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SÉLECTION DE L’HABITAT, REPRODUCTION ET PRÉDATION HIVERNALES CHEZ LES LEMMINGS DE L’ARCTIQUE

Mémoire présenté
à la Faculté des études supérieures de l'Université Laval
dans le cadre du programme de maîtrise en biologie
pour l'obtention du grade de Maître es sciences (M.Sc.)

DEPARTEMENT DE BIOLOGIE
FACULTÉ DES SCIENCES ET DE GÉNIE
UNIVERSITÉ LAVAL
QUÉBEC

2009

Résumé

Nous examinons l'effet du couvert de neige sur la distribution spatiale des nids d'hiver des lemmings variables (*Discrotonyx groenlandicus*) et des lemmings bruns (*Lemmus trimucronatus*) sur l'île Bylot au Nunavut, Canada. Nous validons une méthode permettant de détecter l'activité de reproduction des petits mammifères à l'intérieur des nids d'hiver et étudions l'effet de la structure de l'habitat sur l'occurrence de cette reproduction. Nous évaluons le rôle du couvert nival en tant que protection contre la prédation exercée par l'hermine (*Mustela erminea*) et le renard arctique (*Vulpes lagopus*) sur les nids d'hiver des lemmings. Nos résultats suggèrent que les nids d'hiver des deux espèces de lemmings sont principalement distribués sur des sites où l'hétérogénéité de la micro-topographie est élevée, la pente est forte, le couvert nival est épais et offre une protection thermique et l'abondance des mousses est relativement élevée. Nous démontrons qu'il est possible d'inférer l'occurrence de reproduction hivernale des petits mammifères à partir des fèces récupérées dans les nids d'hiver. Les probabilités d'occurrence de reproduction augmentent dans les sites à faible altitude à l'intérieur des nids de lemmings variables et avec la disponibilité de certaines plantes graminoïdes à l'intérieur des nids de lemmings bruns. L'épaisseur du couvert nival n'influence pas la prédation des nids d'hiver des lemmings par les hermines, mais semble limiter les tentatives de prédation exercées par les renards arctiques. En somme, nous concluons que le couvert nival joue un rôle déterminant sur la structure spatiale des populations de lemmings pendant l'hiver arctique.

Abstract

We investigate the effect of snow cover as a key factor influencing the spatial distribution of winter nests of collared lemmings (*Discrotonyx groenlandicus*) and brown lemmings (*Lemmus trimucronatus*) on Bylot Island, Nunavut, Canada. We validate a method to determine the breeding activity of northern small mammals in their winter nests and examine the effect of habitat structure on their reproduction. We also study the role of snow cover as protection to lemmings against winter nest predation by stoats (*Mustela erminea*) and arctic foxes (*Vulpes lagopus)*. Our results suggest that lemming winter nests of both species are mainly distributed in areas with high micro-topography heterogeneity, steep slopes, deep snow cover providing thermal protection and relatively high abundance of mosses. We demonstrate that analysis of faecal samples can be used to infer breeding activity in small mammal winter nests. The occurrence probability of winter reproduction increases in collared lemming nests located at low elevation and in brown lemming nests surrounded by high graminoid availability. Snow cover did not affect probability of predation of lemming nests by stoats but deep snow cover limited predation attempts by arctic foxes. We conclude that snow cover plays a key role in the spatial structure of wintering small mammal populations in the Arctic.

Avant-Propos

Dans un premier temps, je tiens à remercier mon directeur Gilles Gauthier. Je te remercie pour la confiance que tu as su m'accorder ainsi que pour le soutien et les conseils que tu m'as concédés pour la réalisation de ce projet. Je tiens également à te remercier de m'avoir enseigné et transmis ton dévouement pour la rigueur scientifique. Parallèlement, je désire remercier mon co-directeur Dominique Berteaux. Merci Dominique pour la motivation et les commentaires constructifs que tu m'as alloués. Je remercie chacun de vous de m'avoir permis d'explorer et de mieux comprendre la véritable valeur des terres nordiques.

Je tiens à remercier la grande famille de l'île Bylot. Un merci particulier à Jean-Bastien Lambert et Mylène Marchand-Roi qui m'ont fortement aidé sur le terrain. Merci à Cédric et Don Reid pour vos bons conseils. Merci à Marie-Christine pour ton bon travail essentiel au fonctionnement de l'équipe. Merci Gérald pour ta présence, Madeleine pour m'avoir fait connaître Borat, Marc-André pour tes mille et un coup, Frédéric pour prendre la relève, merci à Arnaud et Cassandra de m'avoir permis d'aller vivre l'expérience des renards avec vous, merci à Laura pour tes rires, merci à Éliane, Nico, Niko, J-F, Antoine, Mélanie et tous les gens qui ont participé de près ou de loin à ce projet. Finalement, je tiens à remercier ma famille, ma blonde et mes amis pour simplement être ce qu'ils sont pour moi.

Ce projet a été réalisé grâce à la participation des organismes suivants: le Centre d'étude nordique, le Ministère des affaires Indiennes et du Nord, le Service canadien de la faune, ArcticNet, le programme de l'Année polaire internationale, l'Étude du plateau continental polaire, le Conseil de recherches en sciences naturelles et en génie du Canada, le Fond de recherche sur la nature et les technologies du Québec, la Fondation canadienne pour l'innovation et Parcs Canada.

Ce mémoire comporte deux articles scientifiques qui seront soumis à des revues spécialisées. Le premier article porte sur la validation d'une nouvelle méthode permettant de déterminer l'activité de reproduction des petits mammifères à partir des fèces récupérées dans les nids d’hiver. D’autre part, le second article s’intéresse à la distribution spatiale des nids d’hiver des lemmings variables et des lemmings bruns, à l’occurrence de reproduction à l’intérieur de ces nids ainsi qu’à la prédation des nids par l’hermine et le renard arctique. Je serai le premier auteur de chacun de ces articles. Pour leur part, M. Gilles Gauthier et M. Dominique Berteaux seront respectivement les second et troisième auteurs.

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La légende des hommes lemmings

Il y a fort longtemps, les hommes lemmings se réveillaient à l'aube de leur vie et s'endormaient à la fin de leurs jours sans trop savoir comment distinguer l'interminable jour de la nuit éternelle. Leur nombre augmentait sans cesse jusqu'à ce que certains d'entre eux sombrent calmement dans un sommeil inlassable que chacun semblait envier. Ainsi, le pouls du cycle vital de ce peuple semblait intemporel. Néanmoins, il fut un jour où l'un de ces hommes lemmings s'interrogea sur ses propres ambitions et il se mit à graver la pierre. Sur son piédestal apparaissent ces mots: «Je suis Ozymandias, le roi des Rois; contemple mon œuvre, Ô tout puissant, et désespère!». Cet être s'autoproclama roi et inventa l'idée du privilège. Cette invention allait se concrétiser sous la forme d'un dispositif ingénieux favorisant le profit individuel sans responsabilité individuelle que l'on désignera seulement plusieurs années plus tard sous le nom de «Société commerciale». Cet être justifia étrangement ses actes par les paroles de Galilée «J'ai du mal à croire que le même Dieu qui nous a dotés d'esprit, de raison et d'intelligence puisse vouloir que nous y renoncions.»

C'est ainsi qu'une simple idée bouleversa l'univers de ces êtres. Le peuple se divisa en deux. D'une part, un jeune homme lemming du nom de Winston Churchill affirmait que la démocratie était la pire forme de gouvernement, à l'exception de toutes les autres. D'autre part, Dom Helder Camara s'exclamait ainsi: «Je nourris un pauvre et l'on me dit que je suis un saint. Je demande pourquoi le pauvre n'a pas de quoi se nourrir et l'on me traite de communiste.». C'est ainsi qu'une guerre sans fin débuta et donna raison aux paroles d'Al Capone: «On obtient plus en demandant poliment une arme à la main qu'en demandant juste poliment.» En effet, les enfants de ces peuples virent le pouvoir politique de Mao Tsé Tung sortir directement du canon d'un fusil. Peu importe le clan de l'un ou de l'autre, cette fois-ci, personne ne s'endormait et la population ne cessait de croître dans cet univers chaotique où d'une manière assez surprenante, chacun avait la prétention d'être du «bon coté». La croissance de la population et celle du chaos semblaient intimement liées. En observant cette augmentation, deux des hommes lemmings discutèrent et le premier, du nom de Albert Einstein, affirma: «Les intérêts composés sont la plus grande force de tout *l'univers.» Le second, du nom de Isaac Newton, songea à la haine impliquée dans ce conflit et s'exclama: «À chaque action correspond une réaction égale.» Quoi qu'il en soit, le nombre d'hommes lemmings ne cessa de croître et permis à Adolf Hittler de rire dans son tombeau blindé en certifiant: «C'est un fait que les masses avalent plus facilement un gros mensonge qu'un petit.»*

Devant cette époque apocalyptique, trois jeunes hommes lemmings se mirent à observer l'océan. L'un d'entre eux, du nom d'André Gide, dit d'une voix incertaine: «Ne découvre de nouvelles terres, que celui qui sait quitter tout rivage.» Le second, du nom de Sun Tzu, l'observa d'un regard perçant et s'attaqua au manque de conviction du premier en lui répondant: «Le vainqueur triomphe avant même de partir à la guerre, le vaincu part à la guerre puis rêve de triomphe.» Le troisième, du nom de Konstantin Tsiolkovsky, regarda ses frères tout en laissant s'étendre le silence puis il les questionna: «La terre est le berceau de l'humanité, mais qui veut passer sa vie entière dans un berceau?» Sur ce, les trois se lancèrent à l'assaut des eaux infinies sans que personne ne puisse en comprendre le véritable sens. Jamais ces hommes lemmings ne revinrent.

Depuis ce jour, les hommes lemmings essaient d'apprendre à reconnaître ce qui les fait avancer et ce qui entrave leur progression. Ils tentent de comprendre leur rôle, car tel que le cita William Shakespeare, le monde entier est une immense scène où tous, hommes et femmes, y sont des acteurs qui y jouent un rôle. Ils savent désormais qu'il n'existe plus grande richesse que le savoir, plus grande pauvreté que l'ignorance. Cela dit, ils se doivent de jouer leur rôle et d'user de ce savoir, car le chant du sage Attikamekw leur révèle qu'ils n'héritent pas la terre de leurs ancêtres, mais qu'ils l'empruntent à leurs enfants. Dans cet univers lointain et près à la fois, les hommes lemmings comprirent le sens des enseignements de Charles Darwin: «Ce n'est pas l'espèce la plus puissante qui survit, mais celle qui s'adapte le mieux aux changements.» Ainsi, ces êtres appliquèrent ce concept et, quand vint le bon moment, ils s'élancèrent vers des eaux infinis afin d'y trouver le sommeil éternel. C'est ainsi que le pouls de la vie recommença à résonner inlassablement dans cet univers intemporel…

Introduction générale

La dynamique cyclique des populations de petits mammifères

Les fluctuations d’abondance périodiques multi annuelles ont fait la renommée des populations de petits mammifères (Elton 1924, Krebs 1978, Fuentes et Campusano 1985, Krebs 1996, Gilg et al. 2003). Nous pouvons définir les cycles de populations comme étant des patrons de fluctuations dans la taille d’une population réglés par une période relativement constante ainsi qu'une forte amplitude (Stenseth et Ims, 1993). Deux principaux types de phénomènes semblent impliqués dans les fluctuations des populations cycliques: les effets directs dépendants de la densité et les effets indirects dépendants de la densité. La réunion de ces deux effets crée le processus d’ordre deux à l’origine de la dynamique cyclique des populations de petits mammifères (Stenseth 1999). Différentes écoles de pensée ont formulé plusieurs hypothèses afin de mettre en lumière le type de facteur (intrinsèque et/ou extrinsèque) impliqué dans ces effets dépendants de la densité.

D’après l’école de pensée des facteurs intrinsèques, la qualité des individus varie selon les phases du cycle et serait responsable de la dynamique cyclique observée (Chitty 1996, Krebs 1978, 1996). Pourtant, une même espèce de petit mammifère peut exprimer des cycles de différentes périodes selon les sites, ou simplement ne pas en exprimer (Hansson et Henttonen 1985). Ce fait suggère qu'il est peu probable que des facteurs intrinsèques génèrent les cycles (Korpimäki et Krebs 1996). Selon l'école de pensée des facteurs extrinsèques, il y aurait deux possibilités. Premièrement, lors des pics de densité, un manque dans la quantité ou la qualité de la nourriture provoquerait la chute de la population (Selas 2006). Deuxièmement, la prédation limiterait l'expansion des populations de lemmings et créerait les cycles, possiblement en combinaison avec des effets intraspécifiques dépendants de la densité (Hansson et Henttonen, 1988, Hanski et al. 1993). Parmi les hypothèses avancées par les différentes écoles de pensée, les hypothèses suggérées par l'école des facteurs extrinsèques privilégiant les interactions trophiques seraient les plus plausibles (Hanski et al. 1993, Korpimäki et Krebs, 1996, Gilg et al. 2006). Ainsi, les processus d'ordre deux observés dans la cyclicité des populations de lemmings pourraient résulter autant d’une interaction spécialisée plante-herbivore que d’une interaction spécialisée prédateur-proie. Il est peu probable que ce système soit régulé par les deux facteurs à la fois. Cette situation tri-trophique résulterait en une dynamique d'ordre trois, ce qui ne correspond pas au comportement observé dans les données à long terme (Stenseth, 1999). Ainsi, les hypothèses du contrôle trophique par le bas (interaction plante-herbivore) et du contrôle trophique par le haut (interaction prédateur-proie) semblent mutuellement exclusives. En ce qui concerne l’hypothèse relative au contrôle trophique par le bas, aucune expérience n'a pu démontrer qu'un apport supplémentaire en nourriture ait pu empêcher la chute d’une population de lemmings et aucune relation n'a pu être établie entre la qualité de la nourriture et les cycles des rongeurs (Henttonen et al. 1987). Par contre, plusieurs évidences semblent supporter l’hypothèse qu’une interaction spécialisée prédateur-proie soit à l’origine des cycles (Korpimäki et Krebs 1996). Selon cette hypothèse, les cycles seraient principalement générés par l'effet densité dépendant indirect imposé par certains prédateurs spécialistes (Gilg 2003, Korpimäki et al. 2005, Gilg et al. 2006). Néanmoins, cette hypothèse ne fait pas encore consensus pour les lemmings (Turchin et al. 2000), notamment à cause de l’absence de démonstration expérimentale à grande échelle (Sundell 2006) et de la difficulté de développer une explication applicable à tous les cycles de populations (Lambin et al. 2006).

En somme, notre compréhension de la dynamique cyclique des populations de mammifères nordiques comporte certaines failles. Stenseth (1999) suggère que cette compréhension fragmentaire des facteurs impliqués dans la dynamique des populations cycliques soit attribuable à la vision restreinte des grandes écoles de pensée. Certaines évidences suggèrent que l’effet des différents facteurs évoqués par ces écoles puisse être modulé par les saisons (Stenseth et al. 2003, Schmidt et al. 2008). Par conséquent, une compréhension globale des cycles de populations des petits mammifères nordiques nécessite la considération de la dynamique de ces populations lors de l’hiver arctique, une période peu documentée qui s'étend de 7 à 9 mois dans les écosystèmes nordiques (Krebs et al. 2002).

Le rôle de l'espace sous nival pour l'écosystème arctique

Les fluctuations périodiques multi annuelles dans l'abondance des populations de petits mammifères constituent un attribut fondamental des écosystèmes nordiques terrestres caractérisés par une alternance entre les périodes estivales et hivernales (Gilg et al. 2003, Hornfeldt et al. 2005, Pitelka et Batzli 2007, Gruyer et al. 2008). Nonobstant le fait que certains cas de cyclicité existent en régions tempérées, ce type de dynamique semble prépondérant dans les régions ayant de longs hivers (Fuller 1975, Hansson et Henttonen 1988, Lambin et al. 2006). En effet, la saisonnalité prononcée des écosystèmes nordiques semble moduler la balance des forces relatives de l'effet des facteurs dépendants de la densité créant ainsi un potentiel d'oscillation essentiel à la génération des cycles de populations (Ostfeld et Tamarin 1986, Tkadlec 2000, Aars et Ims 2002, Smith et al. 2006, Schmidt et al. 2008).

Le potentiel d'oscillation associé à la forte saisonnalité des écosystèmes arctiques est principalement généré par la mise en place du couvert nival lors de la saison froide (Ostfeld et Tamarin 1986, Hansson et Henttonen 1988, Hanski et al. 1993, Ostfeld et Canham 1995). Pendant la saison hivernale, le gradient de température, entre l'air froid et la surface du sol induit une migration ascendante de la vapeur d'eau. Ce processus physique engendre la formation d'une couche de cristaux de neige faiblement liés à la base du couvert de neige et par conséquent de l'espace sous nival (Marchand 1996). La formation de cet environnement particulier est favorisée par l'activité des petits mammifères qui en dépendent pour leur survie et leur reproduction lors de la saison hivernale (Shelford 1943, Korslund et Steen 2006). L'espace sous nival offre aux petits mammifères une isolation thermique contre les conditions climatiques rigoureuses de l'hiver arctique, une accessibilité à la nourriture et une certaine protection contre la pression de prédation exercée par certains prédateurs (Scott 1993, Reid et Krebs 1996, Coulson et Malo 2008).

Puisque les coûts métaboliques des petits mammifères endothermes sont inversement corrélés avec les conditions thermiques ambiantes, l'isolation thermique offerte par le couvert nival serait essentielle à l'atteinte de la balance métabolique vitale de ces individus actifs lors de la saison froide (Chappell 1980). Les coûts énergétiques reliés aux activités des petits mammifères seraient de 15 à 25% moins élevés pour les individus demeurant dans l'espace sous nival par opposition à ceux actifs à la surface du couvert de neige (Chappell 1980). Cette économie métabolique reliée au couvert nival peut atteindre 50% lors des nuits de ciel clair prédominantes pendant l'hiver arctique et par conséquent, elle pourrait jouer un rôle fondamental pour la survie de ces mammifères pendant l'hiver arctique (Chappell 1980, Scott 1993, Reid et Krebs 1996, Ims et al. 2008, Kausrud et al. 2008).

Les contraintes énergétiques chez les petits mammifères s'expriment également au niveau de leur comportement d'approvisionnement. D'une part, la diminution de la photopériode, l'installation du couvert de neige, le gel et le froid, inhérents à l'hiver arctique, inhibent l'activité photosynthétique et la croissance des plantes (Kappen 1993, Hamerlynck et Smith 1994). D'autre part, les petits mammifères nécessitent un apport énergétique alimentaire important en hiver car leur efficacité de digestion est relativement faible, leur taux métabolique est élevé du aux froides conditions thermiques et ils doivent dépenser de l'énergie afin de réchauffer la nourriture ingérée à leur température corporelle (Batzli et Jung 1980, Berteaux 2000, Rammul et al. 2007). Par conséquent, les taux de survie de ces populations sont significativement affectés par l'accessibilité à la nourriture offerte par l'espace sous nival (Korslund et Steen 2006). Cet effet est généré à la fois directement par le processus d'inanition et indirectement via une diminution de la condition physiologique entraînant une hausse de la susceptibilité aux prédateurs et aux pathogènes (Niklasson et al. 2006, Huitu et al. 2007, Beldomenico et al. 2008, Fey et al. 2008).

L’utilisation de l’espace sous nival par les petits mammifères altère également les interactions entre les prédateurs et les proies de l’écosystème arctique (Hansen et al. 1999, Krebs et al. 2003, Gilg et al. 2006). Un couvert de neige relativement épais pourrait limiter la pression de prédation exercée par certains prédateurs nomades et résidants tels le harfang des neiges (*Nyctea scandiaca*) et le renard arctique (*Vulpes lagopus*) (Lindstrom et Hornfeldt 1994, Angerbjorn et al. 1999, Gilg et al. 2006). Ce dernier doit notamment creuser des trous dans le couvert de neige afin d’atteindre les petits mammifères au niveau de l’espace sous nival et serait ainsi affecté par l’état des conditions nivales (Hansson et Henttonen 1985, Lindstrom et Hornfeldt 1994). Par opposition, certains prédateurs spécialistes tels les hermines (*Mustela erminea*) et les belettes (*Mustela nivalis*) sont de petites tailles et ont la capacité de se déplacer au niveau de l’espace sous nival (Korpimaki et Krebs 1996, Korpimaki et al. 2005). Par conséquent, la pression de prédation exercée par ce type de prédateur ne serait pas limitée par la couverture nivale (Erlinge et al. 1983, Hanski et al. 1993, Krebs 1996, Korpimaki et al. 2005).

L’effet des conditions climatiques hivernales

Les fonctions essentielles jouées par le couvert nival pour les populations de petits mammifères pourraient être vulnérable aux conditions climatiques hivernales (Reid et Krebs 1996, Aars et Ims 2002, Solonen 2006, Kausrud et al. 2008). Des températures modérées à l’automne suivies d’une transition rapide vers des températures froides et de fortes accumulations de neige seraient des conditions favorables à la survie hivernale des petits mammifères, et pourraient être les préludes à un pic d’abondance l’année suivante. À l’inverse, de faibles précipitations menant à un faible couvert nival combinées avec des redoux automnaux ou hivernaux créant des épisodes de pluie verglaçante seraient des conditions néfastes pour ces animaux et pourraient conduire à de faibles abondances (Scott 1993, Reid et Krebs 1996). Concrètement, l'occurrence de redoux hivernaux affecte la qualité du couvert nival et par conséquent la protection thermique offerte aux petits mammifères (Ims et al. 2008). De plus, les pluies verglaçantes peuvent engendrer la formation d'une couche de glace au niveau du sol limitant ainsi l'étendue de l'espace sous nival et l'accessibilité à la nourriture (Reid et Krebs 1996, Korslund et Steen 2006). Ces facteurs climatiques affectant les conditions hivernales et leurs effets sur les populations de lemmings sont des phénomènes qui pourraient s'accentuer dans le contexte du réchauffement climatique global actuel (ACIA 2004). Plusieurs modèles climatiques prédisent un réchauffement marqué des températures hivernales dans l'Arctique et une augmentation de la fréquence d'événements extrêmes comme les redoux hivernaux et la pluie verglaçante (Putkonen et Roe 2003). Ainsi, les changements dans les conditions hivernales pourraient affecter la démographie des populations de petits mammifères et être impliqués dans la diminution marquée de l'amplitude des fluctuations de certaines de ces populations (Hornfeldt et al. 2005, Kausrud et al. 2008).

Biologie des lemmings

Deux genres de lemmings sont typiques des écosystèmes arctiques sibérien et nord américain. Le genre *Discrotonyx* habite principalement le haut-Arctique alors que le genre *Lemmus* occupe le bas-Arctique (Stenseth et Ims, 1993). À l'interface entre le haut-Arctique et le bas-Arctique, les deux genres peuvent coexister tel qu'observé dans le nord canadien avec le lemming variable (*Dicrostonyx groenlandicus*) et le lemming brun (*Lemmus trimucronatus*) (Gruyer et al. 2008). La dynamique de population de ces deux espèces de lemming est généralement cyclique à haute latitude (voir Reid et al. 1997 pour une exception) quoique les populations de lemmings bruns subissent habituellement des cycles de plus forte amplitude que les populations de lemmings variables (Stenseth et Ims, 1993).

Le lemming variable se nourrit majoritairement d’herbacées et d’arbustes (*Dryas, Saxifraga, Salix, Pedicularis)* qu'il recherche dans les milieux xériques et mésiques (Negus et Berger 1998) alors que le lemming brun s’alimente principalement de cypéracées, graminées et mousses (*Carex, Dupontia, Arctagrostis, Polytrichum)* qu'il recherche principalement dans les milieux humides (Batzli et al. 1980, Gruyer et al. 2008). Bien que l’utilisation et la disponibilité des ressources, les concepts fondamentaux de la sélection de l’habitat, peuvent fluctuer à travers le temps et les saisons (Schooley 1994, McKnight et Hepp 1998), la majorité des études portant sur la structure spatiale des populations de lemmings touchent à la saison estivale (Batzli et al. 1983, Stenseth et al. 1993, Blackburn et al. 1998). Les quelques études s’intéressant à la saison froide suggèrent que la structure spatiale des populations lors de cette période est principalement reliée à l’accumulation du couvert nival (MacLean et al. 1974, Fuller et al. 1975, Sittler 1995, Reid et Krebs 1996). Selon Rodgers et Lewis (1986), l’occurrence d’un épais couvert nival et d’une grande disponibilité de mousses en milieux mésiques seraient à l’origine d’une migration saisonnière locale des lemmings bruns vers les milieux mésiques.

La saison de reproduction des lemmings variables s'étend de mars à août. Lors de la fonte de la neige au printemps, ils cessent de se reproduire, car la fonte cause des inondations dans l’espace sous nival (Stenseth et Ims 1993). La reproduction de cette espèce serait initiée par l’augmentation de la photopériode au printemps (Nagy et al. 1993, Negus et Berger 1998). Chez le lemming brun, la saison de reproduction s’étend généralement de juin à septembre et serait initiée par un composé chimique que l’on retrouve dans certaines monocotylédones (Stenseth et Ims 1993). Bien que l’activité de reproduction des lemmings bruns soit principalement estivale, cette espèce se reproduit occasionnellement lors de la saison froide pour des raisons méconnues (Millar 2001). L'occurrence de reproduction sous nivale intense engendre une superposition des générations; les jeunes nés durant la saison hivernale atteignent la maturité durant l'été suivant leur naissance et augmentent considérablement le potentiel de croissance des populations (Millar 2001). Certaines études démontrent que la reproduction hivernale serait particulièrement intense les années précédant les pics d'abondance de lemmings (Hansson 1984, Krebs 1993).

Objectifs de l'étude

Les objectifs de ce mémoire se distribuent en trois volets. Le premier volet a pour objectif d'examiner l'effet de la structure de l'habitat sur la distribution spatiale des nids d'hiver des lemmings variables et des lemmings bruns. Le second volet comporte deux objectifs. Le premier objectif est de développer et de valider une méthode permettant d'inférer l'activité de reproduction à l'intérieur des nids d'hiver des petits mammifères. L'élaboration de cette méthode est présentée dans le chapitre 1. Le second objectif de ce volet est de déterminer l'effet de la structure de l'habitat sur l'activité de reproduction des lemmings variables et brun à l'intérieur des nids d'hiver. Le troisième volet a pour objectif d'évaluer le rôle du couvert nival en tant que protection contre la prédation exercée par l'hermine et le renard arctique sur les nids de lemmings.

Nous avons posé les hypothèses que, lors de la sélection des sites de nids d'hiver, les lemmings préfèrent les sites qui offrent une protection optimale contre les stress thermiques et la prédation, et qui maximisent les apports énergétiques. Nos prédictions étaient que les sites des nids d'hiver de lemmings, comparativement à des sites distribués aléatoirement, sont caractérisés par (1) une plus grande hétérogénéité topographique favorisant l'accumulation de neige, (2) un couvert nival plus épais, (3) une plus faible amplitude des fluctuations de température au niveau de l'espace sous nival et (4) une plus grande abondance des espèces végétales clefs pour la subsistance des lemmings en hiver. Nous avons également prédit que ces caractéristiques de l'habitat augmentent les probabilités d'occurrence de reproduction des lemmings à l'intérieur des nids d'hiver. Finalement, nous avons prédit que l'épaisseur du couvert nival n'affecte pas les probabilités d'occurrence de prédation des lemmings dans les nids d'hiver par l'hermine, mais que l'épaisseur moyenne du couvert nival observée aux sites d’événements de tentatives de prédation de nids d’hiver par le renard arctique est inférieure à l’épaisseur du couvert de neige moyen observé au sites des nids d’hiver des lemmings.

Chapitre 1

Validation of a new method to determine the breeding activity of northern small mammals in their winter nests

Résumé

L’occurrence de reproduction sous le couvert de neige lors de la saison froide semble être une importante composante démographique impliquée dans les fluctuations périodiques d’abondance des populations de petits mammifères nordiques. Néanmoins, les conditions arctiques limitent notre capacité à quantifier la reproduction hivernale et par conséquent, celle-ci demeure peu documentée. Dans cette étude, nous décrivons une méthode permettant d’inférer l’occurrence de reproduction à l’aide d’analyses d’échantillons de fèces. Nous validons des critères objectifs fondés sur une expérience en laboratoire à l’aide de hamsters syriens dorés (*Mesocricetus auratus*) en tant que modèle animal. Nous évaluons la méthode et inférons l’occurrence d’activité de reproduction à l’intérieur de nids d’hiver de lemmings variables (*Discrotonyx groenlandicus*) et de lemmings bruns (*Lemmus trimucronatus*) récupérés au printemps dans l’Arctique canadien. La masse individuelle des fèces de hamsters adultes est jusqu’à quatre fois supérieure à celle des fèces de hamsters juvéniles à la date de sevrage. En utilisant des critères simples (distribution bimodale dans la taille des fèces, différence de taille de fèces et proportion de petites fèces), nous démontrons qu’une inspection visuelle d’un échantillon de 30 fèces ou plus est suffisante afin d’inférer l’occurrence de reproduction chez le hamster avec une confiance de >95%. Le même patron de distribution de taille de fèces s’observe chez les lemmings et nous concluons que cette méthode permet de générer un indice quantitatif de l’activité de reproduction hivernale des populations de petits mammifères nordiques.

Abstract

Winter breeding under the snow is thought to be an important ecological adaptation of northern small mammal and potentially a key demographic process in their periodic multiannual fluctuations in abundance. However, arctic conditions limit our capacity to quantify winter reproduction, and it is therefore poorly documented. We describe a method to infer reproduction based on the analyses of faecal samples. We validated objective criteria in controlled laboratory experiments using golden Syrian hamsters (*Mesocricetus auratus*) as a model and we tested the method in winter nests of collared (*Discrotonyx groenlandicus*) and brown lemmings (*Lemmus trimucronatus*) collected in spring in the Canadian Arctic. There was a large difference in individual mass of faeces between adults and juveniles at weaning (up to 4-fold) and they could be easily separated in mixed samples. Using simple criteria (gap in faeces size distribution, size difference, and proportion of small faeces), we showed that visual inspection of 30 or more faeces was sufficient to correctly infer hamster reproduction with an accuracy of >95%. The same patterns were found in the analysis of faecal samples collected from lemming winter nests. We therefore conclude that the method can provide a quantitative index of winter reproductive activity of small mammals under the snow.

Introduction

Periodic multiannual fluctuations in the abundance of small mammals are a major attribute of northern terrestrial ecosystems (Stenseth 1999, Krebs et al. 2003, Gruyer et al. 2008). Cyclic density fluctuations exhibited by northern rodent populations may be related to the seasonality of their environment (Ostfeld and Tamarin 1986, Tkadlec 2000, Schmidt et al. 2008). In particular, winter breeding under the snow is thought to be an important feature of their population dynamics (Hansen et al. 1999, Millar 2001). Even though reproduction in the subnivean layer has been observed in most lemming species (Stenseth and Ims 1993), few studies have quantified this phenomenon because demographic studies are typically conducted during the summer months (Yoccoz et al. 1998). However, a full understanding of the factors that drive the microtine population cycles requires an accurate determination of demographic parameters, including during the winter period (Krebs et al. 2002).

Because of the inaccessibility of most northern field sites during the cold season, the winter reproductive activity of lemmings has been mainly inferred from summer population samples. Age structure of populations at the beginning of the summer has been used to describe winter breeding (Krebs et al. 1995). However, this approach may negatively bias estimates of winter reproduction if snow melt is associated with high juvenile mortality. Overwinter population change estimated by the difference between fall and spring abundance has been used to infer winter demography but in this case reproduction and mortality are confounded (Reid and Krebs 1996, Hansen et al. 1999, Aars and Ims 2002).

Counts of placental scars in females captured in spring can be used to determine the number of litters and their size prior to snowmelt (Koshkina and Kholanski 1962). However, scars last for short and variable periods of time ranging from three to seven weeks (Corthum 1967, Innes and Millar 1987) and two generations of scars could not be distinguished in *Microtus ochrogaster* after 30 days (Martin et al.

1976). Moreover, this method requires sacrificing the animals. MacLean et al. (1974) inferred winter breeding from remains of young in lemming nests collected after snowmelt. However, this method would miss litters where all young survived. Therefore, all of these methods present some drawbacks.

An alternative method to infer lemming reproduction in winter is to discriminate between adult and juvenile faeces in nests used in winter and recovered in spring. This approach has been previously used in Greenland to estimate the winter breeding activity of lemmings (Sittler 1995) but, to our knowledge, this method has never been formally described nor its validity tested. We used this method to determine the occurrence of collared lemming (*Discrotonyx groenlandicus*) and brown lemmings (*Lemmus trimucronatus*) reproduction during the winter in the Canadian Arctic. The aim of this study was to develop objective criteria based on the size of faeces found in lemming winter nests to determine reproductive activity. We assessed the reliability of the method in correctly inferring reproduction by analyzing the faeces of rodents that produced litters in captivity. Because it was impossible to have breeding lemmings in captivity, we used golden Syrian hamsters (*Mesocricetus auratus*) as a surrogate model. Mean body mass of collared lemming, brown lemming and golden Syrian hamster are respectively 45, 55 and 110 grams. Hamsters were selected as surrogate model for their close evolutionary relationship with lemmings (Wilson and Reeder 2005).

Method

Laboratory experiment

We conducted the laboratory experiment at the animal care facility of Université Laval from 2 October to 12 November 2007. We used 10 commercially-bred pregnant golden Syrian hamsters that were housed in individual cages (40x30x20cm). Animals were fed ad libitum with formula food and sunflower seeds throughout the experiment. Nine females gave birth to a litter (mean litter size =

7.0; range 5 to 9) on average 13 days after the start of the experiment but only six litters survived to weaning, which occurred 3 weeks later (3-9 November). At weaning, we collected faecal material accumulated over the previous three days from the six cages where litters had survived. We then separated females from their litter and, after another three days, we collected faecal material from juveniles and adults in their separate cages. This procedure generated three types of faecal samples: (1) a mixture of adults with juveniles near weaning (6-9 November), (2) juveniles alone (9-12 November) and (3) adults alone (9-12 November). Faeces were oven dried during 24 hours at 45^{o}C and then weighed individually (± 0.0001g). All procedures were approved by the Université Laval Animal Care Committee.

Considering the large size difference found between adult and juvenile faeces (see results), we tested if a simple visual inspection of faecal samples could allow us to accurately detect the presence of breeding activity. We performed blind trials to assess our ability to visually detect the presence of juvenile faeces in hamster faecal samples. We used samples of 10, 20, 30, 40, 50, 60, 80 and 100 faeces collected from either reproductive cages (i.e. adult with their young) or cages with only adults. We did not include samples coming from cages with juveniles only because we considered this situation non relevant to field situations. We visually examined each sample and assigned it as being from a cage with reproduction (i.e. presence of juvenile faeces) or from a cage with adult only on the basis of criteria described in the results. The same observer repeated the experiment 10 times on all samples examined in a random order, which allowed us to calculate an error rate in the assignment. The observer had no knowledge of the origin of the samples during the test. Type I error occurred when we assigned “reproduction” to samples coming from cages with lone adults and type II error when we failed to detect reproduction in samples coming from cages where both juveniles and adult were present.

Field data

We collected lemming winter nests during summer 2007 on the south plain of Bylot Island, Sirmilik National Park, Nunavut, Canada (73º08'N, 80º00'W; see Gruyer et al. 2008 for a description of the study area). We sampled collared and brown lemming nests along 74 line transects of 500m long distributed in equal proportion among three habitat types: wet tundra, mesic tundra and along mesic streams. Starting points of these transects were randomly selected from a habitat map of the study area (156 km^2). Details of the sampling protocol are given in chapter 2. All nests encountered along transects were collected, dried and shipped to the laboratory for subsequent analyses. We performed a meticulous dissection of each nest to recover hair and a random sample of 100 faeces per nest. Faeces were dried and weighed individually. Lemming species present in each nest were identified based on the distinctive specific shape of faeces found (MacLean 1974).

Statistical analyses

To determine if the mass of faeces found in juvenile and adult hamster cages differed, we used a Wilcoxon signed rank test. Juvenile and adult faeces found in the same hamster cage or lemming nest represent a combination of two statistical distributions, i.e. one for each age group, hereafter called a finite mixture distribution (Titterington et al. 1985). This distribution arises when samples include heterogeneous populations, each with a different probability density function. The multivariate normal distribution of faeces mass can be represented by a probability density function of the form

$$g(x) = \pi_a f_a(x) + \pi_j f_j(x) \qquad (x \in X)$$

where the mass of individual faeces, x, belongs to the finite mixture distribution X. Parameters π_a and π_j are respectively the proportion of adult and juvenile faeces in the combined sample. The density function of each component of the mixture are defined by f_a and f_j. To estimate the value of unknown parameters (mixing proportions π_i, means μ_i and standard deviation σ_i), we applied a maximum likelihood estimation approach. Given that only the marginal distribution of faeces mass was available, maximum likelihood estimations were computed iteratively using Newton-type method in the maximization step of the Expectation-Maximization algorithm (procedure *Rmix* of R 2.7.1 (CRAN, 2008), see also Dempster et al. 1977, Du 2002). We used a X^2 test to determine if the finite mixture distribution improved model fit compared to the model with a single statistical distribution.

Results

Laboratory experiment

We collected 18 samples of 100 hamster faeces: 6 from reproductive cages (adults with juveniles), 6 from juvenile cages and 6 from adult cages. Mass of faeces found in reproductive cages ranged from 0.6 to 71.9 mg whereas in juvenile cages it ranged from 0.6 to 15.7 mg and in adult cages from 15.2 to 66.6 mg (Fig. 1). Average mass of juvenile faeces was almost 5 times lower than that of adults (7.6 ± 2.2 vs 35.9 ± 10.8 mg (± SE), $z = 7.9$, $n_1 = 6$, $n_2 = 6$, $p < 0.001$). A finite mixture distribution model provided a much better fit to the frequency distribution of the mass of faeces found in reproductive cages compared to a model with a single statistical distribution ($X^2 = 295.4$, df = 3, $p < 0.001$). The finite mixture distribution model estimated the mean mass of juvenile and adult hamster faeces at 8.2 ± 0.2 and 28.9 ± 1.0 mg, respectively, and the proportion of juvenile faeces was estimated to 36 ± 3%.

Based on the previous analyses, we established the following criteria to determine if a faeces sample came from a cage where reproduction had occurred: (1) there was an obvious gap in the size distribution of the faeces, (2) the smaller faeces were approximately 2 to 4 times smaller than the larger ones and (3) the smaller faeces represented at least 33% of the sample. We used these criteria, hereafter called the “reproduction criteria”, as decisive tools to infer reproductive activity based on the visual inspection of faecal samples. We applied these criteria on the samples with variable number of faeces coming either from reproductive or adult cages. We reported 30 detection errors out of 960 trials, of which 4 were Type I errors and 26 were Type II errors. Type I errors were associated with the presence of some particularly small adult faeces whereas Type II errors were associated with the presence of large juvenile faeces. Nevertheless, the error rate decreased rapidly with the number of faeces examined (Fig. 2). When only 10 faeces were examined, we assigned the wrong reproductive status in 11% of the cases but the error rate dropped to less than 4% when 30 faeces or more were examined (Fig. 2). Therefore, our laboratory experiment demonstrated that, on the basis of our criteria, reproductive activity of breeding hamster in captivity could be inferred with accurate confidence ($\geq$95%) by visually examining samples of 30 faeces or more.

Field data

We collected and dissected a total of 193 lemming winter nests, 97 used by collared lemmings, 50 by brown lemmings and 46 by both species. Nests used by both species were excluded from further analyses. On the basis of our reproduction criteria validated with hamsters, we detected breeding activity in 39 collared and 9 brown lemming nests. Number of faeces per nest ranged from less than 20 to >1000 but we only observed signs of reproductive activity in nests with a large amount of faeces (>100).

We quantitatively analysed faecal samples collected in a random sub-sample of 39 lemming nests: 10 collared and 9 brown lemming nests with evidence of reproduction and 10 nests of each species without such signs. Mass of faeces found in reproductive collared and brown lemming nests ranged from 0.4 to 17.7 and 0.7 to 22.6 mg, respectively (Fig. 3). In contrast, mass of faeces found in nests without reproduction signs ranged from 3.1 to 14.6 and 6.2 to 21.7 mg, respectively. A finite mixture distribution model provided a much better fit to the frequency distribution of the mass of faeces found in lemming nests with signs of reproduction compared to a model with a single statistical distribution (collared: $X^2 = 344$, df = 3, $p < 0.001$; brown: $X^2 = 613$, df = 3, $p < 0.001$). The finite mixture distribution models estimated the mean mass of juvenile collared and brown lemming faeces at 2.2 ± 0.1 and 2.6 ± 0.1 mg and of adult faeces at 8.4 ± 0.2 and 12.6 ± 0.2 mg, respectively. The proportion of juvenile collared and brown lemming faeces in nests estimated by the model was 35 ± 2 and 46 ± 2%, respectively. These estimated parameters respect the reproduction criteria developed with the surrogate hamster model.

Discussion

We demonstrated that faeces of adults and juveniles at the time of weaning can be easily distinguished in the nests of small mammals and that they can be used reliably to infer reproduction. Under both field and controlled laboratory conditions, juvenile faeces were abundant in nests and there was a large mass difference between the two types of faeces. However, weighing a large number (up to 100) of individual faeces is time consuming and difficult to apply under field conditions. This is why we developed simple visual criteria based on the relative size differences and the proportion of faeces falling into the smaller size category to infer reproduction. Our blind trials show that this simple visual method can successfully be used to infer reproduction when a minimum number of faeces (≥30) is examined. Overall error rate in assigning reproductive status was low and mostly involved false negative assignments (i.e. failure to detect reproduction when it had occurred) as we very rarely inferred reproduction when it had not occurred (i.e. false positive). We therefore conclude that visual inspection of faeces found in lemming winter nests collected in springs is a simple, quick and inexpensive method to detect winter reproduction of lemmings in their nest.

We must nonetheless recognize a few limitations to the proposed method. First, reproduction is detected only if young are brought to the weaning stage. Indeed, this approach will not detect litters where young died before weaning because faeces of neonatal rodents are not solid and thus cannot be detected. Secondly, lemming faeces are not only present inside their nest as they often tend to be concentrated outside, at the periphery (MacLean 1974). Therefore, required number of faeces and proportion suggested in this paper to infer breeding activity may not apply under all situations. However, we can expect faeces of recently weaned young to be proportionally more abundant inside than outside the nest compared to adults, which would facilitate the detection of reproduction from faeces recovered solely inside nests. Thirdly, conclusions issued from an application of this method are limited by the fact that we measure reproduction rate on nests, not individuals. This approach would only yield an index of reproduction rather than a true reproductive rate, and thus one should remain careful in using these data to study lemming population dynamics.

A potential future development of this method would be to combine faecal counts with hormonal assays. However, because lemming faeces in nests are presumably cumulated over a relatively long period, this method may have some drawbacks (Hirata and Mori 1995, Yamauchi et al. 1999). Pooled hormone concentrations over time could be nonetheless used as suggested by Wildt et al. (1995) and analysis of faecal steroids could provide an additional index of reproductive activity even in nests where young died before weaning.

Despite the limitations outlined above, the possibility of detecting lemming reproductive activity in their winter nests using objective criteria opens up new prospects to further our understanding of the winter ecology of northern small mammals. Inferring reproduction from winter nests rather than from the age structure of lemming populations trapped in spring alleviates biases related to winter juvenile mortality, which can be as high as 65% (Millar 2001). Though lemming reproduction in the subnivean space is thought to be more common in collared than in brown lemmings, intensive winter breeding is considered an essential pre-requisite to reach peak population size during the summer in both species (Krebs 1993). Although this phenomenon remains poorly documented (Stenseth 1999), the method proposed in this paper offers a new approach to test this hypothesis. Ultimately, the application of a robust method to measure the winter breeding activity of northern small mammals should advance our understanding of the demographic processes that drive microtine population cycles.

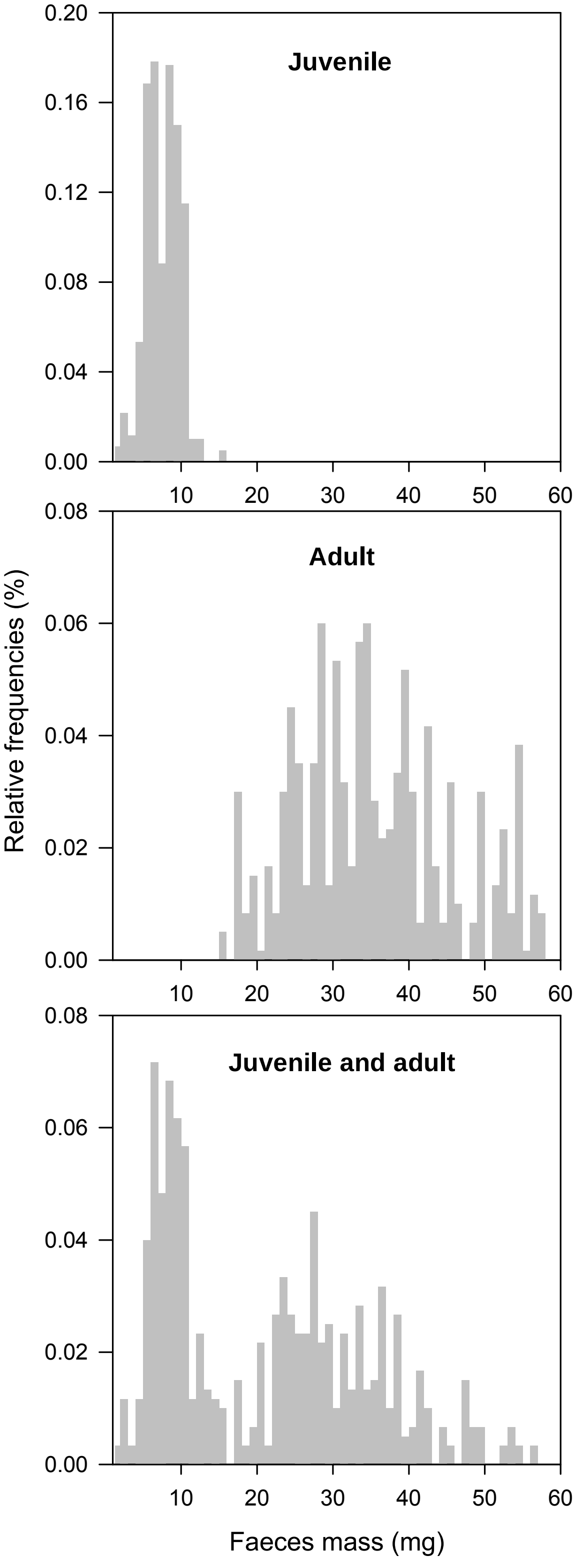

Figure 1. Relative frequencies of hamster faeces mass collected in cages where juveniles only, adults only or both juveniles and adults were present. Each graph is based on 6 cages with samples of 100 faeces / cage.

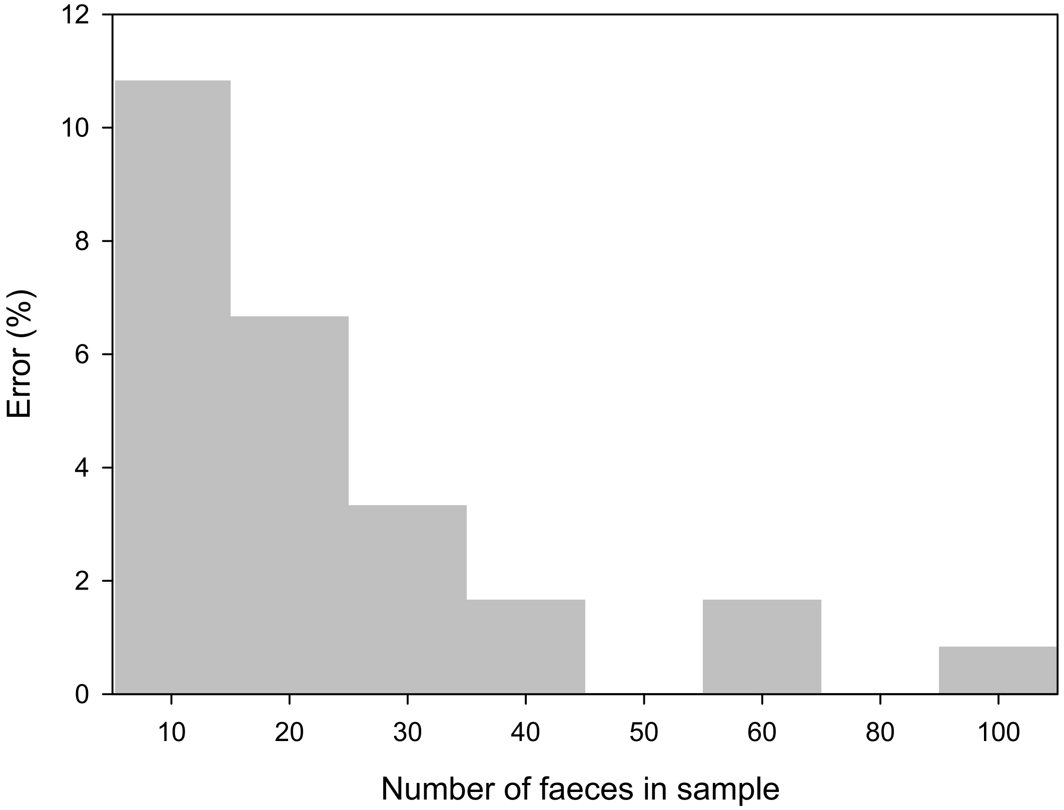

Figure 2. Error rate associated with the determination of reproduction based on the visual inspection of hamster faeces samples in relation to the number of faeces in the sample. Samples came from 6 cages containing adults only (non-reproductive) or adults with juveniles (reproductive). n = 960 trials.

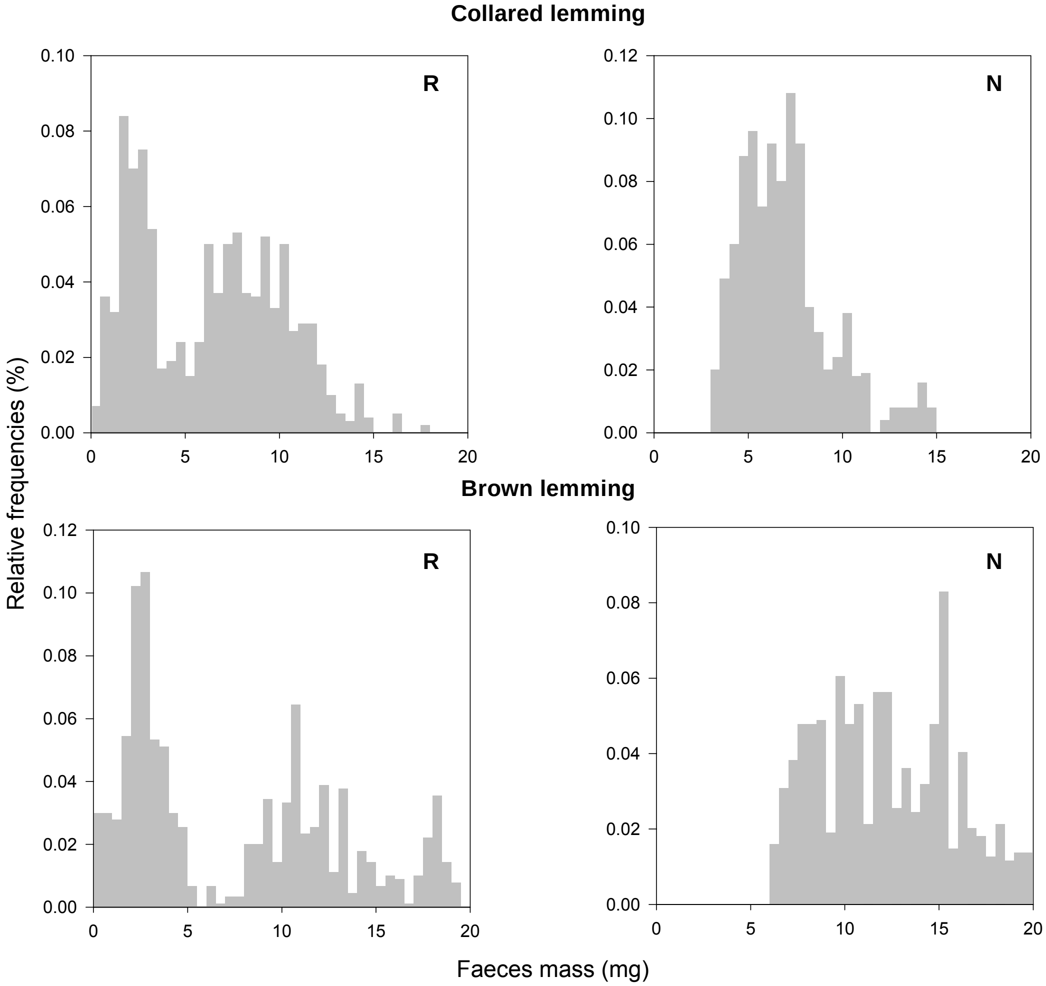

Figure 3. Relative frequencies of faeces mass collected in 10 and 9 reproductive collared and brown lemming nests (R) and 10 non-reproductive nests of each species (N). A total of 100 faeces were weighed in each nest. Nests were used by lemmings during winter 2006-2007 on the south plain of Bylot Island, Sirmilik National Park, Nunavut, Canada.

Chapitre 2

Habitat selection, reproduction and predation of wintering lemmings in the Arctic

Résumé

Pendant l'hiver, le couvert nival modifie fondamentalement la structure et le fonctionnement des écosystèmes nordiques terrestres. L'espace sous nival constitue le principal habitat des petits mammifères lors de cette période et est essentiel à leur survie et possiblement leur reproduction. Dans cette étude, nous examinons l'effet du couvert de neige et de la structure de l'habitat sur la distribution spatiale des nids d'hiver de lemmings variables (*Discrotonyx groenlandicus*) et de lemmings bruns (*Lemmus trimucronatus*) ainsi que sur les probabilités d'occurrence de reproduction et de prédation par l'hermine (*Mustela erminea*) et le renard arctique (*Vulpes lagopus*). Nous avons échantillonné 193 nids d'hiver de lemmings et avons caractérisé la structure de l'habitat à chacun de ces sites ainsi qu'à des sites distribués aléatoirement à deux échelles spatiales. Nous avons suivi l'évolution hivernale de la température au niveau du sol pour un sous échantillon de ces sites. Nos résultats suggèrent que les nids d'hiver sont principalement distribués sur des sites où l'hétérogénéité de la micro-topographie est élevée, la pente est forte, le couvert nival est épais et l'abondance des mousses est relativement élevée. L'effet positif du couvert nival sur la sélection de l'habitat des lemmings en hiver s'effectue indirectement via une diminution de l'amplitude des fluctuations de températures au niveau du sol. La probabilité d'occurrence de reproduction dans les nids de lemmings variables augmente dans les habitats à faible altitude et elle augmente avec la disponibilité de certaines graminoïdes chez le lemming brun. La probabilité d'occurrence de prédation par l'hermine dépend de la densité de nids d'hiver et augmente dans les nids occupés pas le lemming variable. L'épaisseur du couvert nival n'affecte pas la probabilité d'occurrence de prédation des nids par l'hermine, mais limite les tentatives de prédation exercées par les renards arctiques. Nous concluons que le couvert nival joue un rôle clef dans la structure spatiale des populations de petits mammifères pendant l'hiver arctique.

Abstract

Snow cover dramatically changes the structure and functioning of the Arctic ecosystem in winter. The subnivean space is the primary habitat of wintering small mammals and may be critical for their survival and reproduction. We investigate the effect of snow cover and habitat features on the distribution of collared lemming (*Discrotonyx groenlandicus*) and brown lemming (*Lemmus trimucronatus*) winter nests, as well as on the probability of reproduction and predation by stoats (*Mustela erminea*) and arctic foxes (*Vulpes lagopus*). We sampled 193 lemming winter nests and we measured habitat features at all these nests and at random sites at two spatial scales. We also monitored overwinter ground temperature at a subsample of nest and random sites. Our results demonstrate that nests were primarily located in areas with high micro-topography heterogeneity, steep slopes, deep snow cover providing thermal protection (reduced daily temperature fluctuations) and a high abundance of mosses. Probability of reproduction increased in collared lemming nests at low elevation and in brown lemming nests with high availability of some graminoid species. Probability of predation by stoats was density-dependent and increased in nest used by collared lemmings. Snow cover did not affect probability of predation of lemming nests by stoats but deep snow cover limited predation attempt by arctic foxes. We conclude that the snow cover plays a key role in the structure of wintering small mammal populations in the Arctic.

Introduction

Small mammal populations are famous for their phenomenal cyclic fluctuations in abundance (Gilg et al. 2003, Hornfeldt et al. 2005, Pitelka and Batzli 2007, Gruyer et al. 2008). Small mammal species with a wide geographic distribution tend to exhibit more pronounced population cycles at northern latitudes where seasonality is strongest (Hansson and Henttonen 1988, Ims and Fuglei 2005). During the cold and dark Arctic winter, small mammals may spend up to 9 months of the year under the snow. The winter remains the least known period of their annual cycle (Stenseth 1999), yet, this period may play a key role in their population dynamics (Reid and Krebs 1996, Hansen et al. 1999, Korslund and Steen 2006, Kausrud et al. 2008).

At northern latitudes, snow cover dramatically changes the structure and functioning of the ecosystem in winter. Temperature gradients within the snow results in the formation of a stratum of fragile and loosely arranged snow crystals near the ground, which creates a subnivean space, the primary wintering habitat of small mammals (Korslund and Steen 2006). Their survival is dependent upon accessibility to food and protection against harsh temperatures and predators offered by this particular environment (Scott 1993). Small mammals require a high rate of food intake because of their low digestive efficiency and their high metabolic rate enhanced by cold conditions (Barkley et al. 1980, Batzli and Jung 1980, Rammul et al. 2007). Therefore, depletion of winter food may induce a deterioration of their physiological condition and increase mortality (Huitu et al. 2007, Fey et al. 2008). In addition, freeze-thaw cycles induced by warm winter temperature disturb the subnivean space and may lead to the formation of ice at ground level, which prevents rodents from feeding on the vegetation and may increase mortality (Korslund and Steen 2006, Coulson and Malo 2008).

Winter reproduction under the snow occurs in some species of small mammals and is especially common in lemmings (Stenset and Ims 1993, Hansen et al. 1999, Millar 2001). Successful reproduction under the snow is often considered a necessary condition for the occurrence of a peak in abundance in cyclic lemming populations (Millar 2001, Ims et al. 2008). The early onset of a thick and dry snow cover combined with the absence of freezing rain and days with above zero temperatures should favour survival and reproduction (Reid and Krebs 1996, Aars and Ims 2002, Solonen 2006). Recent evidence suggests that population cycles of small mammals of the tundra may be fading out in some areas, especially in Fennoscandia (Hornfeldt et al. 2005). Increased frequencies of freeze-thaw cycles during the winter due to climate warming and their influence on snow conditions has been invoked as a possible cause for the dampening of these cycles (Hornfeldt 2004, Ims et al. 2008). Snow cover alteration may also affect winter predator-prey interactions (Hansen et al. 1999). Even if subnivean specialist predators such as stoats and weasels (*Mustela* sp.) should continue to be efficient predators during winter (Fitzgerald 1977, Sittler 1995), thick snow cover may reduce the success of other predators of small mammals such as arctic foxes (*Vulpes lagopus*) or snowy owls (*Bubo scandiacus*) (Hansson and Henttonen 1985, Lindstrom and Hornfeldt 1994).

During winter, lemmings build nests made of vegetation, which improves insulation from the surrounding environment and allows them to breed (MacLean et al. 1974, Fuller 1977, Sittler 1995). Survey of these nests at snow melt can provide information on the winter ecology of lemmings, including relative population levels (Gilg et al. 2006), habitat use, breeding activity, and predation rate by stoats (Fitzgerald 1977, Sittler 1995). Investigation of factors affecting the spatial distribution of these nests and the occurrence of reproduction and predation may therefore help us to understand the winter ecology of lemmings. Surprisingly, very few studies to date have investigated these factors (but see Gilg (2002) for an exception).

The purpose of our study was to determine ecological factors influencing the spatial distribution of winter nests of collared (*Discrotonyx groenlandicus*) and brown lemmings (*Lemmus trimucronatus*) at various scales, and to examine the effect of habitat structure on the occurrence of reproduction and predation in those nests. Our hypotheses were that lemmings prefer areas providing protection against thermal stress and predation and maximize energy intake. We thus predicted that, compared to random locations, sites of lemming winter nests should have (1) more features affecting snow accumulation such as ground depressions and terrain roughness, (2) deeper snow cover, (3) lower subnivean temperature fluctuations and (4) a greater abundance of key plant species used by lemmings. We further predicted that these habitat variables should increase the probability of occurrence of lemming reproduction in winter nests. Finally, we predicted that snow depth should not affect probability of nest predation by stoats (*Mustela erminea*) whereas nests with shallower snow depth should be more vulnerable to predation by arctic foxes.

Method

Study area

This study was carried out on the south plain of Bylot Island, Sirmilik National Park, Nunavut, Canada in 2007 and 2008 (73º08'N, 80º00'W) (Fig.1). The study area ($156km^2$) includes a large glacial valley surrounded by rolling hills and dominated by two major habitats, wet and mesic tundra. The wet habitat is characterized by sunken polygon tundra forming wet meadows, fens and shallow ponds in lowlands. Vegetation is dominated by graminoids such as *Carex aquatilis* var. *stans*, *Eriophorum sheuchzeri*, and *Dupontia fisheri* (Manseau and Gauthier 1993, Hughes et al. 1994). The mesic habitat is most common in upland areas and is characterized by hummocky tundra. The most common plants are *Salix arctica*, *Cassiope tetragona* and graminoids such as *Arctagrostis latifolia* (Audet et al. 2007). For the purpose of this study, we recognized a third habitat, streams running through upland areas. Previous observations led us to believe that this habitat was heavily used by wintering lemmings.

Two species of lemmings are present: the collared lemming and the brown lemming. The former is primarily associated with dry habitat and feeds mainly on dicotyledons (Negus and Berger 1998), whereas the latter is more common in wetlands and feeds largely on monocotyledons and mosses (Batzli and Pitelka 1983, Batzli et al. 1983). These populations follow 3-4 year cycles at our study site and tend to fluctuate in temporal synchrony, although the amplitude of fluctuations are much larger in brown than in collared lemming populations (Gruyer et al. 2008). Abundance of both species was low in 2006. Collared lemmings increased in 2007 (though brown did not) whereas brown lemmings were very abundant in 2008 (G. Gauthier and D. Duchesne, unpublished data).

Stoats and arctic foxes are resident lemming predators on the island. Avian predators, which are only present in summer, are snowy owls, rough-legged hawks (*Buteo lagopus*), parasitic jaegers (*Stercorarius parasiticus*), long-tailed jaegers (*Stercorarius longicaudus*) and glaucous gulls (*Larus hyperboreus*) (Bety et al. 2002, Gauthier et al. 2004).

Lemming winter nest survey

We estimated lemming nest density during the winter 2006-2007 in early summer 2007 using the line transect method (Buckland et al. 2004). We used 500m transects oriented to the north and distributed in equal proportion among our three habitat types: wet tundra, mesic tundra and mesic streams. Starting points of these transects were randomly selected from a habitat map of the area and we used a GPS receiver to locate these points in the field. Transects in stream habitat followed the meandering course of the water channel. Changes in habitat that occurred while walking transects were noted and transects that covered <300m long in the same habitat type were discarded. We cumulated a total of 36 200m along 74 transect lines. The position of all nests found was recorded using a GPS and perpendicular distance from transect was measured with a measuring tape. Nests were collected in a plastic bag, air-dried in the field and shipped to the laboratory for further analyses. Nests sometimes persist for more than a year, but older nests can be distinguished from those of the previous winter. The material of old nests is bleached and the inner layers show evidence of decomposition (MacLean 1974). According to these criteria, old nests were ignored when encountered.

Lemming nest site selection

We assessed habitat selection by comparing nests sites to random sites at two scales: the landscape and the local scale. We used two scales because resource selection is a hierarchical process and factors affecting selection may differ according to the measurement scale (Johnson et al. 2002, McLoughlin et al. 2004, Boyce 2006). The landscape level corresponds to the scale at which individuals select their home range whereas the local scale represents selection of a site within the home range (Johnson 1980). Random sites at the landscape level were selected along transects distributed in the study area (Fig. 1). Two random points per transect were located at 166-m interval from the start of each transect. To define the local scale, we ran short transects starting in various directions from lemming nests found soon after snowmelt (n = 38). We noted all signs of lemming presence such as leaf clipping, grazing and active runways along these transects (Annexe: Fig. A). Since 52% of signs of lemming presence were concentrated in a radius of 8.5 metres around nests, we used that distance to define the local scale. Random sites at the local scale were systematically distributed in the four cardinal axes at 8.5m from each sampled nest (Annexe: Fig. B). We sampled the habitat at each winter nest and at each randomly located point at the landscape and local scale during summer 2007. This sampling design follows the type III (landscape) and type I (local) designs of protocol A suggested by Manly et al. (2002).

Habitat variables

Habitat variables sampled included topography (elevation, micro-topography, slope and aspect) and flora. Elevation (m) was recorded with a GPS. Micro-topography variables measured were the proportion of the ground covered with depressions and depth of the deepest depression within a 1m radius at each site. The proportion of ground depressions was measured along two 1m lines perpendicular to each other. Along these lines, we measured the proportion of its length passing over depressions > 10cm deep (Annexe: Fig. B). Slope was measured with a clinometer and aspect was evaluated with a GPS. Percent of non-vascular and vascular plant covers were assessed separately and estimated visually in a 50 x 50cm quadrat centered on the site. This method was calibrated and performed by the same observer for every site.

Because the position of lemming nests during the winter 2006-2007 could not be identified before snowmelt, we measured snow depth at these nests and at random sites at the end of the winter 2007-2008. Even though average snow conditions may vary from year to year, the spatial distribution of snow depth is relatively insensitive to annual variations in snowfall (Deems et al. 2008). We thus assumed that relative difference between lemming nests and random sites were constant from 2007 to 2008. Snow depth measurements were carried out from 13 to 16 May 2008 (i.e. shortly before the start of snowmelt) with a graduated metal rod. During this sampling period, we encountered many craters freshly dug into the snow by arctic foxes to attack lemmings in their nests so we measured snow depth at all these sites. These predation attempts were confirmed by the presence of destroyed lemming nests in the freshly dug craters.

We evaluated subnivean thermal conditions over the winter for a randomly selected subsample of 15 nests and 15 random sites at the landscape scale. We recorded temperature at four-hour intervals with ACR System Smart Buttons deployed at 2cm above ground in August 2007. We defined the subnivean period as the period extending from 1 October 2007 to 1 May 2008. From these data, we extracted mean temperature and mean daily temperature fluctuations between minimum and maximum temperature recordings. We also determined snow density at each of these sites in May 2008. Using a snow corer, we weighed a snow core extending from the surface to the ground level and calculated average density by dividing the snow mass by its volume (kg/m^3).

Analysis of lemming nests

In the laboratory, we identified the lemming species using each nest based on faeces recovered from nests. The shape of faeces differs between the two species: collared lemming faeces are dark reddish, about 4-6mm long, blunt at one end and rather pointed at the other end, whereas brown lemming faeces are bright green, about 6-10mm long and rounded at both ends (MacLean 1974). We also assessed the occurrence of reproduction in winter nests on the basis of the mass frequency distribution of lemming faeces recovered from each nest using the method described in chapter 1. Nests that had been depredated by stoats were identified based on the presence of an extensive lining of lemming fur in the nest and lemming remains such as bones (Sittler 1995).

Statistical analyses

Lemming nest density

We estimated lemming nest density using a hazard-rate detection function with a simple polynomial adjustment (Buckland et al. 2004). We evaluated if habitat-specific detection probabilities should be preferred over a global model on the basis of Akaike information criterion (AIC) values (Burnham and Andersion 2002). To evaluate the fit of the detection function to the data, we used Kolmogorov-Smirnov (k-s) and Cramer-von Mises (C-vM) statistics with uniform (W-sq) and cosine weighing (C-sq). Calculations were made with program DISTANCE 5.0 of Buckland et al. (1993). We compared lemming nest density estimated in each habitat with a Mann-Whitney U test and contrasted nest density between the two species with Wilcoxon signed rank tests.

Habitat selection

Habitat data expressed as proportions were normalized using arcsin square-root transformation and all habitat variables were standardized (Sokal and Rohlf 1995). Among habitat variables (topography and snow depth), only the proportion of ground covered by depressions and their depth displayed a high correlation ($r \geq 0.7$). To avoid collinearity problems we applied a principal component analysis (PCA) to these two variables and used the first axis as an index of micro-topography heterogeneity (hereafter referred to as MTH). For the same reasons, we conducted PCAs on plant cover data to extract a small number of components describing major non-vascular and vascular plant communities (separate analyses). To determine the number of principal components retained to describe plant communities, we used an acceleration factor which relies on the second derivative associated with each component (Raiche et al. 2006). There was no collinearity problem among variables (i.e. topography, snow depth and plant communities) of the resulting dataset ($r < 0.55$).

We used resource selection functions (RSFs) to compare lemming nests to random sites (Manly et al. 2002). RSFs were computed for each species at the landscape and local scales with lemming nest presence as the dependent variable and habitat measurements as explanatory variables. To ensure a balanced design at the local scale, we used the means of habitat variables sampled at the 4 random sites around each nest. To estimate RSFs, we used a modification of the generalized estimating equation (GEE), which accounts for spatial autocorrelation (Liang and Zeger 1986, Carl and Kuhn 2007). As suggested by Dormann *et al.* (2007), we assumed that spatial correlation decreased exponentially with increasing distance and we estimated the correlation parameter according to the robust Lagrange multiplier of model residuals using spatial software GeoDA 0.9

(Anselin 2003). Because GEEs are a non-likelihood-based method, AIC cannot be applied for model selection, and we used instead the quasi-likelihood criterion (QIC) (Pan 2001a, b). We determined a set of a priori models to do a preselection of the best variables explaining nest presence among sub-groups (Annexe: Table C and D). Sub-groups were abiotic (topography and snow depth) and biotic (plant communities) factors. Variables included in the best model of each sub-group were combined in a final model selection process. To account for uncertainty in model selection, we calculated the model weight (w_i), which is an index of the relative plausibility of each model on the basis of ΔQIC values (Burnham and Anderson 2002). To determine the relative importance of variables, we summed w_i of all models containing this parameter. To account for the effect of uncertainty in model selection on parameter estimations, we used multi-model inference by averaging parameter estimates and unconditional standard errors across models (Anderson et al. 2000). Two-way interaction terms and quadratic terms (for non-linear effects) associated with biological phenomenon of interest were included when the corresponding variables were present in the best model.

To determine if habitat variables might explain differences in lemming nest densities among habitat types, we used Kruskal-Wallis tests to compare habitat variables measured at random sites (landscape scale) amoung habitats. We performed post-hoc contrasts using Mann-Whitney U test and used Dunn's procedure for multiple comparisons.

Effect of subnivean temperature

We compared subnivean temperatures and snow conditions of lemming nest sites to those of random locations using two sample t-tests or Mann-Whitney *U* tests, depending on the normality of the variables. We examined whether the effect of snow depth on the probability of occurrence of lemming nests was indirectly mediated through an effect on the subnivean microclimatic conditions (i.e. ground temperature) with path analysis. Because subnivean temperature was recorded at a relatively small number of nests, data from both species were pooled for analysis. Predictor variables included in the path analysis were snow depth, mean daily subnivean temperature fluctuations and the plant community PC axis which described the most variation in winter nest site selection at the landscape scale level. We performed analyses on the variance-covariance matrix using the general structural equation models and the reticular action model formulation (McArdle 1980, Bentler 1991). Path analysis assumes that (1) relationships among variables are linear, (2) residuals are normally distributed and (3) correlations among predictor variables are not high. Although we detected a significant quadratic effect, we obtained linearity using a log-transformation. The other assumptions were met in our data. As recommended by Kline (1998), we assessed overall fit of the full model using four tests: the chi-square test, the Bentler-Bonett normed fit index, the Bentler-Bonett non-normed fit index and the standardized root mean square residual. We determined whether dropping non-significant path coefficients significantly reduced model fit by comparing the X^2 goodness-of-fit statistic of the reduced model vs. the more general model. If removing paths did not significantly affect the model fit, reduced models were preferred.

Reproduction and predation in lemming nests

We examined the effect of habitat variables on the probability of occurrence of lemming reproduction in nests with GEEs. Dependent and explanatory variables were the occurrence of reproduction and habitat variables respectively. Analyses followed the same procedure as mentioned above and were conducted separately for each species. Similarly, GEEs were used to examine the effect of habitat variables on the probability of nest predation by stoats. Due to the small number of depredated nests, we pooled both species and compared those to a random subsample of intact nests stratified by habitat in the same proportion as depredated nests. Explanatory variables included snow depth, reproduction occurrence, lemming species and total lemming nest density estimated for the corresponding transect. We compared snow depth between intact nests and nests depredated by stoats using two sample t-tests. Finally, we compared snow depth between a random subsample of intact nests, nests where we observed predation attempt by foxes and a subsample of random sites using Mann-Whitney *U* tests.

Results

Lemming nest density

We found a total of 18 lemming nests in wet tundra, 58 in mesic tundra and 88 along mesic streams (n = 25 transects per habitat except along streams, n = 24). A model with habitat-specific detection functions fitted the data better than one with a common function for all habitats (ΔAIC = 11.6). The width of the effective detection distance was estimated at 10.4 ± 1.8, 3.9 ± 1.0 and 7.1 ± 1.0m (± SE) in wet, mesic and stream habitat, respectively. The detection function models displayed an adequate fit to the data ($p > 0.19$ for all habitats). Total lemming nest density (n/ha) was lower in wet tundra (0.71 ± 1.12) than in mesic tundra and stream habitats (6.14 ± 5.18 and 5.71 ± 5.60; $U = 110$, n = 50, and $U = 87$, n = 49, $p < 0.001$). Nest densities of collared lemming were similar to brown lemmings in wet habitats ($z = 1.31$, n = 25, $p = 0.19$) but tend to be higher in mesic tundra and especially along mesic stream habitat ($z = 1.75$, n = 25, $p = 0.08$ and $z = 3.97$, n = 24, $p < 0.001$, Fig. 2).

Description of plant communities

The first 3 axes of the PCA explained 31% of the total variance of the original non-vascular plant cover data, which included 18 genera. On the first axis (14%), positive scores mainly discriminated the occurrence of lichen species such as *Stereocolon fructilosa* (positive score) from that of some palatable mosses, mainly *Bryum* and *Calliergon* (negative score). The second axis (10%) primarily distinguished the abundance of palatable mosses such as *Polytrichum* (positive score) from the abundance of relatively unpalatable mosses such as *Aulacomnium* and *Tomentyphnum* (negative score). On the third axis (7%), positive values principally depicted the occurrence of relatively unpalatable *Sphagnum* and hepaticophyte species such as *Marchantiopsida*.

For vascular plants, the first four axes explained 20% of the total variance of the original plant cover data (48 species). The first axis (7%) essentially separated forbs typical of mesic habitat (e.g. *Oxyria digyna*, *Renunculus* sp., *Saxifraga* sp.) (positive score) from deciduous shrubs (*Salix* spp.) (negative score). The second axis (5%) described an index of low abundance of plants typical of wet habitats (*Carex aquatilis, Dupontia fisheri* and *Eriophorum scheuchzeri*). The third axis (4%) was associated with a high abundance of plants typical of drier sites such as *Festuca brachyphylla, Astragalus alpinus* and a reduced abundance of *Arctagrostis latifolia*. Finally, the fourth axis (4%) contrasted the abundance of evergreen shrubs typical of hummocky tundra (e,g, *Cassiope tetragona* or *Vaccinium uliginosum;* positive score) from other shrubs such as *Dryas integrifolia* and *Salix reticulata*. Details of both non-vascular and vascular PCAs are given in electronic supplementary material (Annexe: Tables A and B).

Lemming nest site selection

We sampled 193 winter nests, of which 164 were found along transect lines and 29 opportunistically. There were 97 nests used by collared lemmings, 50 by brown lemmings and 46 by both species. Generally, nests of both species were found in areas with a higher proportion of depressions, deeper depressions, steeper slopes and a deeper snow cover than the surrounding (Table 1). They also tended to be characterized by a relatively low abundance of lichens (NONVASC1), a relatively high abundance of palatable mosses (NONVASC2) and a relatively high abundance of deciduous shrubs (VASC1).

At the landscape scale, selection of winter nest site was generally affected by the same variables in both species and our best models explained up to 76 and 68%

(R^2) of the variability in the data for collared and brown lemmings respectively. Micro-topography, slope and snow depth were generally the most influential variables (Table 2). The probability of encountering lemming nests increased with heterogeneity of the micro-topography, slope of the terrain and snow depth (Table 3, Fig. 3). The effect of snow was non-linear as its effect levelled off above 60cm (Fig. 3). In brown lemming, we also found a significant negative interaction between slope and snow depth suggesting that deep snow accumulating in steep slope habitat was less influential than in flat terrain (Table 2 and 3). Elevation and slope aspect did not affect nest site selection and plant variables had a relatively weak influence. A high abundance of palatable bryophytes such as *Polytrichum* (NONVASC2) positively influenced the probability of occurrence of winter nests in both species (Tables 2 and 3). A high abundance of lichen species (NONVASC1) negatively influenced nest site selection of brown but not collared lemmings (Tables 2 and 3). Finally, collared lemmings were negatively influenced by the abundance of *Sphagnum* and hepaticophyte species (NONVASC3).

We examined how selected habitat variables at this scale varied among the three habitats where we sampled lemming nest density (Fig. 2). Stream habitat had the deepest snow cover, steepest slopes and lowest abundance of lichens whereas wet tundra had the shallowest snow cover, flattest terrain, highest abundance of *Sphagnum* and lowest abundance of forbs (Table 4). Mesic tundra was generally intermediate except for lichen (highest abundance) and *Sphagnum* (lowest abundance).

At the local scale, our best models explained up to 68% and 60% (R^2) of the variability in the data for collared and brown lemmings respectively but fewer variables affected the probability of occurrence of lemming nest than at the landscape one (Table 2). Heterogeneity of micro-topography was again the most influential variable in both species but the second most important variable at this scale was lichen abundance (NONVASC1), as nest occurrence increased with a decreasing abundance of lichen and an increasing abundance of some mosses such as *Bryum* (Tables 2 and 3). Snow depth also had a positive effect on nest occurrence at this scale (Tables 2 and 3).

Effect of subnivean temperature

Mean daily temperature fluctuations recorded over the winter was lower at lemming winter nest sites than at random sites (0.96 ± 0.86 (±SE) vs 2.17 ± 1.76ºC; *U* = 59, n = 30, *p* = 0.03). However, mean temperature did not differ significantly between nest and random sites (-17.3 ± 3.8 vs -20.1 ± 5.9ºC; *t* = 1.53, df = 28, *p* = 0.14), nor did mean snow density (142 ± 51 vs 182 ± 80 kg/m^3; *U* = 80, n = 30, *p* = 0.18). The evolution of mean subnivean temperature over winter is given as supplementary material (Annexe: Fig. C).

The covariance matrix of the path analysis model developed to assess the effect of subnivean temperature and snow depth did not differ from the observed covariance matrix (X^2 = 1.29, df = 1, *p* = 0.26; the three other goodness-of-fit tests yielded similar results). Furthermore, since the deletion of non-significant path coefficients did not affect the model fit (X^2 = 0.30, df = 1, *p* = 0.58), the reduced model was preferred. Our final model explained up to 35% of the total variance in nest occurrence probability and revealed that snow depth had a weak positive direct influence on the probability of nest occurrence and a strong indirect influence via an effect on subnivean thermal conditions (Fig. 4). A deeper snow cover decreased subnivean temperature fluctuations, a variable which had a negative effect on lemming nest occurrence.

Factors affecting reproduction

Using the criteria validated in chapter 1, we observed evidence of reproduction in 64 out of 193 winter nests. Signs of reproduction were found in 38% of collared lemming nests (n = 55) and 9% of brown lemming nests (n = 9) and in the 16 nests where both species were identified, reproduction was always only associated with collared lemmings. Our best models explained respectively 32% and 42% of the variation in collared and brown lemming reproduction occurrence (R^2). Probability of reproduction in collared lemming nests increased at low elevation (-0.50 ± 0.21 (β ± SE) and we noted a weak positive effect of forbs availability (0.38 ± 0.22) (Table 2, Annexe: Table G). In contrast, probability of reproduction increased in brown lemmings nest when the abundance of graminoids such as *Arctagrostis latifolia* was high and the abundance of plants typical of drier sites such as *Festuca brachyphylla* and *Astragalus alpinus* was low (VASC3) (-4.71 ± 2.23, Table 2, Annexe: Table H). Other habitat variables such as snow depth and the availability of plants typical of wet habitats had a weak positive effect on probability of reproduction in brown lemming nest.

Factors affecting predation

We found evidence of stoat predation in 11 of the 193 nests sampled. Collared and brown lemmings had used 10 and 2 of these nests, respectively, and 6 of these nests showed signs of collared lemming reproduction. Our best model explained 44% of the variation in the data. Probability of predation by stoats increased along transects where lemming nest density was high (1.41 ± 0.67 (β ± SE)) and when nests were used by collared lemming (3.94 ± 1.96, Table 2, Annexe: Table I). Snow depth did not affect the probability of predation by stoats as this variable did not differ intact and depredated nests (78 ± 41 vs 77 ± 34cm; $t = 0.04$, df = 20, $p = 0.97$). We were able to measure snow depth at 21 craters dug by foxes to depredate lemmings in winter nests. Mean snow cover was deeper at intact lemming nests than at those depredated by foxes (76.6 ± 30.8 vs 39.4 ± 18.2cm; $U = 381$, n = 42, $p < 0.001$). In contrast, mean snow depth did not differ between random sites and lemming nests depredated by foxes (46.9 ± 32.5 vs 39.4 ± 18.2cm; $U = 230$, n = 42, $p = 0.82$).

Discussion

We demonstrated that lemmings are highly selective in their use of winter habitat. Winter nest density varied considerably among habitats and several abiotic and biotic factors explained their habitat selection at both the landscape and local scales. We found strong support for the hypotheses that wintering lemmings prefer areas with deeper snow and a heterogeneous micro-topography, in part because these areas provide a more favourable micro-climate. In comparison, food availability played a relatively minor role in wintering site selection, although it appeared more important in determining weather lemmings would reproduce at a site or not. As expected, snow depth did not affect the probability of predation by stoats but appeared to limit arctic foxes attempting to prey on lemmings in winter nests.

Winter nest site selection

At all spatial scales, heterogeneity of micro-topography emerges as the most important factor determining winter habitat selection of both lemming species. Previous studies showed that lemmings also prefer sites with a rugged micro-topography such as hummocky areas during the summer, possibly because it provides protection against predators (Morris et al. 2000, Predavec and Krebs 2000). We suggest that a rugged micro-topography and its associated ground depressions might act differently during winter. It could offer a refuge against subnivean flood events and increase the probability of formation of a subnivean air space by affecting the pattern of snow drift at a small scale and increasing contact surface area at the ground-air interface (Marchand 1996). The accessibility to food provided by a good subnivean space is essential for overwintering small mammals in the tundra (Korslund and Steen 2006). Therefore, factors enhancing the formation of this air space are probably an essential component of the habitat selection process of wintering lemmings. Although measuring the characteristics of this micro-habitat directly is difficult, future investigations should aim at documenting the effective distribution of the subnivean space.

At both spatial scales, snow depth was fairly important in explaining winter habitat selection of lemmings, though less so in brown lemmings at the landscape scale. This effect was non-linear: lemmings strongly avoided areas with little snow but the effect levelled off above ~60 cm of snow. The path analysis showed that the preference for areas with deeper snow is mainly explained by the more favourable subnivean thermal conditions encountered there. Our results thus confirm the previously assumed role of thermal protection offered by snow cover and corroborate previous observations of an association between lemming winter nests and deep or persistent snow cover (MacLean et al. 1974, Fuller et al. 1975, Rodgers and Lewis 1986, Reid and Krebs 1996). Although average temperature tended to be lower at winter nest sites than random sites, it was especially the daily temperature fluctuation that was reduced by deep snow cover, which suggests that this may be a more important feature for wintering lemmings. This shows that thermal protection is a critical aspect of habitat selection in wintering lemmings, presumably to reduce their energetic requirement, as suggested by Chappell (1980).

Previous studies have suggested that distribution of preferred food is a major factor affecting lemming habitat selection (Batzli et al. 1983). Although lemmings showed a preference for areas characterized by the presence of some moss species at the landscape scale, abiotic factors were clearly much more important than plants in the selection process at this scale. Food availability played a more important role in the habitat selection process at the local scale, along with micro-topography. At this scale, both lemming species preferred areas with a low abundance of lichens and a high abundance of some palatable mosses (e.g. *Bryum*). Previous studies indicated that collared and brown lemmings consume a greater proportion of mosses during winter than during summer (Rodgers and Lewis 1986, Batzli and Pitelka 1983). Although mosses have a low digestibility and sometimes a high content of phenolic compounds (Batzli and Cole 1979, Barkley et al. 1980), they are also rich in multiunsaturated fatty acids such as arachidonic acid, which increases heat production and may help animals to survive in cold climates (Prins 1981). Overall, vascular plants had relatively weak effects on habitat selection of both lemming species in winter compared to other variables.

The higher density of lemming winter nests in the mesic tundra and associated streams than in the wet tundra agrees with other studies (Fuller et al. 1975, Batzli et al. 1983, Rodgers and Lewis 1986). Even brown lemmings, which prefer wet tundra in summer, often perform local migration to mesic habitat in winter (Rodgers and Lewis 1986). The abiotic habitat variables selected by lemmings at the landscape scale can explain some of the differences in nest density observed among our three habitats. Indeed, some habitat variables preferred by lemmings such as snow depth and slope had their highest values in the stream habitat, their lowest values in wet tundra and intermediate values in the mesic tundra. The apparent preference of wintering lemmings for steep slopes may be an indirect effect of habitat configuration in our study area. In contrast to the relatively flat wet tundra, the steep slopes associated with streams may enhance the formation of deep snow drift, which would be favourable to wintering lemmings and thus account for the high ranking of this variable in our RSF analysis.

Factors affecting winter reproduction

Our study confirmed that both lemming species can reproduce under the snow in winter (MacLean et al. 1974, Stenseth and Ims 1993, Krebs et al 1995, Reid and Krebs 1996, Millar 2001) and revealed that reproductive activity was higher in collared than in brown lemmings during winter 2007-2008 at our study site. Although some habitat variables were associated with the occurrence of reproduction, these variables differed among the two species and, globally, our models explained a relatively small proportion of the variation in contrast to previous models explaining nest site selection. In collared lemmings, the greater occurrence of reproduction in nests at low elevation is somewhat difficult to explain. A possible explanation is that low elevation sites may benefit from a more favourable microclimate (less exposure to wind). Even though forbs are an important component of collared lemming diet (Pitelka and Batzli 1993), availability of palatable forage apparently played a relatively minor role in explaining the occurrence of reproduction in this species. In contrast, occurrence of reproduction in brown lemming nests was mostly explained by the presence of some monocotyledons, especially *Arctagrostis latifolia*. Interestingly, Negus and Berger (1998) showed that presence of plant metabolites in soloniferous graminoids triggered the initiation of reproduction in brown lemmings, though not in collared. This may explain why availability of palatable forage was a relatively good predictor of the occurrence of reproduction in the former species but not in the latter.

Factors affecting predation

We found evidence that stoat predation on lemming nests was density dependent. In Greenland, Sittler (1995) found an aggregated pattern of lemming nest occupancy by stoat, which is consistent with density dependent predation. Because we showed that lemmings are highly selective in the location of their nests, this should lead to the concentration of nests in the best habitat patches. Therefore, stoats finding a lemming nest should increase their search effort in the area as the likelihood of finding other nests is probably high. Such area-restricted search is common in predator-prey systems (Hayes and Harestad 2000, Sarnelle and Wilson 2008), especially when prey distribution is aggregated as are lemmings in our area. This would be analogous to a Type III functional response at low prey density (Holling 1959) and may explain the density dependent predation pattern observed. We also found that collared lemmings were more exposed than brown lemmings to stoat predation. Sittler (1995) reported that most lemming nests predated by stoats showed evidence of reproductive activity by lemmings, suggesting that these nests may be more vulnerable to predation. In our study, the occurrence of reproduction was higher in collared than in brown lemming nests but we found weak evidence that nests with reproduction were more likely to be predated. We argue that stoats may show a preference for one lemming species over the other, but evidence to support this hypothesis is lacking.

Our results supported previous suggestions (e.g. Fitzgerald 1977, Reid and Krebs 1996, Gilg et al. 2006) that predation pressure by subnivean specialist predators such as the stoat is unaffected by depth of the snow cover in winter. In contrast, we found evidence that predation attempt by arctic foxes on lemming nests is, at least in part, limited by deep snow, as previously suggested (Hansson and Henttonen 1985, Lindstrom and Hornfeldt 1994). Therefore, deep snow cover may offer a refuge to overwintering lemmings against at least some winter predators. Protection offered by snow cover alters the effective winter predator community and may be involved in the latitudinal cyclicity gradient observed in the dynamic of small mammal populations in Europe and Japan (Stenseth et al. 1999).

Conclusions and perspectives

The present study underlines the role of snow cover as a determinant of the spatial structure of some wintering northern small mammal populations. There is increasing evidence that the winter dynamics of these populations may be dominated by the effect of stochastic climatic events on snow conditions (Ims et al. 2008). Previous studies suggested that freezing rain and frost/thaw events should reduce small mammal winter survival both directly and indirectly (Reid and Krebs 1996, Aars and Ims 2002). Directly, such climatic events reduce the thermal protection offered by snow cover, fragment the subnivean space through the formation of ice crust and can induce water flooding. These phenomena may greatly reduce the probability of individuals surviving the entire winter by increasing thermal stress, reducing food availability and possibly by the drowning of animals during floods (Aars and Ims 2002, Korslund and Steen 2006). Indirectly, mild weather during winter may reduce the protection offered by snow cover against some generalist predators, such as arctic foxes (Lindstrom and Hornfeldt 1994), and increase the competition with mustelid specialists for lemmings (Hansson and

Henttonen 1985, Hanski et al. 1991). Therefore, alterations of winter climatic conditions brought by the current global warming could reduce small mammal winter survival and destabilize their cyclic population dynamic, which would affect the whole arctic ecosystem.

Further studies must focus on mechanisms underlying mortality and reproduction of wintering small mammal populations. Our study recommends that research centered on winter demographic processes need to take into account both the temporal and spatial scales. Such studies should include temporal climatic variability and covers several small mammal population cycles. They should also encompass the transition between seasonal ecosystems with long lasting snow cover and ecosystems with short winter season and include several sites. Ultimately, modelling and experimental approaches could account for the impact of diverging climatic conditions and predator communities on the spatial structure and demography of wintering small mammal populations.

Table 1. Environmental parameters measured at collared and brown lemming winter nests and at random sites at two spatial scales (landscape and local scales; see method for details) during winter 2006-2007 on the south plain of Bylot Island, Sirmilik National Park, Nunavut, Canada. Mean and standard deviation (SD) are reported.

			Collared lemming		Brown lemming	
Variable	Parameter description	Random[1] (n = 148)	Nest (n = 143)	Random[2] (n = 572)	Nest (n = 96)	Random[2] (n = 384)
ELE	Elevation (m)	113 ± 102	158 ± 105	161 ± 107	125 ± 99	126 ± 99
MTH (1)	Micro-topography: Ground depression (%)	18 ± 15	37 ± 17	22 ± 16	38 ± 18	24 ± 17
MTH (2)	Micro-topography: Depression depth (cm)	10.1 ± 5.9	15.1 ± 6.8	11.5 ± 5.1	16.5 ± 8.7	12.4 ± 6.9
SDEPTH	Snow depth (cm)	39.0 ± 27.8	76.0 ± 37.8	54.4 ± 35.2	74.6 ± 42.9	52.0 ± 34.8
SINCLIN	Slope (%)	6.1 ± 2.2	18.9 ± 2.5	13.1 ± 2.5	17.4 ± 3.6	11.1 ± 3.2
EWASPECT	Aspect: E/W (1 = E / -1 = W)	0.11 ± 0.71	0.07 ± 0.71	0.02 ± 0.73	0.06 ± 0.71	-0.01 ± 0.72
NSASPECT	Aspect: N/S (1 = N / -1 = S)	0.01 ± 0.70	-0.09 ± 0.70	-0.02 ± 0.69	0.05 ± 0.70	0.02 ± 0.69
NONVASC1	Index of lichen abundance	-0.15 ± 1.85	-0.39 ± 1.34	0.18 ± 1.48	-0.57 ± 1.39	0.07 ± 1.63
NONVASC2	Index of abundance of palatable mosses	-0.45 ± 1.20	0.20 ± 1.17	0.04 ± 1.34	0.35 ± 1.07	0.08 ± 1.35
NONVASC3	Index of *Sphagnum* abundance	0.34 ± 1.35	-0.12 ± 1.05	-0.09 ± 1.06	0.10 ± 0.99	-0.03 ± 1.14
VASC1	Index of forb abundance	-0.63 ± 1.41	0.23 ± 1.91	0.27 ± 1.91	0.07 ± 2.02	-0.12 ± 1.69
VASC2	Index of low abundance of wet plants	-0.31 ± 1.75	-0.16 ± 1.68	0.24 ± 1.33	-0.40 ± 2.11	-0.09 ± 1.49
VASC3	Index of dry habitat plants	0.18 ± 1.24	-0.09 ± 1.31	-0.04 ± 1.44	0.16 ± 1.70	-0.09 ± 1.27

[1] Landscape scale

[2] Local scale

Table 2. Models explaining habitat selection and occurrence of reproduction and predation in nest of collared and brown lemmings during winter 2006-2007 on the south plain of Bylot Island, Sirmilik National Park, Nunavut, Canada. Shown are best ranked models (ΔQIC<2). Model weight (w_i) is the normalized value of the model based on its ΔQIC. Variables are presented in decreasing order of importance based on the sum of the w_i of models where they appear. DENSITY = nest density (n/ha), SP = species, REPROD = reproduction occurrence. See Table 1 for definition of other variables

Scale	Species	Variables included in the model	ΔQIC	w_i
Landscape	Collared	MTH+SINCLIN+SDEPTH+SDEPTH^2+NONVASC2+NONVASC3+VASC1	0.00	0.50
	(n = 291)	MTH+(SINCLIN*SDEPTH)+SINCLIN^2+SDEPTH^2+NONVASC2+NONVASC3+VASC1	0.26	0.44
	Brown	MTH+SINCLIN+NONVASC2+NONVASC1+SDEPTH+SDEPTH^2	0.00	0.43
	(n = 244)	MTH+(SINCLIN*SDEPTH)+NONVASC2+NONVASC1	0.06	0.41
Local	Collared	MTH+NONVASC1+SDEPTH+VASC2	0.00	0.50
	(n = 286)	MTH+NONVASC1+SDEPTH+SDEPTH^2+VASC2	1.18	0.28
		MTH+(NONVASC1*VASC2)+SDEPTH	1.96	0.19
	Brown	MTH+NONVASC1+SDEPTH	0.00	0.27
	(n = 192)	MTH+NONVASC1+SDEPTH+ELE	0.63	0.19
		MTH+NONVASC1+SDEPTH+SDEPTH^2	1.11	0.15
		MTH+NONVASC1+SDEPTH+NONVASC2	1.24	0.14
		MTH+NONVASC1+SDEPTH+NONVASC2+ELE	1.88	0.10
Reproduction	Collared	ELE+ELE^2+VASC1	0.00	0.17
	(n = 143)	ELE+VASC1	0.32	0.14
		ELE+VASC1+NONVASC3	0.43	0.14
		ELE+SINCLIN	0.82	0.11
		ELE+VASC1+SINCLIN	0.88	0.11
		ELE+NONVASC3+SINCLIN	0.93	0.11
		ELE+VASC1+NONVASC3+SINCLIN	1.12	0.10
		ELE+NONVASC3	1.62	0.07
	Brown	VASC3+VASC2+SDEPTH	0.00	0.41
	(n = 50)	VASC3+VASC2+SDEPTH+SDEPTH^2	1.24	0.22
		VASC3+VASC2+SDEPTH+NONVASC3	1.54	0.19
Predation	Collared/Brown	DENSITY+SP	0.00	0.30
	(n = 22)	DENSITY+SP+REPROD	1.52	0.14

Table 3. Model averaged coefficient (β) estimates with unconditional standard errors (SE) of significant variables in habitat selection models for collared and brown lemmings during winter 2006-2007 on the south plain of Bylot Island, Sirmilik National Park, Nunavut, Canada. See Table 1 for definition of variables.

	Collared lemming				Brown lemming			
	Landscape scale		Local scale		Landscape scale		Local scale	
Variable	β	SE	β	SE	β	SE	β	SE
MTH	1.24	0.22	1.74	0.22	1.17	0.21	1.11	0.21
SINCLIN	0.86	0.26			0.53	0.22		
SDEPTH	1.32	0.26	0.50	0.15	1.00	0.27	0.44	0.17
$SDEPTH^2$	-0.48	0.13			-0.38	0.11		
SDEPTH*SINCLIN					-0.50	0.16		
NONVASC1			-0.95	0.22	-0.42	0.17	-1.03	0.23
NONVASC2	0.74	0.21			0.73	0.23		
NONVASC3	-0.39	0.17						
VASC1	-0.33	0.24						
VASC2			-0.54	0.18				

Table 4. Comparison of habitat variables between wet tundra (n = 50), mesic tundra (n = 50) and mesic stream habitats (n = 48) on the south plain of Bylot Island, Sirmilik National Park, Nunavut, Canada. Mean and SE are given. Variables are compared using Kruskall-Wallis test and means with the same letter do not differ significantly.

Variable	Wet	Mesic	Stream	K-W X^2	*p*
Index of heterogeneity in micro-topography	-0.62±1.34^a	-0.53±1.02^a	-0.41±1.04^a	0.9	0.64
Slope inclination (%)	0.12±0.06^a	0.28±0.12^b	0.35±0.16^b	75.0	<0.001
Snow depth (cm)	25.9±11.4^a	32.2±19.3^a	60.0±34.8^b	39.0	<0.001
Index of lichen abundance (NONVASC1)	-0.30±2.09^a	1.06±1.35^b	-1.19±1.23^a	39.7	<0.001
Index of palatable mosses abundance (NONVASC2)	-0.26±1.12^a	-0.51±1.26^a	-0.61±1.24^a	2.8	0.24
Index of *Sphagnum* abundance (NONVASC3)	1.00±1.53^a	-0.20±1.15^b	0.16±0.98^b	19.7	<0.001
Index of forb abundance (VASC1)	-1.52±0.62^a	-0.18±1.29^b	-0.11±1.66^b	39.1	<0.001

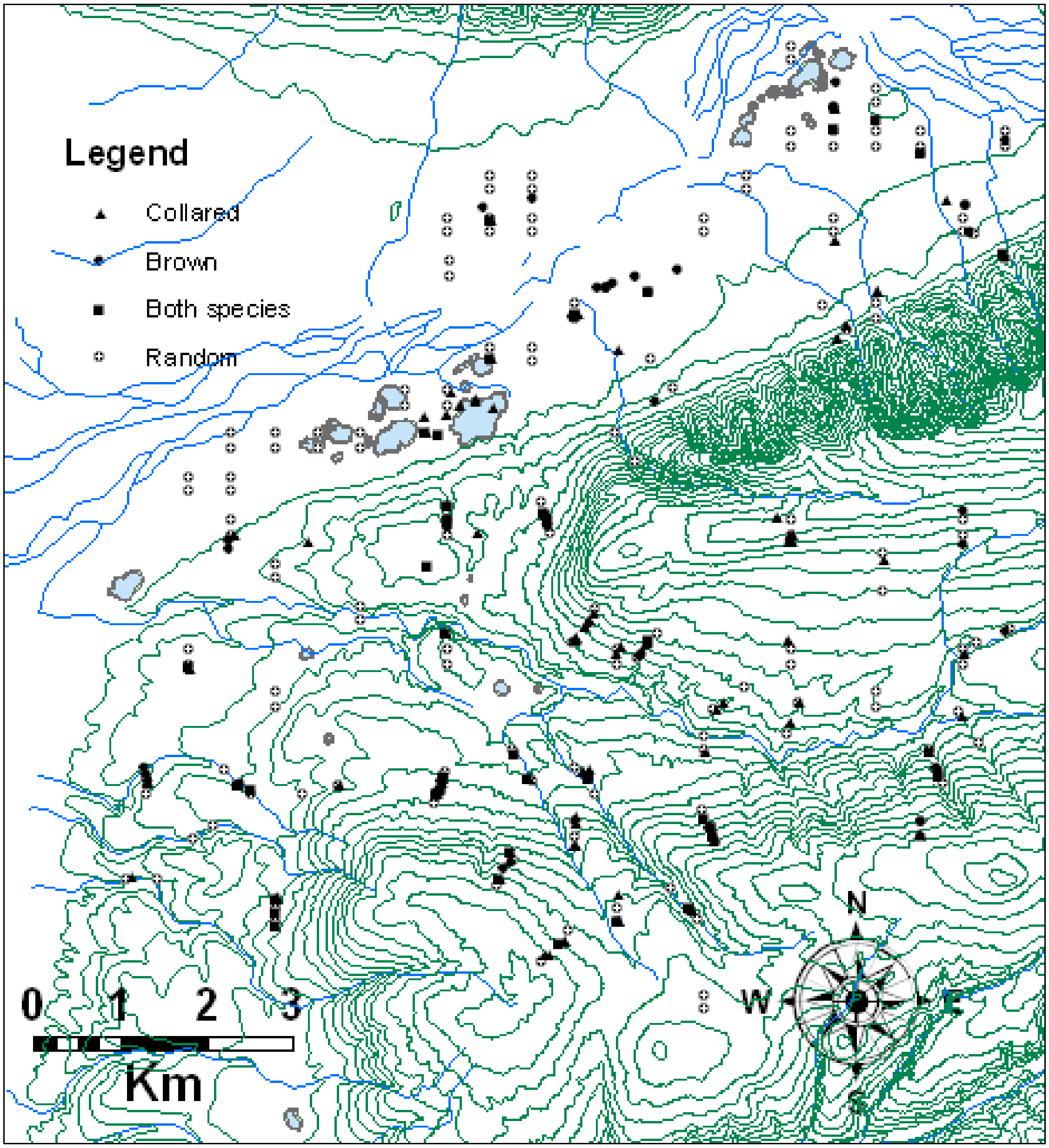

Figure 1. Locations of collared and brown lemming winter nests and random sites sampled in summer 2007 on the south plain of Bylot Island, Sirmilik National Park, Nunavut, Canada (73º08'N, 80º00'W). Transect positions are represented as two consecutive random sites.

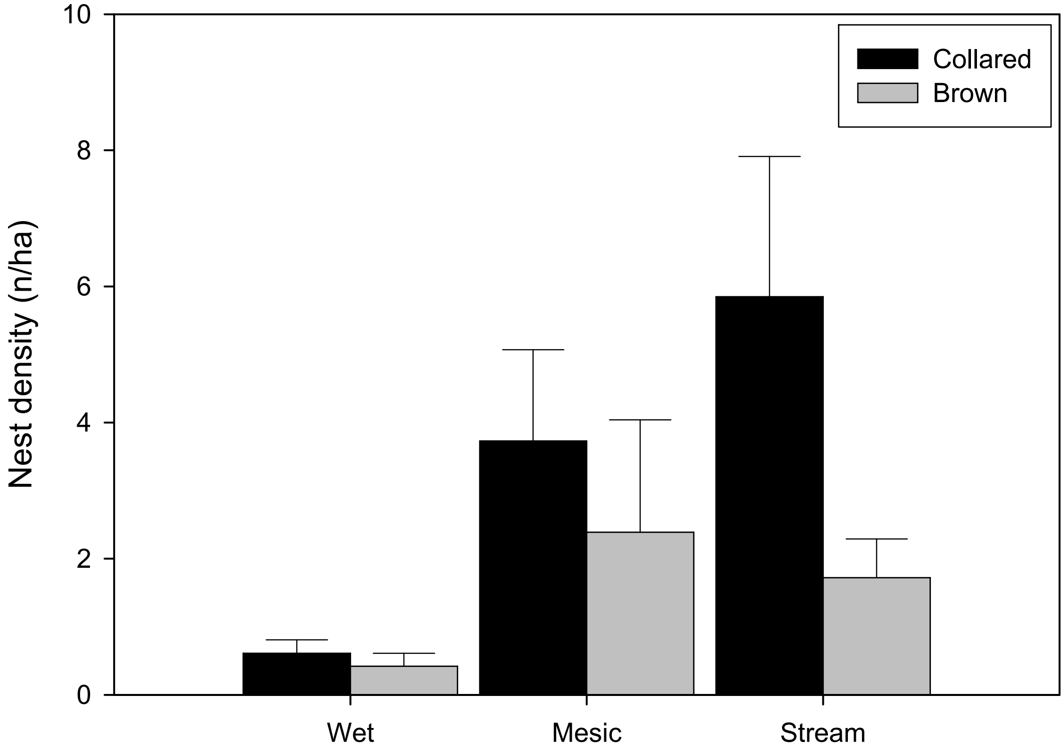

Figure 2. Winter nest density of collared and brown lemmings in wet, mesic tundra and stream habitat sampled in summer 2007 on the south plain of Bylot Island, Sirmilik National Park, Nunavut, Canada.

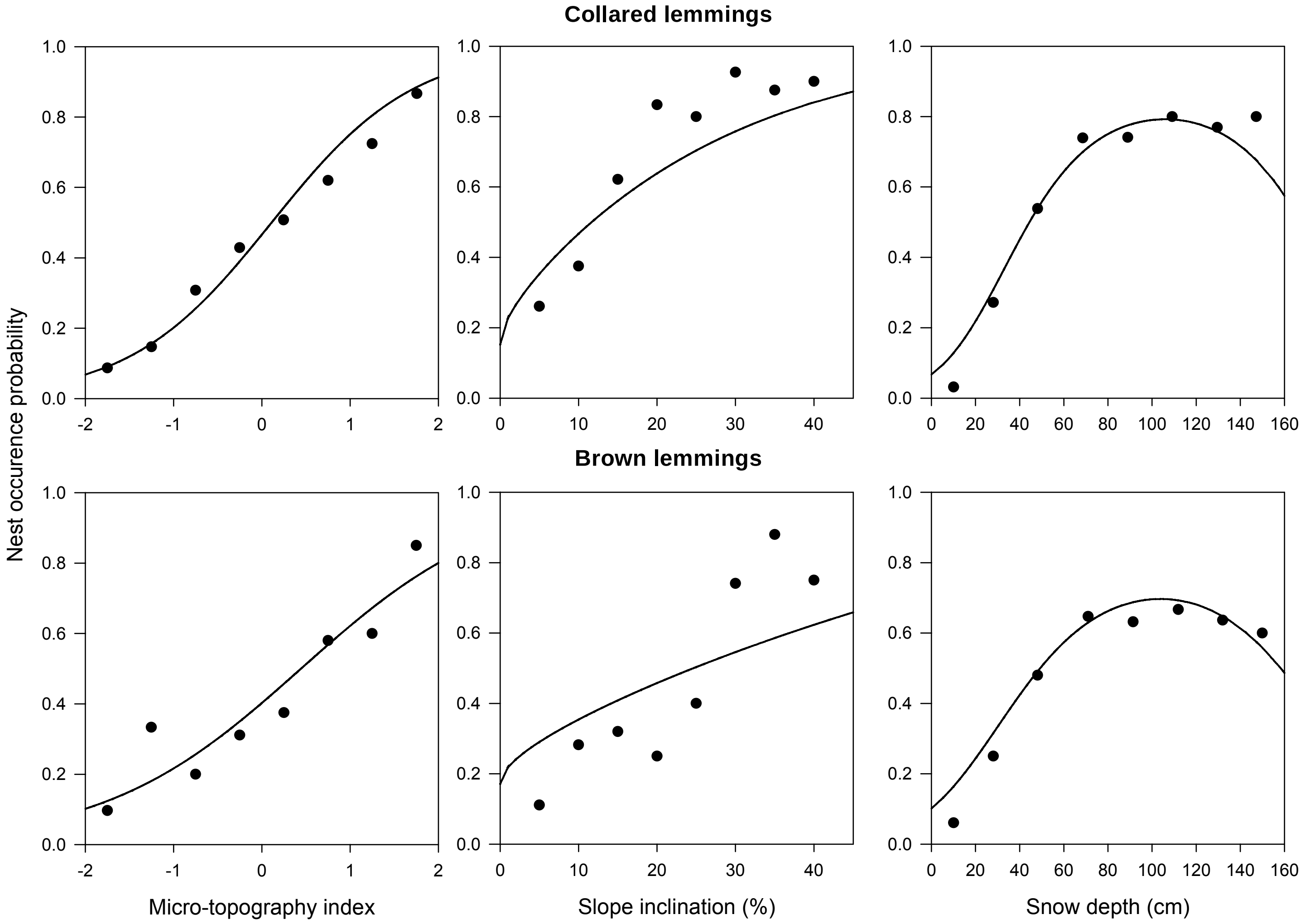

Figure 3. Occurrence probability of collared and brown lemming winter nests in relation to micro-topography, slope and snow depth at the landscape scale during winter 2006-2007 on the south plain of Bylot Island, Sirmilik National Park, Nunavut, Canada. The line is the prediction from the best model (Table 2) and the dots the observed values.

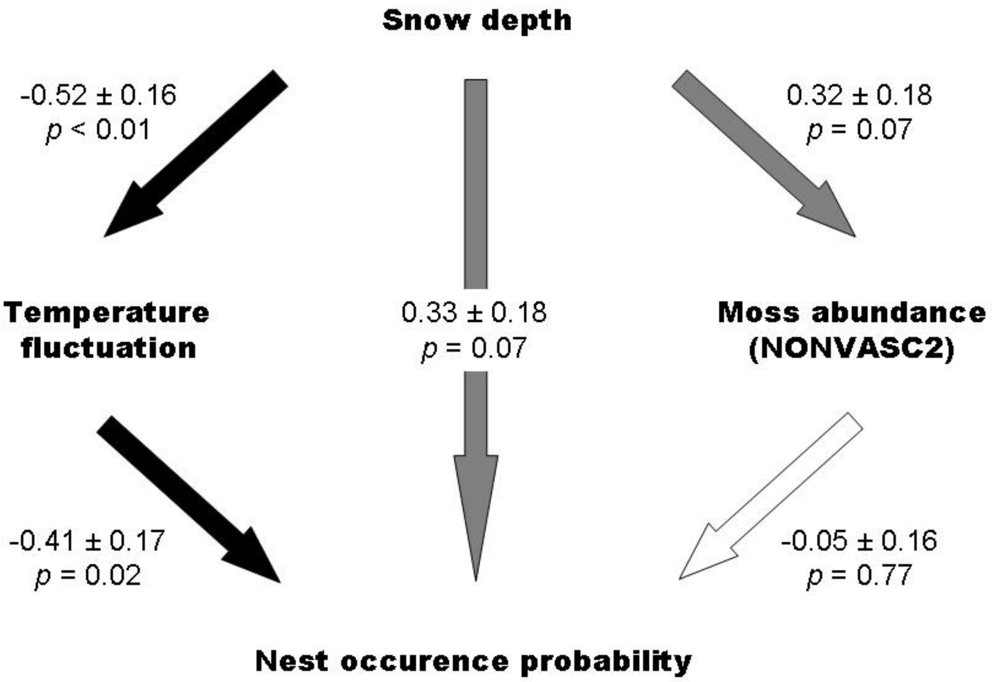

Figure 4. Path diagram showing the direct and indirect effects of snow depth on the probability of occurrence of collared and brown lemming nests during winter 2006-2007 on the south plain of Bylot Island, Sirmilik National Park, Nunavut, Canada. Path coefficient estimates, standard errors and *p*-values are given for each tested path. Significant paths are shown in black, non-significant ones in white and those approaching significance in grey (n = 30).

Conclusion générale

Dans la présente étude, nous mettons en relief le rôle du couvert nival en tant que déterminant de la structure spatiale hiémale des populations de lemmings variables et de lemmings bruns et nous validons une nouvelle méthode permettant de détecter l'activité de reproduction des petits mammifères à l'intérieur des nids d'hiver. L'approfondissement de nos connaissances de l'écologie hivernale de ces populations ainsi que la validation de ce nouvel outil s'inscrivent dans le processus de compréhension de l'impact des conditions climatiques hivernales sur la dynamique cyclique des populations de petits mammifères nordiques. Lors de la saison hivernale, l'installation du couvert nival semble jouer un rôle prédominant dans la balance des forces relatives des facteurs dépendants de la densité à l'origine des cycles de population (Ostfeld et Tamarin 1986, Tkadlec 2000, Aars et Ims 2002, Smith et al. 2006, Schmidt et al. 2008). Pourtant, très peu d'études se sont intéressées à cette période du cycle annuel des populations de petits mammifères nordiques (Fuller et al. 1975, Reid et Krebs 1996, Hansen et al. 1999, Korslund et Steen 2006). Par conséquent, ce mémoire représente l'une des études les plus approfondies traitant de la structure spatiale des populations de petits mammifères en hiver et propose un outil permettant de quantifier leur reproduction hivernale, une composante majeure de la démographie de ces populations.

Concernant notre premier volet, nos travaux démontrent l'influence de plusieurs composantes abiotiques et biotiques de la structure de l'habitat sur la sélection des sites de nid d'hiver des lemmings variables et des lemmings bruns à l'île Bylot. Notre étude confirme l'importance de la protection thermique offerte par le couvert nival en tant que déterminant de la distribution spatiale des lemmings tel que proposé par certaines études (MacLean et al. 1974, Fuller et al. 1975, Rodgers et Lewis 1986, Reid et Krebs 1996). La sélection des sites favorisant l'accumulation d'un couvert nival épais serait essentielle au maintien thermo-métabolique des lemmings lors de la saison froide (Chappell 1980). D'autre part, bien que la distribution réelle de l'espace sous nival n'ait pu être mesurée lors de cette étude, nos travaux suggèrent que le couvert nival puisse également affecter les populations de petits mammifères via une interaction avec la structure micro topographique de la toundra arctique. Cette structure topographique est probablement sélectionnée par les lemmings en été pour la protection qu'elle offre contre les prédateurs (Morris et al. 2000, Predavec et Krebs 2000), mais les causes de cette sélection hivernale aux deux échelles étudiées pourraient différer. En effet, l'hétérogénéité de la micro-topographie pourrait d'une part offrir des refuges aux petits mammifères contre les événements d'inondation et d'autre part, favoriser la formation de l'espace sous nival en augmentant la surface de contact entre l'air et le sol (Marchand 1996). L'accessibilité à la nourriture offerte par l'espace sous nival étant essentielle à la survie des petits mammifères nordiques (Korslund et Steen 2006), les facteurs favorisant la formation de cet espace semblent être une composante importante du processus de sélection des sites de nids d'hiver chez les lemmings.

De plus, notre étude démontre l'importance de la disponibilité des bryophytes en tant que déterminant de la sélection des sites de nids d'hiver des lemmings variables et bruns à l'échelle locale. Certaines études suggèrent que les lemmings intègrent une plus grande proportion de bryophytes dans leurs régimes alimentaires lors de la saison froide que lors de la saison estivale (Rodgers et Lewis 1986, Batzli et Pitelka 1983). Ce comportement serait relativement commun chez les herbivores de l'écosystème arctique (Prins 1981). La présence de composés secondaires phénoliques implique une faible digestibilité chez les mousses (Batzli et Cole 1979), mais ces dernières sont riches en acides gras insaturés tels que les acides arachidoniques (Prins 1981). Ce type de composé permettrait une forte production de chaleur chez les endothermes et favoriserait ainsi la survie des petits mammifères et de leurs jeunes lors de la saison froide dans l'Arctique (Prins 1981). Par contre, bien que les plantes vasculaires soient intégrées dans le régime alimentaire hivernal des lemmings (Batzli et Jung 1980, Batzli et Pitelka 1983), elles n'eurent qu'un effet relativement faible sur la distribution spatiale de leurs nids d'hiver dans notre étude.

Globalement, nos travaux suggèrent une convergence des facteurs affectant la sélection des sites de nid d'hiver entre les lemmings variables et les lemmings bruns. Cette réalité se concrétise par l'observation de fortes densités de nids des deux espèces en milieux mésiques et surtout le long des ruisseaux qui traversent ces milieux par opposition aux milieux humides. Nous soulignons ainsi les différences de structure spatiale des populations de lemmings bruns entre les saisons estivales et hivernales (Batzli et al. 1983, Rodgers et Lewis 1986, Gruyer et al. 2008). À notre connaissance, aucune étude ne s'est intéressée directement aux interactions interspécifiques liées à la migration locale des populations de lemmings bruns, occupant principalement les milieux humides en été, vers les milieux mésiques, généralement occupés par le lemming variable lors de la saison estivale. Considérant que les contraintes énergétiques soient à l'origine de l'influence de la protection thermique et de la disponibilité des mousses sur la sélection de l'habitat d'hiver des lemmings, le réchauffement global risque de modifier la convergence des facteurs affectant la sélection des sites de nid d'hiver des deux espèces de lemmings. Éventuellement, cette modification risque d'affecter la migration locale saisonnière et la composante démographique dépendante de la densité impliquée dans les interactions interspécifiques de ces espèces.

En ce qui a trait à notre second volet, nous proposons une méthode permettant d'inférer l'occurrence d'activité de reproduction chez les petits mammifères à l'aide de la distribution de fréquences de la masse des fèces récupérées dans les nids d'hiver. Brièvement, la méthode proposée est fondée sur l'occurrence de fèces générées par la présence de juvéniles avant le sevrage dans les nids d'hiver. L'interprétation des paramètres démographiques générés par cette approche indirecte est néanmoins limitée par le fait que nous mesurons un taux de reproduction sur des nids d'hiver et non sur des individus (Cole 1954, 1960, De-Camino-Beck et Lewis 2008). Ainsi, l'approche proposée génère un indice de reproduction et non un taux de reproduction per capita. En conséquence, cette méthode devrait être utilisée avec précaution dans l'analyse de la dynamique des populations de petits mammifères. Nonobstant cette limitation, l'avènement de cette nouvelle approche permettant de quantifier rapidement la reproduction hivernale ouvre de nouvelles perspectives dans l'étude des phénomènes démographiques chez les petits mammifères nordiques. L'occurrence de reproduction en hiver, favorisée par de bonnes conditions nivales et climatiques (Reid et Krebs 1996, Aars et Ims 2002), engendre une superposition de l'atteinte de maturité chez plusieurs générations et par conséquent, augmente considérablement le potentiel de croissance des populations (Millar, 2001). Ce phénomène démographique semble être un prélude à l'atteinte des pics d'abondance chez les petits mammifères nordiques (Hansson, 1984, Krebs, 1993, Stenseth 1999). Par conséquent, notre capacité à quantifier ce phénomène démographique était un préalable essentiel à notre compréhension des processus démographiques impliqués dans la dynamique cyclique de ces populations.

Notre étude confirme les capacités de reproduction des lemmings variables et des lemmings bruns lors de la saison froide dans l'Arctique (MacLean et al. 1974, Stenseth et Ims 1993, Krebs et al 1995, Reid et Krebs 1996). Nos travaux suggèrent que la variabilité spatiale dans l'occurrence de la reproduction à l'intérieur des nids d'hiver est principalement influencée par la topographie chez les lemmings variables et par la disponibilité de certaines plantes graminoïdes chez les lemmings bruns. L'effet des plantes vasculaires sur l'occurrence de reproduction à l'intérieur des nids de lemmings bruns pourrait s'expliquer par le fait que, contrairement au lemming variable, cette espèce de lemming initie la reproduction en fonction d'un composé chimique que l'on retrouve à l'intérieur de ce type de plante (Negus et Berger 1998).

Notre troisième volet, relatif à la prédation, démontre principalement que les conditions nivales ne semblent pas limiter la pression de prédation exercée par les prédateurs spécialistes telle que l'hermine. Par opposition, nos observations suggèrent que les tentatives de prédation exercées par le renard arctique sur les nids d'hiver des lemmings seraient partiellement limitées par l'épaisseur du couvert nival. La somme de ces observations évoque l’influence du couvert nival sur le fonctionnement des communautés prédateur-proie dans l’écosystème arctique. L’installation d’un épais couvert nival dans les écosystèmes nordiques ayant de longs hivers semble protéger les petits mammifères contre certains prédateurs généralistes, et par conséquent offrir une exclusivité partielle des proies de l’espace sous nival aux prédateurs spécialistes tels que les mustélidés (Hansson et Henttonen 1985, Lindstrom et Hornfeldt 1994, Hanski et al. 1991). Cela dit, la régulation hiémale des communautés de prédateurs et de proies, via l’installation du couvert de neige, semble être impliquée dans le gradient latitudinal de cyclicité observé en Europe ainsi qu’au Japon (Hansen et al. 1999, Stenseth et al. 1999).

En conclusion, le présent mémoire souligne l’importance des rôles du couvert nival sur la structure spatiale de certaines populations de petits mammifères nordiques lors de la saison froide. Plusieurs études suggèrent que les conditions du couvert nival, influencées par les conditions climatiques hivernales, auraient également une influence importante sur la dynamique de ces populations (Reid and Krebs 1996, Kausrud 2008). En effet, l’occurrence de pluies verglaçantes et de redoux hivernaux semble affecter la survie de ces populations en hiver (Aars et Ims 2008). A priori, ces événements climatiques peuvent affecter la qualité de la protection thermique offerte par le couvert nival et fragmenter l’espace sous nival en générant une couche de glace au niveau du sol (Korslund et Steen 2006). Par conséquent, la survie des petits mammifères est affectée par une augmentation des stress thermiques et une réduction de la capacité de support du milieu induite par une diminution de l’accessibilité à la nourriture (Chappell 1980, Korslund et Steen 2006). A posteriori, les conditions climatiques reliées aux redoux hivernaux peuvent affecter l’accumulation du couvert nival et réduire la protection offerte aux petits mammifères contre certains prédateurs généralistes (Hansson et Henttonen 1985). Par conséquent, l’augmentation de l’effet densité dépendant relié à la prédation exercée par ce type de prédateur risque de perturber la dynamique des communautés de prédateurs et de proies des écosystèmes nordiques terrestres (Lindstrom et Hornfeldt 1994). Ces faits suggèrent que le réchauffement global impliquant un changement directionnel à long terme et une augmentation des températures régissant les conditions climatiques de l'hiver arctique pourrait affecter les conditions nivales, réduire la survie des petits mammifères et agir en déstabilisant la dynamique cyclique de ces populations.

Ce contexte impose l'approfondissement de nos connaissances des mécanismes impliqués dans la démographie hivernale des populations de petits mammifères. Concrètement, nous suggérons que la protection thermique offerte par le couvert nival, la distribution de l'espace sous nival fournissant l'accessibilité aux ressources alimentaires, les interactions interspécifiques causées par la convergence de la sélection de l'habitat en hiver, l'occurrence de reproduction à l'intérieur des nids ainsi que la protection partielle offerte par le couvert de neige contre les tentatives de prédation par les prédateurs généralistes doivent être pris en compte dans les futures études de la dynamique hivernale des populations de petits mammifères nordiques. Ce mémoire suggère que les prochaines études portant sur la mortalité et la reproduction des petits mammifères nordiques devraient non seulement travailler sur une échelle temporelle, mais également considérer la dimension spatiale qui semble fortement influencer les populations de petits mammifères nordiques. Ces études doivent couvrir une période de temps suffisante afin d'inclure une variabilité temporelle des conditions climatiques sur plusieurs cycles de populations de petits mammifères. Au niveau de l'échelle spatiale, ces études doivent être suffisamment bien représentées géographiquement afin d'inclure une transition entre les écosystèmes dominés par de longs hivers et les écosystèmes affectés par une courte période hiémale. En somme, les approches de modélisation et les méthodes expérimentales pourraient être combinées afin étudier l'effet des conditions climatiques et des communautés de prédateurs sur la structure spatiale et la démographie des populations de petits mammifères nordiques.

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Annexe

Table A. Eigenvectors derived from principal component analyses on the correlation matrix of the 18 non-vascular plants sampled in 2007 and 2008 on the south plain of Bylot Island, Sirmilik National Park, Nunavut, Canada

Genus	NONVASC1	NONVASC2	NONVASC3
Aulacomnium.sp.	0.31	-0.51	0.49
Bryum sp.	-0.50	0.24	0.09
Calliergon sp.	-0.42	0.02	-0.07
Campylium sp.	0.07	0.02	0.09
Dicranella sp.	0.04	0.01	0.12
Dicranum sp.	0.44	0.07	0.23
Drepanocladus sp.	-0.38	0.16	-0.19
Marchantiopsida	0.41	-0.14	0.41
Hepaticophyta	0.04	0.52	0.36
Lichens	0.54	0.31	-0.34
Meesia sp.	-0.36	-0.08	0.16
Pleurozium sp.	0.54	-0.38	-0.11
Pohlia sp.	-0.06	0.34	0.22
Polytrichum sp.	0.38	0.51	0.35
Rhacomitrium sp.	0.40	-0.01	-0.31
Sphagnum	-0.09	-0.09	0.38
Stereocolon fruticulosa	0.64	0.18	-0.26

Table B. Eigenvectors derived from principal component analyses on the correlation matrix of the 48 vascular plant species sampled in 2007 and 2008 on the south plain of Bylot Island, Sirmilik National Park, Nunavut, Canada

Species	VASC1	VASC2	VASC3	VASC4
Alopecurus alpinus	0.25	-0.18	0.06	0.00
Alopecurus pratense	0.07	0.03	-0.05	-0.07
Arctagrostis latifolia	-0.31	0.06	-0.31	-0.18
Arnica angustifolia	-0.02	-0.02	0.02	0.04
Astragalus alpinus	-0.22	0.33	0.42	-0.07
Cardamine belidifolia	0.06	0.17	-0.21	-0.20
Carex aquatilis	-0.28	-0.43	0.20	-0.01
Carex membranacea	-0.04	0.00	-0.12	-0.06
Cassiope tetragona	-0.13	0.10	-0.24	0.40
Cerastium alpinum	0.40	0.03	0.14	0.01
Draba sp.	0.44	0.00	-0.02	-0.21
Dryas integrifolia	-0.17	0.20	-0.01	-0.42
Dupontia fisheri	-0.23	-0.63	0.26	0.10
Epilobium latifolium	-0.01	0.10	0.15	-0.05
Equisetum arvense	-0.12	-0.16	0.11	-0.16
Eriophorum angustifolium	-0.16	-0.08	-0.16	0.22
Eriophorum scheuchzeri	-0.17	-0.48	0.23	0.05
Festuca brachyphylla	-0.01	0.25	0.53	0.04
Hierochloe alpina	-0.07	0.06	0.00	0.25
Juncus sp.	0.31	-0.07	0.04	-0.17
Luzula confusa	0.07	0.35	-0.06	0.22
Luzula nivalis	0.52	0.15	-0.39	0.10
Oxyria digyna	0.63	-0.02	-0.10	0.05
Oxytropis maydelliana	-0.09	0.20	0.20	-0.02
Papaver radicatum	0.34	0.05	0.01	0.05
Pedicularis arctica	-0.08	-0.23	0.24	0.06
Pedicularis hirsuta	-0.02	0.13	-0.17	-0.08
Pedicularis lanata	0.03	0.10	0.06	0.08
Pedicularis sudetica	-0.13	-0.27	0.08	0.11
Poa sp.	-0.01	0.31	0.34	0.21
Polygonum viviparum	-0.16	0.40	0.16	-0.29
Potentilla hypartica	0.35	0.16	0.21	0.22
Pyrola grandiflora	-0.05	0.08	-0.12	0.30
Renunculus sp.	0.57	-0.25	0.04	-0.01
Salix arctica	-0.31	0.51	0.05	0.03
Salix herbacea	-0.13	0.13	-0.31	0.34
Salix reticulata	-0.30	0.23	0.02	-0.38
Salix ritchardsoni	-0.12	-0.14	0.01	-0.20
Sagina caespi	0.33	0.08	0.32	0.06
Saxifraga cernua	0.42	-0.14	0.11	-0.14
Saxifraga hirculus	0.02	0.02	0.05	0.14
Saxifraga nivalis	0.59	-0.02	0.00	-0.11
Saxifraga oppositifolia	0.43	0.13	0.09	-0.17
Saxifraga tricuspidata	0.05	0.12	0.41	0.22
Senecio congestus	-0.04	-0.23	0.09	0.01
Silene uralensis	0.16	-0.02	0.05	-0.06
Stellaria longipes	0.13	0.26	0.32	0.24
Vaccinium uliginosum	-0.04	0.02	-0.14	0.37

Table C. Models explaining habitat selection for winter nest in collared lemming at the landscape scale. ΔQIC indicates the difference between a model and the model with the lowest QIC value. Model weight (w_i) is the normalized value of the model based on its ΔQIC. Variables are shown in decreasing order of importance based on the sum of the w_i of models where they appear.

Variables included in the model	ΔQIC	w_i
MTH+SINCLIN+SDEPTH+SDEPTH^2+NONVASC2+NONVASC3+VASC1	0.00	0.50
MTH+(SINCLIN*SDEPTH)+SINCLIN^2+SDEPTH^2+NONVASC2+NONVASC3+VASC1	0.26	0.44
MTH+(SINCLIN*SDEPTH)+NONVASC2+NONVASC3+VASC1	4.41	0.05
MTH+SINCLIN+SINCLIN^2+SDEPTH+NONVASC2+NONVASC3+VASC1	9.87	0.00
MTH+SINCLIN+SDEPTH+NONVASC2+NONVASC3+VASC1	12.2	0.00
MTH+SINCLIN+SDEPTH+NONVASC2*VASC1+NONVASC3	12.3	0.00
MTH+SINCLIN+SDEPTH+NONVASC2+NONVASC3	13.0	0.00
MTH+SINCLIN+SDEPTH+NONVASC2+NONVASC3*VASC1	13.3	0.00
MTH+SINCLIN+SDEPTH+NONVASC2+VASC1	15.7	0.00
MTH+SINCLIN+SDEPTH	21.0	0.00
MTH+SINCLIN+SDEPTH+NONVASC3+VASC1	21.1	0.00
MTH+SINCLIN+SDEPTH+VASC1	22.0	0.00
MTH+SINCLIN+NONVASC2+NONVASC3+VASC1	23.9	0.00
MTH+SDEPTH+NONVASC2+NONVASC3+VASC1	27.1	0.00
SINCLIN+SDEPTH+NONVASC2+NONVASC3+VASC1	46.7	0.00
NONVASC2+NONVASC3+VASC1	136	0.00
NONVASC2+NONVASC3	140	0.00
VASC1	150	0.00

Table D. Models explaining habitat selection for winter nest in brown lemmings at the landscape scale. ∆QIC indicates the difference between a model and the model with the lowest QIC value. Model weight (w_i) is the normalized value of the model based on its ∆QIC. Variables are shown in decreasing order of importance based on the sum of the w_i of models where they appear.

Variables included in the model	∆QIC	w_i
MTH+SINCLIN+NONVASC2+NONVASC1+SDEPTH+SDEPTH^2	0.00	0.43
MTH+(SINCLIN*SDEPTH)+NONVASC2+NONVASC1	0.06	0.41
MTH+(SINCLIN*SDEPTH)+SINCLIN^2+SDEPTH^2+NONVASC2+NONVASC1	2.84	0.10
MTH+SINCLIN+SINCLIN^2+NONVASC2+NONVASC1+SDEPTH	6.31	0.02
MTH+SINCLIN+NONVASC2+NONVASC1+SDEPTH	6.54	0.02
MTH+SINCLIN+NONVASC2+NONVASC1+SDEPTH+ELE	7.14	0.01
MTH+SINCLIN+NONVASC2+NONVASC1+SDEPTH+ELE+VASC1+VASC4	9.41	0.00
MTH+SINCLIN+NONVASC2+NONVASC1	10.3	0.00
MTH+SINCLIN+NONVASC2+SDEPTH+ELE	11.7	0.00
MTH+NONVASC2+NONVASC1+SDEPTH	11.9	0.00
MTH+SINCLIN+NONVASC2+NONVASC1+ELE	11.9	0.00
MTH+SINCLIN+NONVASC2+SDEPTH	12.2	0.00
MTH+SINCLIN+NONVASC1+SDEPTH+ELE	12.5	0.00
MTH+SINCLIN+NONVASC1+SDEPTH	13.5	0.00
MTH+NONVASC2+NONVASC1+SDEPTH+ELE	14.3	0.00
MTH+SINCLIN+SDEPTH+ELE	17.0	0.00
SINCLIN+NONVASC2+NONVASC1+SDEPTH+ELE	35.1	0.00
SINCLIN+NONVASC2+NONVASC1+SDEPTH	42.7	0.00
NONVASC2+NONVASC1+VASC1+VASC4	90.1	0.00
NONVASC2+NONVASC1	93.0	0.00
VASC1+VASC4	106	0.00

Table E. Models explaining habitat selection for winter nest in collared lemmings at the local scale. ΔQIC indicates the difference between a model and the model with the lowest QIC value. Model weight (w_i) is the normalized value of the model based on its ΔQIC. Variables are shown in decreasing order of importance based on the sum of the w_i of models where they appear.

Variables included in the model	ΔQIC	w_i
MTH+NONVASC1+SDEPTH+VASC2	0.00	0.50
MTH+NONVASC1+SDEPTH+SDEPTH^2+VASC2	1.18	0.28
MTH+(NONVASC1*VASC2)+SDEPTH	1.96	0.19
MTH+NONVASC1+SDEPTH	7.00	0.02
MTH+NONVASC1+VASC2	7.12	0.01
MTH+SDEPTH+VASC2	18.0	0.00
MTH+SDEPTH	33.0	0.00
NONVASC1+SDEPTH+VASC2	71.6	0.00
NONVASC1+VASC2	91.9	0.00
NONVASC1	92.8	0.00
VASC2	104	0.00

Table F. Models explaining habitat selection for winter nest in brown lemmings at the local scale. ∆QIC indicates the difference between a model and the model with the lowest QIC value. Model weight (w_i) is the normalized value of the model based on its ∆QIC. Variables are shown in decreasing order of importance based on the sum of the w_i of models where they appear.

Variables included in the model	∆QIC	w_i
MTH+NONVASC1+SDEPTH	0.00	0.27
MTH+NONVASC1+SDEPTH+ELE	0.63	0.19
MTH+NONVASC1+SDEPTH+SDEPTH^2	1.11	0.15
MTH+NONVASC1+SDEPTH+NONVASC2	1.24	0.14
MTH+NONVASC1+SDEPTH+NONVASC2+ELE	1.88	0.10
MTH+NONVASC1+SDEPTH+ELE+NONVASC2+VASC2+VASC3	2.97	0.06
MTH+NONVASC1+ELE	4.24	0.03
MTH+NONVASC1+ELE+NONVASC2	4.35	0.03
MTH+NONVASC1	5.44	0.02
MTH+SDEPTH+ELE+VASC2+VASC3	8.65	0.00
MTH+SDEPTH+ELE	17.6	0.00
MTH+SDEPTH+ELE+NONVASC2	18.9	0.00
NONVASC1+SDEPTH+ELE	28.0	0.00
NONVASC1+SDEPTH	28.3	0.00
NONVASC1+SDEPTH+ELE+NONVASC2	29.0	0.00
NONVASC1+NONVASC2	41.4	0.00
NONVASC1+NONVASC2+VASC2+VASC3	43.3	0.00
VASC2+VASC3	55.1	0.00

Table G. Models explaining the occurrence of reproduction in collared lemming nests. ∆QIC indicates the difference between a model and the model with the lowest QIC value. Model weight (w_i) is the normalized value of the model based on its ∆QIC. Variables are shown in decreasing order of importance based on the sum of the w_i of models where they appear.

Variables included in the model	∆QIC	wi
ELE+ELE2+VASC1	0.00	0.17
ELE+VASC1	0.32	0.14
ELE+VASC1+NONVASC3	0.43	0.14
ELE+SINCLIN	0.82	0.11
ELE+VASC1+SINCLIN	0.88	0.11
ELE+NONVASC3+SINCLIN	0.93	0.11
ELE+VASC1+NONVASC3+SINCLIN	1.12	0.10
ELE+NONVASC3	1.62	0.07
NONVASC3	3.91	0.02
VASC1	4.67	0.02
VASC1+NONVASC3	5.69	0.01
VASC1+NONVASC3+SINCLIN	7.56	0.00

Table H. Models explaining the occurrence of reproduction in brown lemming nests. ΔQIC indicates the difference between a model and the model with the lowest QIC value. Model weight (w_i) is the normalized value of the model based on its ΔQIC. Variables are shown in decreasing order of importance based on the sum of the w_i of models where they appear.

model	ΔQIC	wi
VASC3+VASC2+SDEPTH	0.00	0.41
VASC3+VASC2+SDEPTH+SDEPTH^2	1.24	0.22
VASC3+VASC2+SDEPTH+NONVASC3	1.54	0.19
VASC3+VASC2	3.78	0.06
VASC3+SDEPTH	4.59	0.04
VASC3+VASC2+NONVASC3	4.87	0.04
VASC3+SDEPTH+NONVASC3	5.76	0.02
SDEPTH	7.41	0.01
VASC2+SDEPTH	8.15	0.01
VASC2+SDEPTH+NONVASC3	9.36	0.00
NONVASC3	10.7	0.00

Table I. Models explaining the occurrence of stoat predation in lemming nests. ∆QIC indicates the difference between a model and the model with the lowest QIC value. Model weight (w_i) is the normalized value of the model based on its ∆QIC. Variables are shown in decreasing order of importance based on the sum of the w_i of models where they appear.

model	∆QIC	wi
DENSITY+SP	0.00	0.30
DENSITY+SP+REPROD	1.52	0.14
REPROD	2.12	0.10
DENSITY+SP+SDEPTH	2.55	0.08
DENSITY	2.56	0.08
SDEPTH	3.49	0.05
SP	3.83	0.04
DENSITY+REPROD	4.00	0.04
SP+REPROD	4.44	0.03
REPROD+SDEPTH	4.86	0.03
REPROD+SDEPTH	4.86	0.03
DENSITY+SDEPTH	5.49	0.02
DENSITY+SP+REPROD+SDEPTH	5.78	0.02
SP+SDEPTH	6.37	0.01
SP+REPROD+SDEPTH	7.61	0.01
DENSITY+REPROD+SDEPTH	9.36	0.00

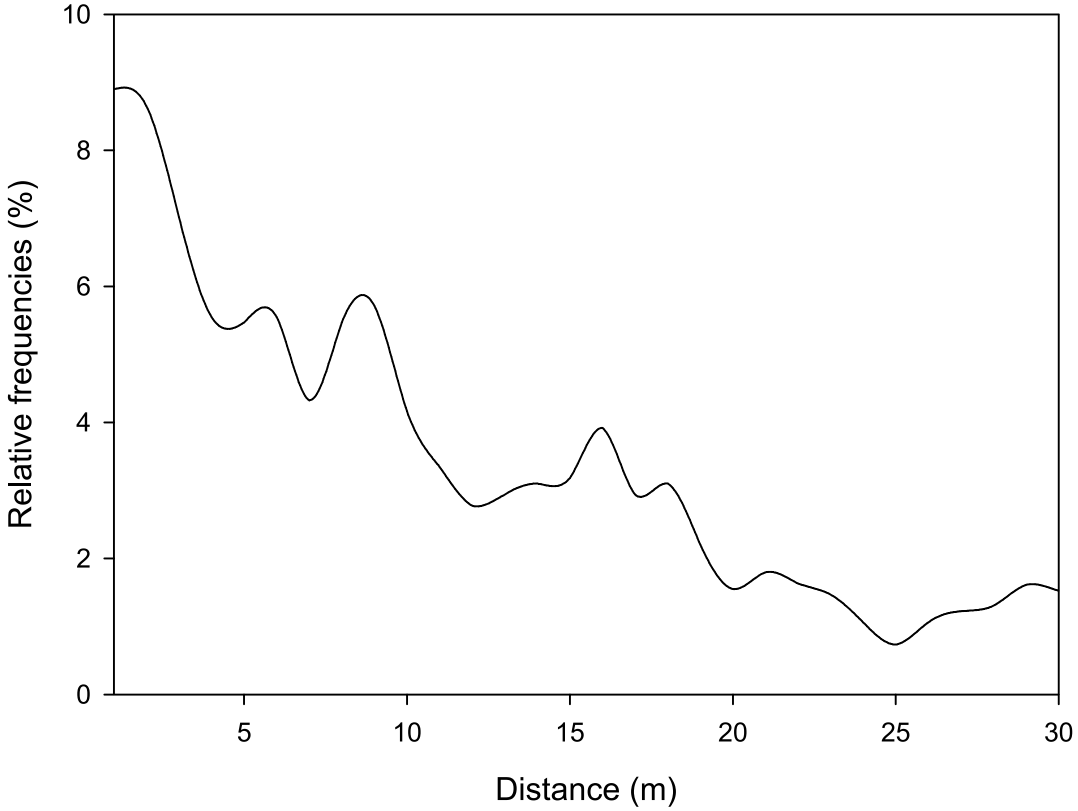

Figure A. Frequency distribution of signs of lemming activity according to distance from their nests on the south plain of Bylot Island, Sirmilik National Park, Nunavut, Canada

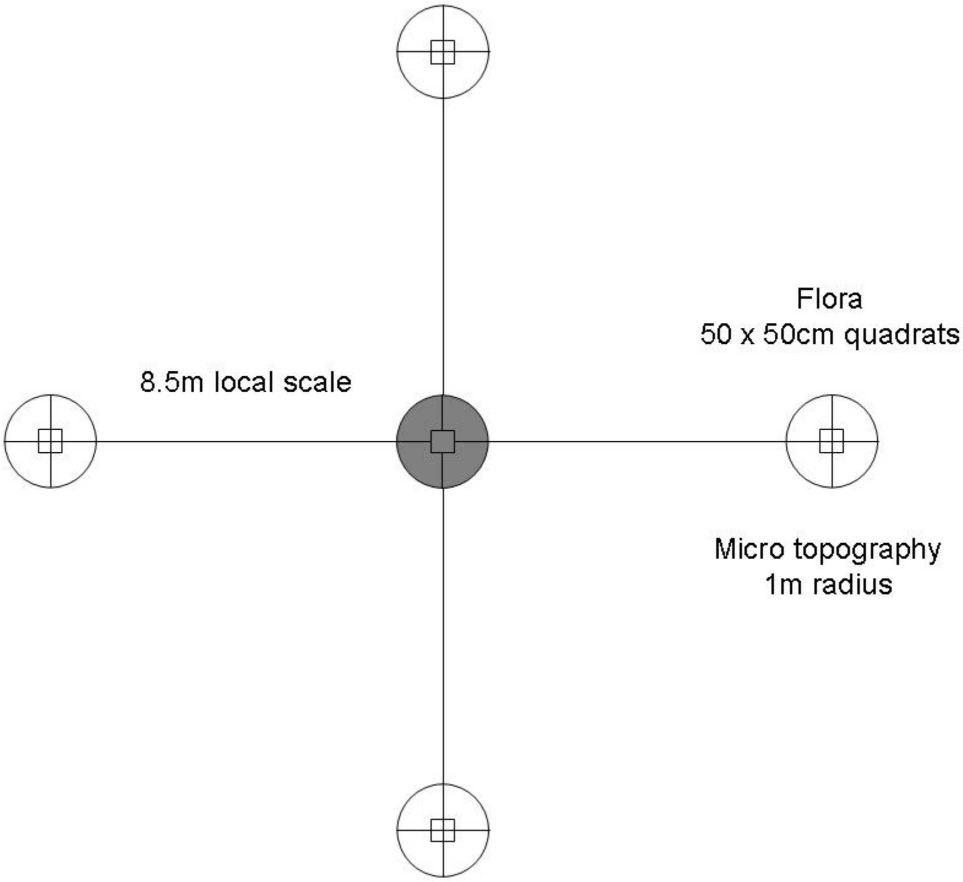

Figure B. Local scale habitat sampling design. The grey site represents the position of the lemming nest.

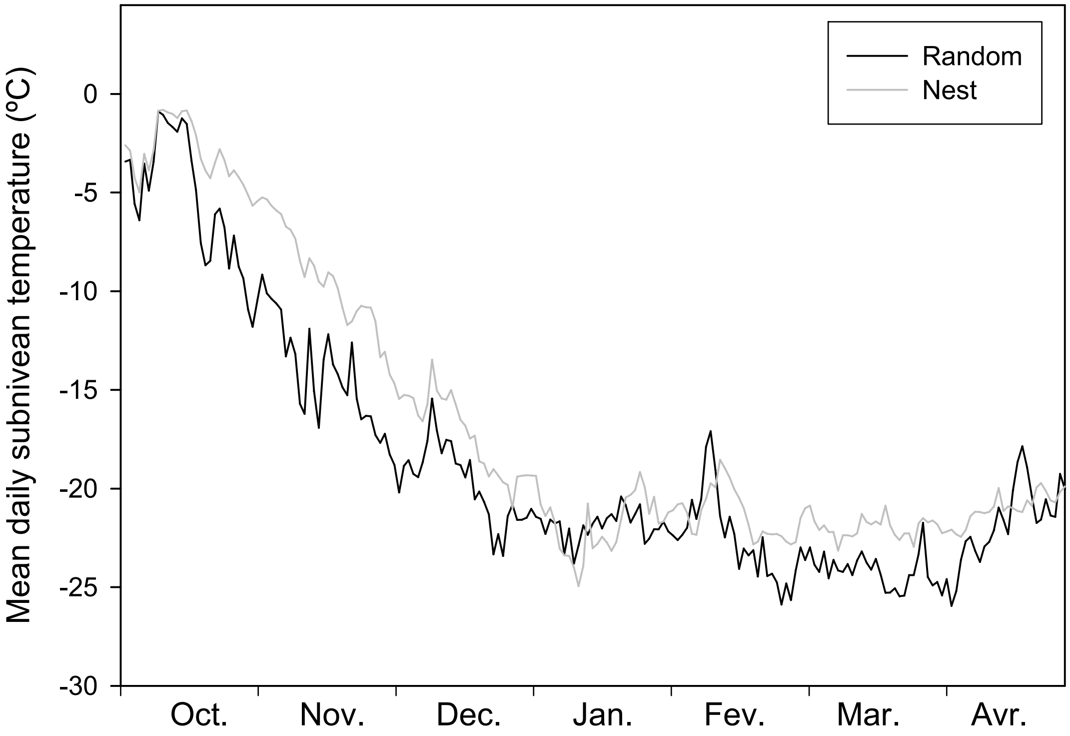

Figure C. Evolution of the mean subnivean temperature at random and real lemming winter nest sites during winter 2007-2008 on the south plain of Bylot Island, Sirmilik National Park, Nunavut, Canada (n = 15 loggers for each treatment).