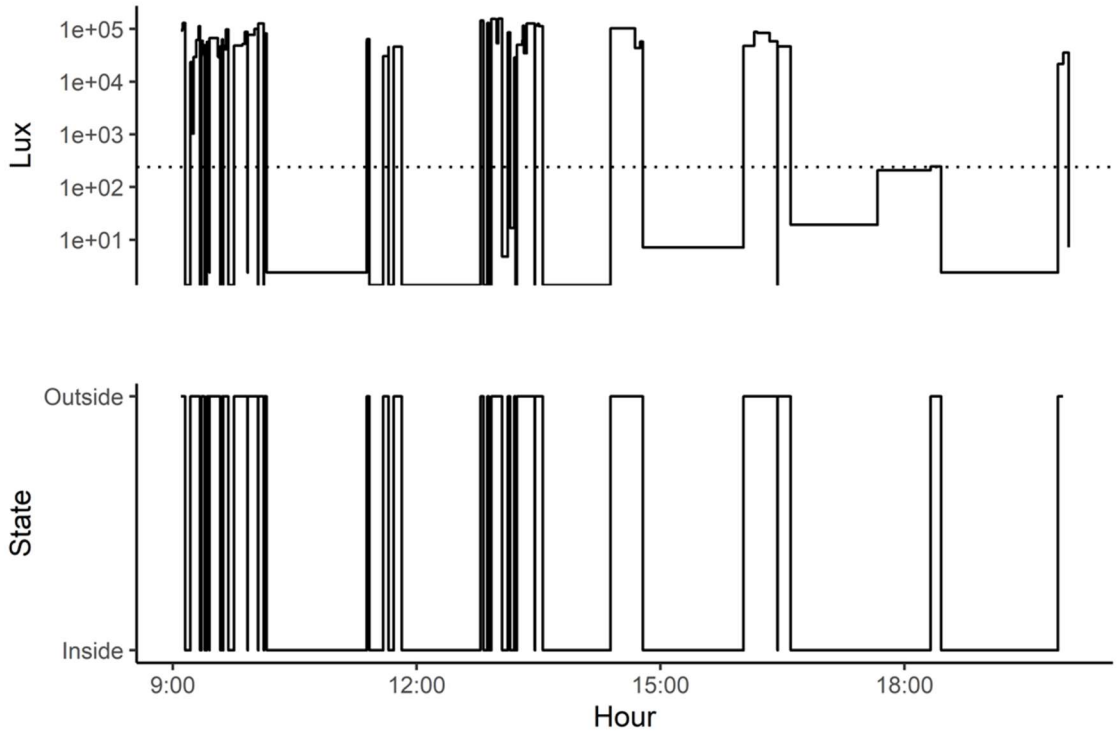

Fig. A1.3. Example of light intensities (lux) recorded by a photosensitive collar equipped on a brown lemming individual on Bylot Island, NU, Canada. Above: continuous light intensity (Lux) on a logarithmic scale over time, with the threshold fixed at 240 lux (dotted line) that separate states of the lemming being inside or outside its burrow. Long periods without changes in lux (flat horizontal lines) indicate no transitions and that the rodent is constantly in darkness. Below: state of lemming being either inside or outside a burrow derived from the recorded light intensity threshold.

During daylight hours, different individuals simultaneously recorded similar light intensity values, confirming consistency of readings among collars (Fig. A1.4). Weather patterns, total or partial (e.g., in the shadow of a plant) exposure to the sun, and dirt on the heat shrink sleeve are all factors that may have contributed to the large variability among recordings taken at the same time of day but on different small rodents. From these values,

we derived the state of the lemming (in- or outside its burrow) by discretizing the recorded light intensity by the previously programmed transient amplitude threshold of 240 lux, which was used to record the transition between low and high light intensities. Above it, the lemming was considered outside its burrow. Whether the individuals were at the very entrance of the burrow or further from it is unknown, and this information will influence the degree to which lemming are available to predators (Schmidt et al. 2008). The results showed a behavioral pattern characterized by continuous bouts of activity outside burrows interrupted by prolonged stays inside burrows. Similar repetitive pattern of activity was also observed in captivity for brown lemmings with running wheels (Swade & Pittendrigh 1967) or semi-natural conditions for other fossorial mammals such as bank voles (Jędrzejewska & Jędrzejewski 1990) and meadow voles (Webster & Brooks 1981) where general activity was highly fluctuating within 24h periods. High frequency recordings will allow to examine how physiological (e.g., sex, reproductive condition), external (e.g., predation and habitat) parameters and their interactions could affect movements and other behaviors like the use of refuges. Indeed, such parameters have been shown to be important in how fossorial cricetid rodents use burrows as refuges (Harper & Batzli 1996).

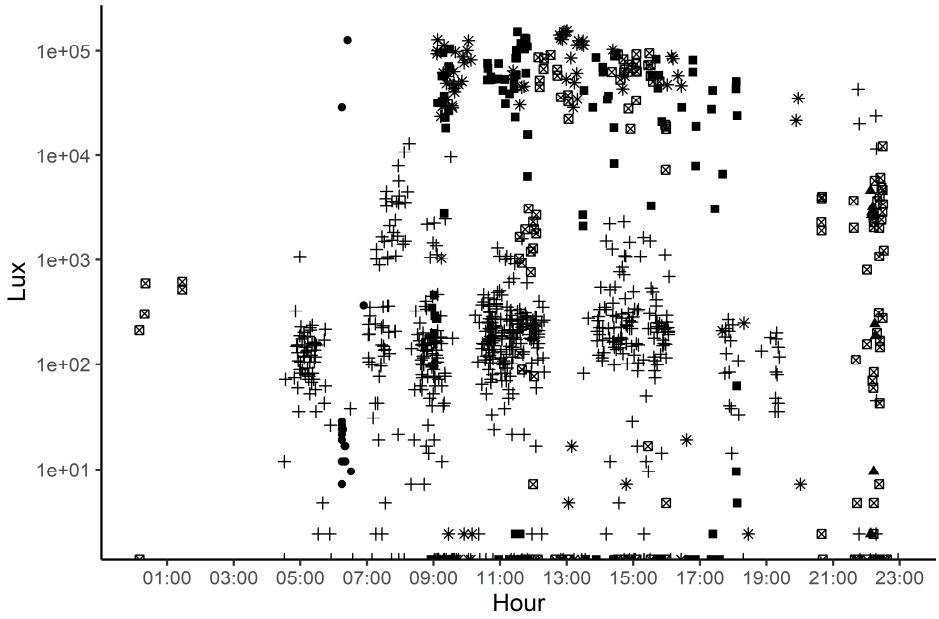

Fig. A1.4. Light intensities (lux) recorded by photosensitive collars equipped on seven brown lemmings, each represented by a different symbol, on Bylot Island, NU, Canada between the 10th and 18th of August 2021. Symbols are used to differentiate individuals.

We found that the batteries, that made up 41% of the total PCB mass, were largely sufficient to record light transitions for at least 72 hours in the field and expected to last 20 days from theoretical calculations. Unfortunately, we could not test the longevity of the collars for longer periods in the field due to logistical constraints due to the COVID-19 pandemic situation. Additionally, 50% of the retrieved collars contained data. This proportion will be increased by making sturdier connections among all the electronic elements of the collar. Nonetheless, our objectives were fulfilled by developing a fully functional photosensitive collar that can be deployed on rodents of the Arctic tundra with so far no known health risks or impact on behavior. Moreover, this passive recording system that can be set on all Arctic small mammals is one a step further towards revealing some of the most cryptic behaviors with very high details and without observer bias (Smith & Pinter-Wollman 2021).

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