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Introduction

Changements dans l’écosystème arctique

Les écosystèmes de la planète sont en évolution continuelle, mais récemment le rythme des changements semble s’être accéléré et ceci serait en partie imputable aux changements climatiques (Callaghan 2004, IPCC 2007). On remarque un accroissement des températures au niveau planétaire, particulièrement dans l’Arctique (IPCC 2007, Hannah 2011). Le régime de précipitation aux latitudes élevées devrait aussi subir des changements importants. On s’attend à une augmentation des précipitations sous forme de pluie pour l’hiver, l’automne et le printemps (IPCC 2007). Cette augmentation sera associée à une plus courte période avec présence d’un couvert nival et une diminution de la qualité de celui-ci (Callaghan et al. 2004, Kohler et Aanes 2004, Derksen et Brown 2012; voir section « Écologie hivernale des populations de lemmings et couvert nival » pour une définition de qualité de la neige). Ces altérations abiotiques sont susceptibles de créer des impacts majeurs sur les écosystèmes arctiques (Callaghan et al. 2004, Ims et Fuglei 2005, Ims et al. 2008). Les variations de la qualité du couvert nival vont influencer directement les paramètres démographiques de certaines espèces dans l’Arctique (Courtin et al. 1991, Hörnfeldt 2004, Ims et al. 2008, Kausrud et al. 2008) et perturber les interactions trophiques (Aars et Ims 2002, Callaghan et al. 2004, Mech 2004, Ims et Fuglei 2005). Par exemple, un déclin drastique de certaines populations de caribou (*Rangifer tarandus*) et de bœuf musqué (*Ovibos moschatus*) dû à un couvert nival de mauvaise qualité, notamment par l’entremise de la formation d’une couche de glace au sol, a été documenté (Forchhammer et Boertmann 1993, Miller et Gunn 2003, Kohler et Aanes 2004, Chan et al. 2005). Les changements climatiques prennent de l’ampleur et de telles altérations dans le climat sont susceptibles d’avoir des répercussions sur tous les écosystèmes de l’Arctique. Cependant, nos connaissances face aux impacts potentiels qu’auront ces derniers sur la faune et la flore, surtout en hiver, restent assez limitées.

Cycle de population des micromammifères dans l’Arctique

Dans l’Arctique, les micromammifères et en particulier les lemmings (*Lemmus* spp. et *Dicrostonyx* spp) constituent un maillon important de la chaîne alimentaire. Ils sont parmi les herbivores les plus abondants des régions nordiques (Gauthier et al. 2004) et sont également la principale proie pour la majorité des prédateurs mammaliens et aviaires (Krebs et al. 2003, Ims et Fuglei 2005). Bien que les rongeurs aient une courte durée de vie, leur potentiel de croissance de population est très élevé car ils atteignent la maturité sexuelle rapidement et peuvent se reproduire plusieurs fois par année (Millar 2001).

Les rongeurs des régions nordiques sont connus pour subir des fluctuations d'abondance interannuelles très importantes (Krebs 1996, Pitelka et Batzli 2007). Ces fluctuations d'abondance sont généralement caractérisées par de très fortes amplitudes entre les pics et les creux, pouvant atteindre un facteur de 100 (Korpimäki et Krebs 1996, Boonstra et al. 1998) et sont souvent régulières avec une périodicité variant de 3 à 5 ans (Krebs 1996, Getz 2006a, Gruyer et al. 2008). Ces deux éléments permettent de qualifier les fluctuations d'abondance des rongeurs de l'Arctique comme étant des cycles de population (Krebs 1996). À l'échelle locale, c'est-à-dire sur un même site dont la superficie peut varier de centaines ou de milliers de km^2, les différentes espèces de micromammifères auraient tendance à avoir des cycles synchrones (Korpimäki et Krebs 1996, Krebs et al. 2002, Gruyer et al. 2008). Par contre, ces cycles d'abondance peuvent varier dans le temps et l'espace entre les populations d'une même espèce (Reid et al. 1997, Erlinge et al. 1999, Angerbjörn et al. 2001). Il existerait un gradient latitudinal en relation avec le couvert nival où les populations au nord auraient tendance à subir des cycles d'abondance interannuels de plus fortes amplitudes que celles plus au sud (Hansson et Henttonen 1985, Stenseth et Ims 1993b, Hanski et al. 2001, Ims et al. 2008). Depuis deux décennies, on assiste toutefois à la disparition des cycles de petits mammifères dans certaines régions de l'Arctique dont en Scandinavie (Ims et Fuglei 2005, Ims et al. 2008) et au Groenland (Gilg et al. 2009), un phénomène encore mal compris mais où les changements climatiques pourraient jouer un rôle (voir section « Écologie hivernale des populations de lemmings et couvert nival »).

Facteurs pouvant expliquer les cycles d'abondance

Depuis qu'Elton (1924) a décrit les cycles de population chez les petits mammifères, plusieurs scientifiques ont tenté et tentent toujours d'élucider leurs causes. De nombreuses hypothèses ont été formulées pour expliquer ce phénomène, mais aucun consensus n'a encore été atteint (Stenseth et Ims 1993b, Krebs 1996, Gauthier et al. 2009). Malgré le fait qu'on peut considérer l'écosystème arctique comme simplifié par rapport à ceux des latitudes plus basses, celui-ci demeure difficile à étudier, spécialement en hiver.

Les séries temporelles historiques provenant de Scandinavie et d'Alaska nous démontrent que les cycles d'abondance de lemmings semblent être réguliers depuis longtemps (i.e. plus de 50 ans) (Stenseth 1999, Pitelka et Batzli 2007). Pour que les cycles soient aussi réguliers à long terme, il est peu probable qu'ils soient dus à des effets indépendants de la densité (Krebs 2001), quoique ceux-ci aient sûrement un rôle à jouer dans la fréquence et l'amplitude des cycles (Hörnfeldt 2004). Ces effets environnementaux jouent probablement un rôle dans l'amplification ou l'atténuation des autres facteurs pouvant limiter les populations de lemmings (Stenseth 1999, Ims et Fuglei 2005).

Les facteurs dépendants de la densité qui peuvent limiter les populations de petits mammifères sont soit de nature externe, comme la prédation, ou intrinsèque, comme des changements qualitatifs ou génétiques chez les individus (Krebs 1996, Boonstra et Hochachka 1997). Par contre, quels que soient les facteurs responsables de ces cycles, il semble admis que ces facteurs doivent agir avec délai sur les processus démographiques afin de générer une dynamique cyclique (Stenseth 1999, Krebs 2001, Begon et al. 2006, Gilg et al. 2009, Inchausti et Ginzburg 2009). Certains auteurs ont suggéré que les populations de lemmings pourraient s'autoréguler (Stenseth et al. 1996, Boonstra et Hochachka 1997). Ceci peut être possible si le taux de croissance intrinsèque diminue avec l'augmentation de la densité (Krebs 2001). Cette diminution pourrait s'opérer de plusieurs façons. L'augmentation des interactions sociales pourrait faire augmenter le stress dans la population et engendrer des effets comportementaux, comme l'interférence (Sutherland 1996) ou des effets physiologiques et/ou génétiques qui pourraient avoir des répercussions à long terme sur les individus (Krebs 1996, Sinclair et al. 2003). Pour l'instant, les preuves empiriques que les lemmings sont limités par des facteurs intrinsèques sont relativement minces (Boonstra et al. 1998, Stenseth 1999) quoique le rôle des effets maternels dans la dynamique cyclique de plusieurs espèces aurait pu être sous-estimé (Inchausti et Ginzburg

2009). Les parasites peuvent également avoir une forte influence sur la dynamique de populations animales, notamment chez les Tétraonidés (Cattadori et al. 2005, Holmstad et al. 2005). Malheureusement, pratiquement aucune information n'existe sur l'effet des parasites sur les populations des micromammifères de l'Arctique (voir Pedersen et Greives 2008 pour un exemple en zone tempérée).

En ce moment, deux hypothèses jouissent d'un plus grand support, celle où les cycles de petits mammifères nordiques seraient dus aux interactions prédateurs-proies, donc à un contrôle par le haut du réseau trophique (Korpimäki et Krebs 1996, Reid et al. 1997, Angerbjörn et al. 1999, Hanski et al. 2001, Korpimäki et al. 2005, Gilg et al. 2006) et celle où ils seraient plutôt dus aux interactions plantes-herbivores, donc à un contrôle par le bas (Turchin et al. 2000, Turchin et Batzli 2001, Pitelka et Batzli 2007, Oksanen et al. 2008).

Interactions plantes-herbivores et cycles de population

Selon l'hypothèse du contrôle par les ressources ou producteurs primaires (i.e. végétaux), l'abondance des herbivores serait déterminée par l'abondance et la disponibilité des ressources alimentaires (Polis et Strong 1996, Polis 1999). Dans l'Arctique, où la productivité primaire est faible (Gauthier et al. 1996), cette interaction plante/herbivore devrait, selon cette hypothèse, être dominante dans le contrôle de la dynamique des populations d'herbivores (Pitelka et Batzli 2007, Oksanen et al. 2008). Les lemmings sont sélectifs dans leur choix de nourriture et s'alimentent de plantes à faible valeur digestive (Batzli et Cole 1979, Batzli et Jung 1980, Hickie et al. 1982, Negus et Berger 1998), ce qui les obligent à rechercher de la nourriture continuellement pour survivre (Searle et al. 2006) et pour se reproduire. Les ressources peuvent devenir limitantes lorsque le nombre de lemmings dépasse la capacité de support de leurs milieux. Certains chercheurs ont des raisons de suspecter que la population déclinerait par épuisement des ressources et que ceci serait suffisant pour générer les cycles de population (Moen et al. 1993, Moen et Oksanen 1998, Huitu et al. 2003, Pitelka et Batzli 2007, Olofsson et al. 2012). Notamment, dans les montagnes de Finlande, des signes de broutement sévère par le lemming de Norvège (*Lemmus lemmus*) ont été détectés lors d'une année de pic modéré, suggérant que les ressources alimentaires pourraient limiter les populations de lemming (Virtanen et al. 2002).

Il a aussi été suggéré que le manque d'accessibilité à la nourriture durant la saison hivernale puisse entraîner un déclin des populations (Korslund et Steen 2006). Toutefois, cette dernière hypothèse, qui n'implique pas nécessairement un épuisement des ressources, peut être difficile à vérifier car son effet serait modulé par un facteur externe, le climat. Une autre hypothèse alternative pour expliquer le cycle via le contrôle par les ressources est que la qualité nutritive des plantes soit réduite (Seldal et al. 1994, Pitelka et Batzli 2007) et entraîne par conséquent une réduction de la survie ou du taux de reproduction chez les lemmings. En présence de broutement intense, les plantes peuvent augmenter leur défense chimique en générant une plus grande quantité de composés secondaires (phénols ou autres) ce qui diminuerait leur palatabilité et leur digestibilité (Clausen et al. 1989). Par contre, aucune relation n'a encore été établie entre la diminution de la qualité des ressources alimentaires et la baisse de densité durant la phase de déclin du cycle (Jonasson et al. 1986, Getz et al. 2006b).

Interactions prédateurs-proies et cycles de population

La deuxième hypothèse, selon laquelle les populations d'herbivores sont régulées par les prédateurs, semble être mieux supportée pour expliquer les cycles d'abondance des lemmings. De nombreuses études ont mis en cause l'effet de la prédation comme initiateur du cycle des lemmings (Korpimäki et Krebs 1996, Reid et al. 1997, Angerbjörn et al. 1999, Wilson et al. 1999, Hanski et al. 2001, Gilg et al. 2003, Korpimäki et al. 2005). La capacité de reproduction des lemmings est tellement élevée (taux de croissance potentiel maximal étant estimé à 2.44% par jour; Stenseth et Ims 1993a) que la prédation par les spécialistes résidents (i.e. les mustélidés) semble être insuffisante à elle seule pour contrôler le cycle (Angerbjörn et al. 1999, Hanski et al. 2001). Il est donc nécessaire, pour amorcer la phase de déclin du cycle durant l'été, que la pression de prédation exercée provienne de plusieurs espèces de prédateurs en plus de l'hermine (*Mustela erminea*), notamment le renard arctique (*Vulpes lagopus*) et plusieurs espèces de rapaces (Korpimäki et al. 2005). Cette pression excèderait alors le taux de recrutement des lemmings et contribuerait à faire diminuer l'abondance tout au long de la saison estivale (Reid et al. 1995, Gilg 2002, Gilg et al. 2006).

Étant le seul prédateur pouvant avoir facilement accès aux lemmings dans leurs tunnels durant l'hiver (Bjørnstad et al. 1995, Sittler 1995, Krebs et al. 2003, King et Powell 2007), l'hermine jouerait un rôle clé dans le cycle d'abondance en maintenant les populations de lemmings à basse densité après que les prédateurs aviaires aient quitté pour l'hiver (Hanski et al. 2001, Gilg et al. 2006, Gilg et al. 2009). L'hermine, avec des portées moyennes de 8 à 10 jeunes, a un fort potentiel reproductif (King et Powell 2007) et elle répondrait numériquement de façon décalée à l'augmentation d'abondance des lemmings (Sittler 1995, Klemola et al. 1999, Gilg et al. 2006). Elle aurait également une forte réponse fonctionnelle puisqu'en présence de hautes densités de proies elle augmenterait de façon disproportionnée son taux de capture afin de se faire des réserves de nourriture en prévision d'un déclin de population de sa proie (Jędrzejewska et Jędrzejewski 1989, King et Powell 2007).

L'hermine serait aussi susceptible d'inhiber indirectement la reproduction chez les rongeurs en engendrant un niveau de stress élevé. À haute densité de prédateurs, les rongeurs limiteraient leurs activités afin de mieux échapper à la prédation (Henttonen et al. 1987, King et Powell 2007). Chez le lièvre d'Amérique (*Lepus americanus*), l'élévation du stress due à de fortes densités de prédateurs peut se propager aux jeunes via des effets maternels et inhiber la reproduction sur plus d'une génération, accentuant ainsi l'impact des prédateurs (Sinclair et al. 2003). Certains chercheurs ont également observé que les hermines sélectionneraient comme proies les femelles allaitantes et les nids avec des jeunes (Sittler 1995), probablement parce que ceux-ci sont moins mobiles et donc plus facilement repérables à l'odorat, ce qui amplifierait leur impact. L'hermine pourrait donc maintenir à basse densité les populations de lemmings durant les années suivant le pic jusqu'au déclin de leur propre population (Hanski et al. 2001, Gilg et al. 2006) dû au manque éventuel de nourriture.

La faible abondance de prédateurs aviaires comme le harfang des neiges (*Bubo scandiaca*) et le labbe à longue queue (*Stercorarius longicaudus*) durant la saison hivernale jouerait aussi un rôle dans les cycles d'abondance des micromammifères (Hanski et al. 2001). Une faible pression de prédation hivernale sur les petits mammifères suite à la diminution des populations d'hermines lors du creux permettrait d'amorcer la remontée de leur nombre. Un exemple de la situation inverse nous est livré à Pearce Point (TN) où les lemmings variables (*Dicrostonyx groenlandicus*) ne sont pas cycliques probablement parce que les populations de prédateurs peuvent se maintenir durant toute l'année à l'aide de proies alternatives (Reid et al. 1997).

Habitats utilisés par les lemmings et compétition

Dans l'Arctique canadien, deux espèces de lemmings se côtoient habituellement, le lemming brun (*Lemmus trimucronatus*) et le variable (Jarrell et Fredga 1993). Lorsque les deux espèces coexistent, le lemming brun montre habituellement de fortes fluctuations d'abondance, tandis que celles du variable sont beaucoup plus modérées (Batzli et al. 1983, Negus et Berger 1998, Gruyer et al. 2008).

Les deux espèces démontrent une certaine ségrégation au niveau de l'habitat durant l'été. Les lemmings bruns préféreraient des habitats plus humides que les variables (MacLean et al. 1974, Batzli et al. 1983), mais il est possible que ces derniers soient partiellement exclus de ces habitats par les lemmings bruns plus compétitifs (voir plus bas). En effet, l'utilisation de l'habitat par les lemmings variables semble plus limitée lors des années de pic d'abondance de lemmings bruns comparée aux années de creux de cette espèce. La différence majeure dans leur utilisation de l'habitat proviendrait toutefois de leurs préférences alimentaires (Batzli 1993, Rodgers et Lewis 1985). Les lemmings bruns préfèreraient les monocotylédones et les lemmings variables les dicotylédones (Rodgers et Lewis 1985), mais une étude récente à l'Île Bylot montre cependant que les deux espèces peuvent s'alimenter en grande partie de Salicaceae, une dicotylédone abondante dans l'Arctique canadien (E. Soininen et G. Gauthier, communication personnelle). En hiver, les deux espèces de lemmings partageraient néanmoins les mêmes habitats, principalement les milieux mésiques et le long des ravins formés par les cours d'eau (Duchesne et al. 2011b). Au printemps, les lemmings bruns passeraient d'habitats plus élevés et plus secs, à des habitats plus humides et plus bas après les inondations causées par la fonte de la neige (Batzli et al. 1983, Pitelka et Batzli 1993).

La compétition entre les espèces sympatriques de lemmings semble davantage se manifester au niveau de l'espace plutôt que des ressources alimentaires (Hansson et Henttonen 1985, Morris et al. 2000), la compétition serait donc sous forme d'interférence (Morris et al. 2000). En effet, les expériences de Morris et al. (2000) montrent que la sélection de l'habitat par le lemming brun en été (i.e. préférence pour les milieux humides) ne serait pas influencée par la densité de lemming variable, tandis que celle du lemming variable, qui tend à se distribuer dans tous les habitats à faible densité de brun, serait influencée par la densité de *Lemmus*. Ces résultats supportent l'hypothèse que le lemming brun pourrait exclure le variable de son habitat préféré par interférence.

Il est aussi possible que la prédation et la compétition interspécifique interagissent ensemble. Chez les rongeurs, l'espèce compétitivement dominante (habituellement la plus grosse) est souvent plus vulnérable à la prédation ou préférée par les prédateurs, comme c'est le cas pour plusieurs espèces de campagnols en Scandinavie (Hanski et Henttonen 1996). Toutefois, chez les lemmings, la situation inverse semble prévaloir car les lemmings variables (i.e. l'espèce potentiellement dominée) subissent apparemment des taux de prédation plus élevés que les bruns, même en période de forte abondance de lemmings bruns (Duchesne et al. 2011b, Therrien 2012). Quelle que soit la raison, il semble établi que les lemmings variables subissent une plus forte pression de prédation que les lemmings bruns en tout temps.

Écologie hivernale des populations de lemmings et couvert nival

Les lemmings sont actifs tout l'hiver et ils sont mieux adaptés aux conditions hivernales de l'Arctique que les autres espèces de rongeurs (Stenseth et Ims 1993a). Ceci est particulièrement vrai pour le lemming variable qui montre des adaptations physiologiques plus marquées comme une grande résistance aux chocs hypothermiques (Batzli et al. 1983, Malcolm et Brooks 1993, Stenseth et Ims 1993c). Pendant la période hivernale, qui peut durer jusqu`à 9 mois aux hautes latitudes, les lemmings sont confinés sous le couvert nival où les effets du froid et possiblement de la prédation sont moins ressentis (Gilg et al. 2006, Korslund et Steen 2006, Kausrund et al. 2008, Duchesne et al. 2011b). Les lemmings ont aussi la capacité de se reproduire sous la neige durant l'hiver (Millar 2001, Stenseth et Ims 1993b). La majorité des informations sur la période hivernale nous provient des nids d'hiver construits par les lemmings (MacLean et al. 1974, Sittler 1995, Duchesne et al. 2011b) afin de mieux s'isoler des températures très froides et sauver de l'énergie (Casey 1981). La sélection du site pour l'emplacement des nids d'hiver semble être grandement influencée par la topographie, avec une préférence marquée pour les dépressions et les endroits où la neige est plus épaisse (Sittler 1995, Duchesne et al. 2011b, Reid et al. 2012). MacLean et al. (1974) ont observé que les nids les plus gros et les mieux isolés étaient ceux où il y avait de la reproduction et que les nids plus petits n'abritaient que des adultes, probablement des mâles ou des femelles non reproductrices.

Une conséquence de leur fort potentiel de reproduction en hiver combiné avec un taux de prédation relativement faible serait que les densités les plus hautes sont atteintes à la fin de la saison hivernale (Henttonen et Kaikusalo 1993, Gilg et al. 2002, Ims et Fuglei 2005, Getz et al. 2006a). Au contraire, la forte pression de prédation subie après la disparition du couvert nival causerait le plus souvent une chute de population estivale (Stenseth et Ims 1993b, Gilg et al. 2006). Le couvert nival pourrait donc être un facteur ayant une grande influence sur la démographie des lemmings (Ims et Fuglei 2005, Kausrud et al. 2008). Les variations des caractéristiques du couvert nival peuvent affecter la qualité et la sélection de l'habitat hivernal (Reid et al. 2012), qui à son tour peut influencer la survie, spécialement celle des jeunes nés durant l'hiver, et possiblement aussi la reproduction (Yoccoz et Ims 1999, Aars et Ims 2002). Le couvert nival peut également affecter la démographie en réduisant la disponibilité de la nourriture, notamment lorsqu'une couche de glace se forme au sol ou en limitant l'accès aux prédateurs (Ims et Fuglei 2005, Kausrud et al. 2008, Gilg et al. 2009, Duchesne et al. 2011b). Plusieurs considèrent d'ailleurs qu'un couvert nival de qualité est une condition essentielle pour avoir une explosion de population menant à un pic d’abondance de lemmings (MacLean et al. 1974, Aars et Ims 2002, Korslund et Steen 2006, Ims et al. 2008, Kausrud et al. 2008).

Pour être considéré de bonne qualité, pour un micromammifère, un couvert de neige devrait posséder certaines caractéristiques. Premièrement il devrait permettre la formation d’une couche de neige de faible densité ainsi qu’un espace sous-nival à sa base, qui faciliterait le fouissage ainsi que la circulation d’air et permettrait assez d’espace pour que les micromammifères l’habitent et s’y nourrissent (McKay et Adam 1981, Marchand 1996, Sanecki et al. 2006). Deuxièmement, il devrait isoler les micromammifères des variations extrêmes des températures externes et des événements météorologiques les plus froids (Pomeroy et Brun 2001, Duchesne et al. 2011b, Reid et al. 2012). Troisièmement, il devrait empêcher la formation de glace au sol dû aux pluies hivernales et aux épisodes de gel et dégel (Korslund et Steen 2006). Quatrièmement, il devrait persister assez longtemps pour que les effets positifs mentionnés plus haut soient ressentis tout au long de la saison froide.

En dépit du rôle clé que pourrait jouer la période hivernale et son couvert nival dans la dynamique des populations de lemmings, elle demeure très peu étudiée comparée à la courte période estivale. La survie des petits mammifères pourrait être grandement affectée par le climat lors des périodes précédant l’établissement d’une couche de neige permanente, surtout si celle-ci tarde à s’installer à l’automne, puisqu’ils ne sont ni isolés des températures extrêmes ni protégés des prédateurs (Courtin et al. 1991, Ims et al. 2008). Au printemps, une fonte de neige accélérée pourrait aussi augmenter les risques d’inondation dans les tunnels et ainsi avoir des répercussions négatives sur la survie et la reproduction (Courtin et al. 1991).

Plusieurs ont suggéré qu’un couvert nival de mauvaise qualité dû au réchauffement climatique pourrait être la cause de la perte de cyclicité rapportée plus haut chez certaines populations nordiques (Aars et Ims 2002, Hörnfeldt et al. 2005, Ims et al. 2008, Gilg et al. 2009). En particulier, les épisodes de pluie hivernale ou verglaçante ainsi que l’alternance de périodes de gel et dégel durant l’hiver pourraient avoir des conséquences néfastes sur les populations de lemmings en entraînant l’effondrement de l’espace sous-nival (Callaghan et al. 2004) et en diminuant la qualité du couvert nival (Aars et Ims 2002, Korslund et Steen 2006). La compaction et la cristallisation de la neige dues aux phénomènes mentionnés précédemment réduiraient en effet la capacité isolante de celle-ci (Pomeroy et Brun 2001) et la diminution de l'épaisseur du couvert nival rapprocheraient les températures de l'espace sous-nival de celles de l'extérieur (Taylor et Buskirk 1996). Ces phénomènes climatiques stimuleraient également la formation de glace au sol ce qui limiterait l'accessibilité aux ressources alimentaires en encapsulant les plantes dans la glace (Forchhammer et Boertmann 1993, Kohler et Aanes 2004, Korslund et Steen 2006, Stien et al. 2012).

Le modèle d'étude : les lemmings à l'île Bylot

L'île Bylot au Nunavut constitue un écosystème terrestre arctique relativement complexe où une large communauté de prédateurs et de proies interagissent entre eux (Gauthier et al. 2004, 2011). Sur ce site, deux espèces de lemmings sont sympatriques, le brun et le variable (Gruyer et al. 2008; Fig. 1.1). Les deux espèces sont caractérisées par des cycles interannuels d'une périodicité de trois ou quatre ans (Stenseth et Ims 1993b, Gruyer et al. 2008) et leurs abondances varient généralement en synchronie (Krebs et al. 2002, Gruyer et al. 2008). À l'île Bylot, le cycle des lemmings bruns est représenté par des variations d'abondance de très forte amplitude (>40 fois) et celui des lemmings variables par des variations de faible amplitude (~4 fois; Gruyer et al. 2008). En 2004-2005, Gruyer et al. (2010) a rapporté des densités estivales moyennes relativement faibles de 0,5 à 2,4 individus/ha pour le brun et 0,4 à 0,5 individus/ha pour le variable à l'île Bylot. Toutefois, le suivi à long terme à ce site a depuis montré que les densités pouvaient atteindre 20 individus/ha ou plus pour le brun lors de pics d'abondance (Krebs et al. 2012). Ces données sont comparables avec celles obtenues à Atkasook en Alaska, où le lemming brun et le variable sont présents et à Pearce Point aux Territoires du Nord-Ouest où l'on retrouve seulement le lemming variable (Batzli et Jung 1980, Krebs et al. 1995, Reid et al. 1995). Au Groenland, où seulement le lemming variable est aussi présent, les densités sont également comparables (de < 0,1 individus/ha à ~12 individus/ha; Gilg 2002, Gilg et al. 2006). Des densités beaucoup plus élevées durant les années de pic ont par contre été observées à Barrow en Alaska pour le lemming brun (>100 individus/ha; Pitelka et Batzli 2007). La comparaison des densités entre les sites d'étude est toutefois très difficile à faire à cause de différences dans les méthodes d'estimation et le choix des sites pour mesurer l'abondance.

Une grande diversité de prédateurs aviaires (rapaces, labbes, goélands) et mammaliens (renards, hermines) consomment les lemmings à l'Île Bylot et certains prédateurs spécialistes comme l'hermine (Fig. 1.2), le harfang des neiges et la buse pattue s'en alimentent presqu'exclusivement (Gauthier et al. 2011, Gilg et al. 2006, Therrien 2012). L'abondance annuelle des prédateurs spécialistes est grandement influencée par les fluctuations d'abondance de ces rongeurs (Gauthier et al. 2004, Gilg et al. 2006, Therrien 2012, Legagneux et al. 2012). Parmi les prédateurs généralistes (i.e. qui s'alimentent de proies alternatives en faible abondance de lemming), le renard arctique (Fig. 1.3), qui réside à l'année dans l'Arctique, semblerait être le plus affecté par le cycle des lemmings et répondrait numériquement de façon instantanée aux fluctuations d'abondance (Gauthier et al. 2004, Tarroux et al. 2012). Pour les prédateurs généralistes, les œufs et les jeunes de la grande oie des neiges (*Chen caerulescens atlantica*), un herbivore qui se reproduit en abondance sur ce site en été, sont aussi une proie importante, surtout durant les années de creux de lemmings (Bêty et al. 2002, Gauthier et al. 2004).

Présentement, pour l'île Bylot, on possède peu d'information sur les effets du climat sur les populations de lemmings, sur la prédation par l'hermine et par le renard arctique lorsque le couvert nival est présent et sur l'utilisation de l'habitat et des ressources alimentaires durant cette période.

Objectifs de la thèse

La littérature sur les populations cycliques de petits mammifères est extrêmement vaste et plusieurs générations de scientifiques les ont étudiées (Krebs 1996). Cependant, le jour où un chercheur élucidera complètement le phénomène de cyclicité chez ces rongeurs semble encore loin et représente un Saint Graal de l'écologie. De plus, l'hiver, considéré comme une période importante pour les rongeurs de l’arctique, reste un trou noir de connaissances et c’est pourquoi, pour faire suite aux travaux de Duchesne et al. (2011a, b), mon projet s’intéresse principalement à l’écologie hivernale des lemmings.

L’objectif principal de cette thèse est d’évaluer le rôle du couvert nival, de la prédation par l’hermine et le renard arctique et des ressources alimentaires pendant la période hivernale sur le cycle d’abondance et les paramètres démographiques des lemmings bruns et variables à l’île Bylot. Plus spécifiquement, mon projet vise à évaluer 1) les effets de l’augmentation expérimentale de l’épaisseur du couvert nival sur les paramètres démographiques des petits mammifères de l’arctique, 2) l’effet de la qualité et de la persistance de la neige sur l’amplitude et la fréquence du cycle des lemmings, 3) l’impact du broutement par les lemmings sur la végétation pendant la période hivernale, 4) l’effet de l’épaisseur et de la dureté de la neige sur la prédation par l’hermine et le renard, ainsi que 5) la pression de prédation exercée par l’hermine pendant les périodes hivernales et estivales sur les deux espèces de lemmings. Un sixième objectif, qui consistait à déterminer les patrons de déplacement et d’utilisation de l’habitat des lemmings durant la période critique de fonte de la neige au printemps, n’a pas pu être réalisé mais a quand même permis l’évaluation d’une technique de trappage des lemmings sous la neige. Les résultats obtenus lors de cette thèse permettent de mieux comprendre l’écologie hivernale des lemmings et d’améliorer nos connaissances sur les mécanismes derrière le fonctionnement des cycles d’abondance des micromammifères.

Organisation de la thèse

Le premier chapitre évalue les effets de l’augmentation expérimentale du couvert de neige sur divers paramètres démographiques des lemmings et campagnols (*Microtus oeconomus*), ainsi que sur la prédation par l’hermine et la petite belette (*Mustela nivalis*). Testée sur trois sites différents de l’Arctique canadien et donc le fruit d’immenses efforts sur le terrain et d’une collaboration entre plusieurs chercheurs, cette étude est la première à répondre aux questions relatives à l’effet direct de la neige sur la démographie à l’aide d’un dispositif expérimental. Un premier volet de cette expérience s’adressant à la sélection de l’habitat a aussi fait l'objet d'un article publié dans *Oecologia* et dont je suis co-auteur, (voir Reid et al. 2012).

Le deuxième chapitre évalue quant à lui l'effet de la qualité et de la persistance de la neige sur les amplitudes et la fréquence du cycle du lemming brun. Très peu d'études ont tenté d'expliquer les effets qu'ont les différentes caractéristiques de la neige sur les fluctuations d'abondance des petits mammifères. Contrairement à d'autres études qui ont intégré directement des paramètres climatiques dans des équations permettant de modéliser le cycle et qui tentaient donc d'expliquer directement les mécanismes générant le cycle, j'ai plutôt simulé des cycles d'abondance pour voir ensuite comment divers paramètres reliés à la neige pouvaient expliquer la différence entre les cycles simulés et observés. J'ai pu ainsi vérifier directement quels sont les effets du couvert nival sur le cycle, sans tenter d'expliquer les causes de celui-ci.

Le troisième chapitre est une note où j'évalue une technique de trappage de petits mammifères sous la neige. Communiquer les échecs, autant que les succès est une phase critique pour améliorer les techniques utilisées en écologie, spécialement lorsque des données empiriques permettent d'expliquer les causes possibles de l'échec. Ceci devient particulièrement important quand des investissements significatifs en temps, comme dans notre cas, et financiers sont déployés.

Le quatrième chapitre aborde une question relative à l'hypothèse du contrôle par le bas. Dans ce chapitre, j'évalue un des prérequis pour cette hypothèse, soit que lors de la saison froide, lorsque les plantes ont cessé de croître, on devrait détecter un impact significatif des lemmings sur la végétation. L'expérience a été menée dans les habitats hivernaux préférés des lemmings, les combes à neige en bordure de ravins et en milieu mésique, donc aux endroits où l'impact sur la végétation devrait être maximal.

Le cinquième chapitre traite de l'effet de la neige sur la prédation sur les lemmings par l'hermine et le renard arctique. Beaucoup d'études avancent l'hypothèse, trop souvent utilisée de façon spéculative, que la neige a un effet négatif sur la prédation par le renard, mais pas nécessairement par celle exercée par l'hermine. Pour répondre à cette question, j'évalue donc dans ce chapitre l'effet qu'ont l'épaisseur et la dureté de la neige sur les probabilités de prédation par ces deux prédateurs.

Finalement, le sixième chapitre s'attaque à l'hypothèse du contrôle par le haut. L'hermine est le seul prédateur contraint à rester sur le site lors de l'hiver et est donc potentiellement le seul pouvant maintenir une pression de prédation pendant cette saison, puisque le renard peu quitter la terre ferme pour la banquise (Soper 1944, Chesemore 1968, Tarroux et al. 2010). L'hermine pourrait avoir un rôle critique dans la dynamique du cycle des lemmings. Cependant la prédation exercée par ces prédateurs reste très peu étudiée. Dans ce chapitre, j'évalue les patrons de prédation de ce prédateur sur les populations de lemmings et j'estime, à partir d'observations estivales, la réponse totale potentielle de ce prédateur.

Figure 1. En haut, lemming brun juvénile (A) et adulte (B). En bas, lemming variable. Le dos du lemming brun est brun et celui du variable est gris argenté alors que le ventre est roux chez les deux espèces. La ligne noire sur le dos est caractéristique du variable (C) et ses griffes avants sont très développées (D) comparativement à celles du brun. Photo A prise par Stéphanie Pellerin, photos B, C et D prises par Hugo Mailhot-Couture.

Figure 2. Hermine mâle juvénile en pelage d'été, photographiée près d'une tanière à l'île Bylot en 2010 par Étienne Godin.

Figure 3. Renard arctique adulte en pelage d'été et marqué avec des étiquettes d'oreilles et un émetteur satellite Argos. Photo prise par Meggie Desnoyers.

Chapitre 1

Demographic response of tundra small mammals to a snow fencing experiment

Bilodeau, F., Reid, D.G., Gauthier, G., Krebs, C.J., Berteaux, D. & Kenney, A.J. 2013. Demographic response of tundra small mammals to a snow fencing experiment. Oikos (in press). doi: 10.1111/j.1600-0706.2012.00220.x.

Résumé

Le couvert de neige constitue un élément environnemental clé pour la faune de la toundra qui va être affecté par les changements climatiques. L'altération du couvert de neige pourrait affecter la dynamique des populations de petits mammifères aux hautes latitudes, qui sont actifs tout l'hiver et se reproduisent sous la neige. Nous avons testé expérimentalement l'hypothèse qu'un couvert de neige plus épais augmenterait les densités et les taux de reproduction hivernale, mais que la prédation par les mustélidés pourrait être plus élevée aux endroits où les densités de petits mammifères sont plus élevées. Nous avons augmenté l'épaisseur du couvert de neige en installant des clôtures à neige sur trois sites dans l'Arctique Canadien (Île Bylot, Nunavut, l'Île Herschel et Komakuk Beach, Yukon) sur des périodes variant de 1 à 4 années. Les densités de nids d'hiver étaient plus élevées là où le couvert de neige avait été augmenté, mais les densités au printemps n'ont pas augmenté dans les zones expérimentales. Les lemmings se déplacent probablement des zones de fort enneigement, leurs habitats hivernaux préférés, vers leurs habitats estivaux pendant la période de fonte de la neige, lorsque les avantages associés à un couvert de neige plus épais sont disparus. Notre traitement n'a pas eu d'effet sur les signes de reproduction dans les nids d'hiver, sur la proportion de femelles reproductrices ni sur la proportion de juvéniles capturés au printemps, ce qui suggère que le couvert de neige plus épais n'a pas augmenté la reproduction. Nos résultats sur la prédation étaient incohérents à travers les sites puisque la prédation par les mustélidés était plus élevée dans la zone expérimentale pour un site, mais plus basse aux deux autres sites et n'était pas plus élevée dans les agrégations de nids. Bien que cette expérience nous a procuré plusieurs pistes sur l'impact qu'a le couvert de neige sur la dynamique des populations des petits mammifères de la toundra, elle nous a aussi exposé les défis et les difficultés associés avec des expériences à grande échelle ayant pour but de manipuler un facteur climatique critique.

Abstract

Snow cover is a key environmental component for tundra wildlife that will be affected by climate change. Change to the snow cover may affect the population dynamics of high-latitude small mammals, which are active throughout the winter and reproduce under the snow. We experimentally tested the hypotheses that a deeper snow cover would enhance the densities and winter reproductive rates of small mammals, but that predation by mustelids could be higher in areas of increased small mammal density. We enhanced snow cover by setting out snow fences at three sites in the Canadian Arctic (Bylot Island, Nunavut, and Herschel Island and Komakuk Beach, Yukon) over periods ranging from 1 to 4 years. Densities of winter nests were higher where snow depth was increased but spring lemming densities did not increase on the experimental areas. Lemmings probably moved from areas of deep snow, their preferred winter habitat, to summer habitat during snow melt once the advantages associated with deep snow were gone. Our treatment had no effect on signs of reproduction in winter nests, proportion of lactating females in spring, or the proportion of juveniles caught in spring, which suggests that deep snow did not enhance reproduction. Results on predation were inconsistent across sites as predation by weasels was higher on the experimental area at one site but lower at two others and was not higher in areas of winter nest aggregations. Although this experiment provided us with several new insights about the impact of snow cover on the population dynamics of tundra small mammals, it also illustrates the challenges and difficulties associated with large-scale experiments aimed at manipulating a critical climatic factor.

Introduction

Climatic conditions in the Arctic are changing rapidly with increasing temperature and shifting precipitation regimes (Solomon 2007, Hannah 2011). These changes will inevitably affect the snow cover, a key environmental component of the tundra for many animals (Chan et al. 2005, Forchhammer et al. 2005, Tyler et al. 2008, Gilg et al. 2009,). During the winter, snow provides a vital protective cover for tundra plants and for some wildlife species, most notably small mammals that live under the snow (Callaghan et al. 2004). Arctic small mammal populations are famous for their multi-annual population cycles (Stenseth 1999, Krebs et al. 2002, Ims and Fuglei 2005, Pitelka and Batzli 2007, Gruyer et al. 2008), the causes of which are still far from fully understood (Krebs 2011). Recently, lemming and vole cycles have become less regular, and with a reduced amplitude, in several parts of northern Fennoscandia and Greenland (Hörnfeldt 2004, Hörnfeldt et al. 2005, Ims et al. 2008), a phenomenon that may have far-reaching consequences for the whole tundra food web. Changes in snow cover, including its depth, duration and density, have been invoked to explain these new patterns (Kausrud et al. 2008, Gilg et al. 2009, Ims et al. 2011), but the role played by snow cover in the population dynamics of small mammals is still poorly known and largely based on correlative evidence.

Small mammals are active throughout the long Arctic winter, which can last up to 8 months at high latitudes. During this time, they live and even reproduce in the sub-nivean space (MacLean et al. 1974, Sittler 1995, Duchesne et al. 2011a), which is formed in the depth hoar of the snowpack. Specific conditions are required for the establishment of a low-density snow layer near the ground, which facilitates tunnelling by small mammals and air circulation (McKay and Adam 1981, Marchand 1996, Sanecki et al. 2006). Deeper snow increases the chances of a sub-nivean space forming by providing a higher temperature gradient between the ground and the ambient air (Marchand 1982, Sanecki et al. 2006). Deep snow reduces the probability of ground icing, due to rain or early melting, especially if the snow cover forms quickly in the early winter (Bergsten et al. 2001, Rixen et al. 2004). Deep snow can also restrict access to small mammals by predators such as foxes (Angerbjörn et al. 1999, Gilg et al. 2006), although this may be less applicable to mustelids which can hunt lemmings under the snow (Reid and Krebs 1996). It is thus not surprising that previous studies have reported a preference of lemmings for deep snow areas in winter (Formozov 1969, Sittler 1995, Duchesne et al. 2011b, Reid et al. 2012). However, because mustelids frequently concentrate their hunting effort in areas of high small mammal densities (Klemola et al. 1999, Hellstedt and Henttonen 2006), deep snow areas could potentially attract those predators if lemmings aggregate there. Snow depth is thus a central factor during winter and could affect several demographic parameters of small mammals.

Testing the effect of climatic factors on animal population dynamics is challenging, especially when based on correlations (Krebs and Berteaux 2006). For instance, the possibility of having to deal with chance events such as extreme weather conditions, or our inability to control climate, may seriously hamper our ability to detect meaningful relationships (Cowie 2007). In order to circumvent these problems, we implemented a large-scale snow manipulation experiment to examine the effect of increased snow cover on the population dynamics of arctic small mammals. A strength of our approach was the use of spatial replicates (over several years) at 3 sites in the Canadian Arctic, two of which were separated by >2000 km. We used rows of snow fence on large grids (>7 ha) to trap drifting snow during winter. In a previous paper, we showed that our manipulation increased snow depth on the experimental grids, created a more favourable sub-nivean temperature regime and influenced the spatial distribution of lemming and vole winter nests (Reid et al. 2012). Therefore, our manipulation improved the winter habitat quality of small mammals.

In this paper, we examine the effects of our snow manipulation on small mammal demographic parameters. Our first two hypotheses were that deeper snow would increase the density and the reproductive rate of small mammals. We thus predicted that winter density (nests) and spring density (individuals), and reproduction in winter (proportion of winter nests with evidence of reproduction) and spring (proportion of reproductive females and of juveniles) would be higher on our snow-manipulated grids than on our control grids. Our third hypothesis was that deeper snow would increase predation rates by mustelids because of increased lemming density. We thus predicted that the intensity of mustelid predation on small mammals in winter nests would be higher on our snow-manipulated grids and higher in aggregated nests.

Material and methods

Study sites

We conducted the study at three sites in the Canadian Arctic. The first is in the Qarlikturvik glacial valley (50 km^2) of Bylot Island, Sirmilik National Park, Nunavut Territory (73° 08 ’N, 80°00’ W). The study area consists of tundra polygons, thaw lakes and ponds that form wetlands interspersed with mesic tundra at the bottom of the valley, surrounded by extensive, mesic tundra on the nearby slopes and hills. The second is on Herschel Island, Yukon Territory (69˚ 34’ N, 138˚ 54’ W). It is a post-glacial island (112 km^2) composed mostly of upland habitats dominated by tussock tundra and dwarf shrub heath. The third is at Komakuk Beach, Ivvavik National Park, on the North Slope of Yukon Territory (69˚ 35’ N, 140˚ 11’ W). This is a mainland site (12 km^2) mainly composed of wet tundra on a coastal plain (see Reid et al. 2012 for more details).

At all sites the small mammal community is quite simple. On Bylot Island, the only rodent species present are brown and collared lemmings (*Lemmus trimucronatus* and *Dicrostonyx groenlandicus*) and both species exhibit multiannual cycles, although the former species exhibits much stronger fluctuations in abundance (Gruyer et al. 2008). At Herschel, the same lemming species are present and fluctuate with substantial amplitude (Krebs et al. 2011), and the only other rodent species present, in very small numbers, is the tundra vole (*Microtus oeconomus*). At Komakuk Beach, brown lemmings and tundra voles are common, collared lemmings are rare, and all species remain at fairly low densities (Krebs et al. 2011); no other rodent species are found at this site. In winter, the main predators are mustelids (ermine, *Mustela erminea*, at Bylot Island, and least weasel, *Mustela nivalis*, in north Yukon) and the Arctic fox (*Vulpes lagopus*) at all sites. The red fox (*Vulpes vulpes*) is also present in small numbers at all sites and the wolverine (*Gulo gulo*) at Herschel Island and Komakuk Beach only.

Snow fence experiment

At all sites we set up two trapping grids at least 600 m apart, one for the experimental treatment and one as a control. Pairs of grids were set up in similar habitats and were dominated by mesic tundra, a habitat used by lemmings during winter (Duchesne et al. 2011b). On Herschel and Komakuk, all trapping grids were 9 ha (300 x 300 m) and on Bylot the control grid was 10.9 ha (330 x 330 m) and the experimental one 7.3 ha (270 x 270 m). In summer 2007 (Bylot and Herschel), and summer 2008 (Komakuk), we installed 5 parallel rows of 1.5 m high snow fence in the experimental grids to enhance snow depth. Fences were made of orange, UV-resistant plastic. Fence rows were set up perpendicular to the dominant wind and the spacing between rows ranged from 30 to 50 m. On Bylot, we fenced the entire width of the experimental grid, although fenced areas varied between years because 10 to 30% of the fence collapsed every winter but was repaired annually. At Herschel and Komakuk, only half of the experimental grids were fenced (see Reid et al. 2012 for more information about the experimental set up). The experiment lasted 4 years on Bylot Island (2008-2011), 2 years on Herschel Island (2008-2009) and 1 year at Komakuk (2009).

The effect of the fence on snow depth was measured annually on Bylot and on Herschel, either before or at the beginning of snow-melt (end of May to beginning of June on Bylot, late April on Herschel). No measurements could be taken at Komakuk because we could not reach the site before snowmelt. While suitable to compare snow depth among treatments within years, these data should not be used to make inter-annual comparisons due to differences in the timing of snow measurements each year. We measured snow depth at 2 to 5-m intervals along multiple transects perpendicular to the fence on both experimental and control grids. These results have been reported by Reid et al. (2012) but we will briefly summarize here the information relevant to the interpretation of the data that we present.

Lemming winter nests

Most of our information on the winter biology of arctic small mammals comes from winter nests (MacLean et al. 1974, Sittler 1995, Duchesne et al. 2011a). Lemmings and voles build nests for insulation against cold temperatures and to save energy during winter (Casey 1981). These nests are made mainly of grasses and sedges and are easily spotted at close range after snowmelt. It is possible to determine whether brown or collared lemmings used the nest based on the length, form and color of faeces left behind (MacLean et al. 1974, Duchesne et al. 2011a). Collared lemmings have dark reddish faeces about 4-6 mm long, while brown lemmings produce green faeces about 6-10 mm long. Lemmings regularly reproduce under the snow in their winter nests (Millar 2001, Stenseth and Ims 1993b). Juveniles have smaller faeces than adults, which allowed us to detect if there was reproduction in a nest following the criteria of Duchesne et al. (2011a). Nests made by voles at Komakuk were differentiated from those of brown lemmings by size of green faeces (<6 mm long and thinner for voles), and the association of nests with typical soil and humus digging and deposits along runways made by *Microtus*.

When weasels prey on small mammals in their winter nests, they often line the nest with their prey's fur and use the nest themselves, or they leave rodent body parts and partially eaten carcasses in the nest (MacLean et al. 1974, Sittler 1995). It is thus possible to obtain an index of weasel predation rate on small mammals during winter by counting nests with fur lining or rodent remains.

Each spring, we systematically counted all winter nests on our control and experimental grids by walking along lines spaced 5 to 10 m apart. Because this distance is less than the effective detection distance of those nests in most habitats (Duchesne et al. 2011b), we assumed a probability of detection of 1 for nests in this census. Revisits of these sites throughout the summer confirmed that >99% of the nests had been detected by our spring survey. Therefore, our winter nest densities (number of nests per grid / grid size) lacked a variance estimate. All nests on Bylot Island and Komakuk Beach were carefully inspected to determine if reproduction or mustelid predation had occurred using the criteria outlined above. On Herschel Island, winter nests were examined for mustelid predation only.

Species using winter nests and winter reproduction could not be determined on Herschel due to time restraints.

Live-trapping

We live-trapped rodents on the control and experimental grids at all sites every year using Longworth traps to obtain mark-recapture estimates of abundance. The trapping grids were laid out in a Cartesian plane of rows and columns, with numbered stakes spaced every 30 m at Bylot Island and every 20 m at the two Yukon sites. At each stake on Bylot, and every second stake in Yukon, we set out a Longworth trap pre-baited with apple near signs of lemming use or burrows (the total number of traps per grid ranged from 100 to 144). We typically had 3 trapping sessions during the summer but we report here only the first one, which occurred as soon as possible after snow melt (mid-June on Bylot, early to mid-June in north Yukon). Trapping sessions lasted for 3 days (Bylot) or 2 days (north Yukon) and traps were checked twice a day on Bylot and 4 times a day in Yukon. Traps were occasionally closed during inclement weather. This design typically yielded 6-8 trapping occasions and we considered the populations closed during this period, a reasonable assumption considering the short duration of our trapping sessions. All individuals caught were identified to species, sexed, and weighed (± 1 g) with a spring scale. Small mammals were individually marked with ear-tags in Yukon or internal PIT tags on Bylot (Gibbons and Andrews 2004) and all recaptures were noted.

For each female, we assessed reproductive status based on nipple size, vaginal condition, and pelvic separation. The number of pregnant and lactating females divided by the total number of adult females caught gave us an estimate of the proportion of reproductive females in spring just after snowmelt. The weight of each individual provided us with an index of its age (juvenile or adult). All individuals that weighed < 33 g for brown lemmings and tundra voles and < 40 g for collared lemmings were considered juveniles (Framstad et al. 1993, Gruyer et al. 2010). This gave us an estimate of reproductive activity during late winter based on the proportion of juveniles among all captured individuals in the spring-time population.

Statistical analyses

All density estimates were carried out in DENSITY 4.4 (http://www.otago.ac.nz/density) using Efford's maximum likelihood estimates (Efford et al. 2004, Borchers and Efford 2008), which accounts for the spatial structure of our trapping grids. All parameter settings in DENSITY 4.4 were similar to those used by Krebs et al. (2011). In spring 2010 at Bylot Island, trapping had to be done when snow was still present due to a late snow-melt, which reduced the number of effective traps by 50% in the control and 26% in the experimental grids. Because the effective trapping area had to be corrected, we estimated abundance with program CAPTURE implemented in MARK 4.2 (White and Burnham 1999). To estimate density, we divided abundance by the size of the effective trapping area following Gruyer et al. (2010) (see also Williams et al. 2002). The number of different individuals trapped per grid ranged from 0 to 65 and recapture of previously marked animals was relatively high. When the number of captured individuals was too low for analysis in DENSITY (i.e. < 4 individuals), we used the minimum number known to be alive and divided this number by the effective trapping area (Krebs et al. 2011). Density estimates were obtained for each species separately.

The models of Otis et al. (1978) were used to test for variations in capture and movement probabilities. We tested models where capture and movement probabilities were set to vary as a function of time, behavioural response to capture, and individual heterogeneity (see Gruyer et al. 2010 for more details). The best models for our data were selected with Akaike's Information Criterion (AIC; Burnham and Anderson, 2002).

We used general linear models to test for differences between the experimental and control grids (i.e. treatment) in winter nest and spring densities, as well as for an effect of site and interaction between treatment and site. We also tested for a species × treatment interaction separately for the sites where the information was available. Because small mammal densities differed considerably among years (due to their cyclic fluctuations of abundance), and among sites, we first log-transformed density estimates (both winter nests and live trapping data). We then standardized data by subtracting the annual, site-specific mean densities from the individual values of the experimental and control grids. We thus conducted the analyses on the deviations in densities of the control and experimental grids with respect to the annual, site-specific mean. Standardizing the data this way allowed us to use each year and site as replicates in the statistical analysis. We compared reproductive rates (both from winter nests and live-trapping) and predation rates by mustelids between our control and experimental grids using log-linear models. The effects of site, and interactions between site or species and treatment, were also tested. All data from the experimental grids used in the analyses for Herschel and Komakuk were taken from the treated half only (see Reid et al. 2012). For statistical analyses, we used R 2.11 (R Development Core Team 2010).

To examine our prediction that predation rate would be higher in aggregated nests, we calculated the local nest density around every nest in a given area. The mean nearest-neighbour distance between winter nests (calculated using the "spatstat" package in R; Baddeley and Turner 2005) varied between 9.3 and 17.0 m depending on sites and years. Based on that and a visual inspection of the spatial distribution of nests, we chose a 25-m radius zone centered on the nest to calculate density around every individual nest and to assess those nests located in aggregations. To test if mustelid predation was higher in aggregations of nests, we used a logistic regression with local nest density as the independent variable. The model was run separately for each year, site and treatment with sufficient data (9 datasets with individual n ranging from 15 to 176). For these analyses, we applied the sequential Bonferroni correction to maintain the experiment-wise error rate at a reasonable level. We set the significance level as $1 - (1 - 0.05)^{1/9} = 0.0057$, which means that if the smallest probability encountered in our tests exceeded this value, then all other tests would be declared non-significant (Sokal and Rohlf 1995).

Results

Effect of experimental treatment on snow depth

Our experimental enhancement of snow depths on experimental grids was a partial success. On average, the fences increased snow depth by only 5.5 to 13.1 cm (23 to 38% depending of the site and year) over the entire experimental grid. However, fences had a strong local effect within 10 m on either side of each fence row. In these areas, snow was on average 18.2 to 40.2 cm deeper (72 to 108%) on the experimental than on the control grids (Fig. S1; see Reid et al. 2012 for details). Consequently, we conducted two separate analyses for winter nest data: one using the entire experimental grid compared to the control, and one using only nests located within 10 m on either side of a fence row (hereafter referred to as the deep snow zone) compared to the control. Monitoring of ground temperature near the snow fences and on the control grids showed that temperature became warmer near the fence during late fall and this difference persisted throughout the winter (Fig. S2). This suggests that snow accumulated rapidly near the fence rows in early winter and that this effect persisted until spring.

Effect on densities

On Bylot Island, winter nest counts and spring live-trapping density estimates indicate that brown and collared lemmings reached peak densities in 2008, were very low in 2009, increased again to high densities in 2010 and increased further in 2011. On Herschel Island, live trapping showed that brown lemmings reached peak densities in 2008 whereas collared lemmings reached their highest densities in 2007 and 2010 (i.e. pre and post-treatment years; Krebs et al. 2011). No clear cyclic fluctuations could be detected for any small mammal species at Komakuk (Krebs et al. 2011). Voles were in very low densities at Herschel compared to lemmings but were the dominant species at Komakuk.

The treatment affected winter nest densities ($F_{1,18}$ = 5.46, P = 0.031) and despite a significant interaction between site and treatment ($F_{2,18}$ = 10.47, P < 0.001), the treatment effect was present at all three sites; only its magnitude varied (Fig. 1). Density of small mammal winter nests was on average 1.5 times higher on the experimental than on the control grids for the same years. When we repeated the analysis by restricting the experimental grid data to the deep snow zone, results were similar but the treatment effect was much stronger as nest densities were on average 3.3 times higher in this deep snow zone than on the control grids (treatment: $F_{1,18}$ = 26.63, P < 0.001; site ×treatment: $F_{2,18}$ = 10.88, P < 0.001). On Bylot Island and Komakuk, all species reacted similarly to the treatment over the entire grids (species × treatment: $F_{2,12}$ = 2.57, P = 0.118) and, although a significant interaction was found for the deep snow zone ($F_{2,12}$ = 7.71, P = 0.007), all species reacted positively to the treatment and only the magnitude of the reaction varied among them, with a much stronger effect on brown lemming, the most abundant species on Bylot Island.

The previous patterns were not repeated in the mark-recapture estimates of rodent density in spring, soon after snow melt (Fig. 2). Overall, there was no treatment effect ($F_{1,24}$ = 0.02, P = 0.894) but we found a significant site × treatment interaction ($F_{1,24}$ = 3.92, P = 0.034). This interaction shows conflicting results between sites and thus a conservative approach would be to say that we cannot detect an effect of treatment. Therefore, we found partial support for our first hypothesis because, although density of winter nests was increased by our experimental treatment, it had no effect on spring density.

Effect on reproduction

The proportion of winter nests showing signs of reproduction did not differ between the experimental and control grids (χ^2= 0.900, df = 1, P = 0.343; Fig. 3), and there were no site × treatment (χ^2 < 0.001, df = 1, P = 0.988) or species × treatment interactions (χ^2= 0.644, df = 2, P = 0.725). Results were similar for the analysis restricted to the deep snow zone of the fences (treatment: χ^2 = 0.807, df = 1, P = 0.369; site × treatment: χ^2 = 0.146, df = 1, P = 0.702; species × treatment: χ^2 = 1.796, df = 2, P = 0.407).

Spring live-trapping revealed the same patterns. Proportion of reproducing females in spring did not differ between experimental and control grids (treatment: χ^2 = 1.124, df = 1, P = 0.289; site × treatment: χ^2 = 0.169, df = 2, P = 0.919; species × treatment: χ^2 = 0.007, df = 2, P = 0.997; Fig. 4). Similar results were obtained for the proportion of juveniles among individuals caught in spring (treatment: χ^2 = 0.008, df = 1, P = 0.930; site × treatment: χ^2 = 1.775, df = 2, P = 0.412; species × treatment: χ^2 = 1.528, df = 2, P = 0.466; Fig. 5). Therefore, we found no support for our hypothesis of an enhanced reproductive rate on the experimental grids.

Effect on predation

The proportion of small mammal winter nests predated and used by mustelids tended to be lower in the experimental than in the control grids at Bylot and Komakuk but the opposite trend was detected at Herschel (site × treatment: $\chi^2 = 6.85$, df = 2, P = 0.033; Fig. 6). The same pattern was detected when we compared the deep snow zone of experimental grids to the control (site × treatment: $\chi^2 = 10.26$, df = 2, P = 0.006). On Bylot and Komakuk, the effect of the treatment on predation rates was similar for all species (treatment × species, entire grid: $\chi^2= 1.106$, df = 2, P = 0.575; deep snow zone: $\chi^2= 0.395$, df = 2, P = 0.821). Therefore, as two sites out of three did not show higher predation rates on the experimental grid, our prediction that winter predation should increase on our snow-manipulated grids was not supported.

Across all sites, grids and years with sufficient data, only Herschel showed a trend for a negative effect of nest density on predation rate by mustelids in the control grid in 2008 ($\beta = -0.71 \pm 0.42$; $F_{1,89} = 5.90$, P = 0.017) and 2009 ($\beta = -0.75 \pm 0.55$; $F_{1,51} = 6.88$, P = 0.011). However, these tests were not significant based on the Bonferroni-corrected significance level ($\alpha = 0.0057$). Our initial prediction that predation would be higher in aggregated nests, such as those found on the snow-manipulated grid, was thus not supported.

Discussion

Population densities

Previous studies showed that lemmings tend to aggregate in areas of deeper snow (Duchesne et al. 2011b, Reid and Krebs 1996). Our experimental manipulation clearly demonstrated a cause-effect relationship between snow depth and lemming habitat use in winter as the density of winter nests increased on our experimental grids, with the greatest increase found in areas of deepest snow along the fence. This suggests that normal snow conditions on the widespread mesic tundra habitats at our three sites offer less than optimal conditions for wintering lemmings. Greater snow depth provides benefits to lemmings, potentially as superior protection against cold temperatures, and improves the quality of the snowpack compared to adjacent areas with shallower snow depth (Marchand 1982, Duchesne et al. 2011b, Reid et al. 2012). Although all rodent species reacted positively to the treatment, the effect was apparently greatest on brown lemmings in the deepest snow areas near the fence. One possibility is that this species showed a stronger preference for deep snow areas than the collared lemming or tundra vole. Alternatively, because the brown lemming is behaviourally dominant over the collared lemming (Morris et al. 2000), it is also possible that it limited occupation of those areas by the latter species through interspecific competition.

It is unclear if the increase in winter nest density that we observed is a genuine population increase or simply the consequence of a redistribution of individuals from areas surrounding our grids due to improved overwintering habitat quality near the snow fences (i.e. aggregative numerical response). Small rodents probably redistribute themselves in autumn in the process of finding the areas with the earliest accumulations of deeper snow (Reid et al. 2012). However, the absence of an increase in reproductive rate on our experimental grids does not support the hypothesis that our manipulation caused a real population increase in winter (i.e. a reproductive numerical response).

The lack of consistently higher spring densities on treatment grids compared to controls, despite an increase in winter nests, suggests that some individuals composing the winter rodent population on our grids may have moved away before or at snowmelt. In conjunction with this study, we have discovered that, even though winter nest densities explain up to 64% of the variance in mark-recapture population estimates in the subsequent spring, a sizeable amount of variation remains unexplained, suggesting a role for other ecological factors in re-distributing the population between seasons (Krebs et al. 2012). It is possible that the scale of our treatment may not have been sufficiently large to account for small mammal inter-seasonal movements though the distance moved by lemmings between seasons remain unknown. During the process of snow melt, the sub-nivean space generally becomes colder than the ambient air (Bilodeau et al. 2013c); basal ice frequently forms with the re-freezing of melt water at the ground, and melt water puddles develop in hollows (Pomeroy and Brun 2001). Therefore, at snow melt, areas of deep snow may offer a poorer environment for lemmings than areas with a thinner snow pack. Lemmings probably disperse from these poorer quality areas to better drained sites or even to the first areas that become snow free (Batzli et al. 1983, Pitelka and Batzli 1993). These movements may also be stimulated by seasonal changes in other habitat conditions such as food quality because food plants will grow earlier on snow-free sites.

Higher winter density on the treatment area could have increased density-dependent effect through food depletion compared to the control, hence favouring dispersal of small mammals away of these areas in spring. However, we found little support for this hypothesis as we did not detect any obvious signs of lemming overgrazing after snow-melt in our areas of highest winter nest density contrary to what has been reported elsewhere under high lemming density (e.g. Moen et al. 1993). Moreover, monitoring of the impact of lemming winter grazing on vegetation with exclosures on Bylot Island showed little effect in their preferred wintering habitat (snowbeds) even during years of peak lemming abundance (F. Bilodeau et al. unpublished data).

Reproduction

It is surprising that our manipulation did not enhance winter reproduction, at least based on the indices that we used, considering that it had a strong effect on the local abundance of winter nests. The increase in winter nest abundance we observed near the fence, where snow accumulation started early during the winter and was greatest, was likely due to an increase in the sub-nivean temperature (on average, sub-nivean temperature were 1.5 to 4.5^{o} C warmer near the fence than on the control areas; Reid et al. 2012). Chappell (1980) estimated an energy savings for lemmings in the subnivean space of about 30 kJ/d for a 10°C increase in temperature (equivalent to about 50% of basal metabolic rate), and daily energy expenditures of between about 135 and 240 kJ at the height of winter. Thus, although the increases in subnivean temperature that we observed near the fences would have meant some energy savings for lemmings, this energetic advantage may not have been large enough to enhance reproduction. Our results are also consistent with Duschesne et al. (2011b) who found a negligible effect of enhanced thermal protection due to higher snow depth on probability of reproduction in winter nests. However, Duchesne et al. (2011b) also found an association between the presence of some vascular plants and the probability of winter reproduction in brown lemmings. Thus, it is possible that the low abundance of some plant species, and especially graminoids, may have hindered reproduction on our experimental plots.

The timing of snow accumulation in fall may be a critical factor determining the intensity of winter reproduction. If snow accumulation is too small before the onset of the coldest winter months, it is possible that reproduction will be delayed until temperatures begin increasing toward the end of winter and become more clement across an entire region, regardless of the difference in snow accumulation between our treated and control grids. Reid and Krebs (1996) found that the intensity of cold stress experienced by collared lemmings during the September and October period of photoperiod-induced changes in body morphology and, before the onset of deeper winter snow, explained the majority of the variance in rate of population growth during the entire winter. In areas where snow accumulates rapidly early in winter, individuals under a deeper snow cover may start reproducing earlier and have more or larger litters. Also, warmer temperatures on the experimental grid may have enhanced survival or growth rates of juveniles, although the absence of an increase in the proportion of juveniles caught at snow-melt does not support this hypothesis. The lack of an effect of our experiment on the proportion of reproductive females in spring, soon after snow-melt, is less surprising because reproductive activity is usually reduced or nil during the snow melt period (Negus and Berger 1998, Millar 2001).

Predation

Contrary to what we predicted, experimental areas where snow depth was enhanced did not have a higher predation index by mustelids despite a higher density of lemming nests and, at a finer scale, aggregations of winter nests did not increase the probability of being predated on our grids. A winter nest lined with fur by a weasel is a clear indication that the weasel killed lemming(s) using that nest. However, if the weasel subsequently used that nest as a starting point to forage in the surrounding area, it may encounter other winter nests and kill their occupants without necessarily using their nests. Therefore, the number of nests used by weasels may provide an underestimation of the true predation rate, and possibly a variable estimate of the predation rate depending on the degree of nest aggregation. It is also possible that the increase in winter nest density near the fence was not high enough to elicit a response by weasels but we believe that it is unlikely because the density of winter nests recorded near the fence was comparable to the density measured in preferred lemming winter habitat at our study sites (Duchesne et al. 2011b, F. Bilodeau et al. unpublished data).

Another potential issue is the scale of our experiment. It is noteworthy that the proportion of winter nests predated by weasel for most of our site by year combinations were low (< 5% of nests), and often nil. This suggests that weasels were at very low densities, or that they did not visit and establish themselves on our grids. In choosing our grids, we avoided the highest quality winter habitats for lemmings, where snow was known to form deeper drifts because of large-scale landscape topography. So, the search pattern of weasels for areas of deeper snow, and therefore higher likelihood of lemmings, may have easily missed our relatively small scale snow depth enhancements. The home ranges of Arctic weasels in winter are not documented, but based on published information on summer ranges, are likely to be larger than our study grids and dependent on the probability of finding high concentrations of prey (Klemola et al. 1999, King and Powell 2007).

Other studies, also relying on winter nest sampling, have found that probability of predation by mustelids increased in areas of high lemming nest densities at the landscape level (Sittler 1995), including at one of our study sites (Bylot Island; Duchesne et al. 2011b). Data from Bylot also show that predation is highest in riparian habitat (Bilodeau et al. in prep.), suggesting that weasels forage more in such habitats where snow is consistently deeper than elsewhere. Thus, habitat may be more important in affecting weasel foraging decisions than lemming density or snow depth per se.

The challenges of experimental climate manipulations

Several aspects of the snow cover such as its duration, density or depth could affect the population dynamic of tundra small mammals (Kausrud et al. 2008, Gilg et al. 2009, Ims et al. 2011). Our experiment, which was designed to manipulate only one of them, has provided us with several new insights about the impact of snow depth on the demography of small mammals. However, it also illustrates the difficulties associated with an experiment aimed at manipulating a key climatic factor and the experiment's relevance for assessing the impact of climate change on animal populations. We were able to experimentally manipulate snow depth, a key climate-related factor, but at a relatively local scale. The treatment affected the spatial distribution of small mammals, as evident in the changing densities of their winter nests, but apparently had little effect on other demographic parameters such as reproduction and predation rate. This raises the important issue of spatial scale of ecological experimentation in the Arctic. Although fairly large and logistically difficult to accomplish, our snow depth experiment perhaps still covered too small an area to encompass some of the inter-seasonal movements of small rodents and, most likely, the within-winter movements of one of their chief predators, weasels. The question of scale may be too logistically difficult to overcome, and we may have to be satisfied in some situations with mensurative assessments of relationships between demographic parameters and possible causative factors at more appropriate landscape scales. Our experiment also stresses the need to develop additional and potentially more sensitive indices of winter demographic parameters of lemmings and their predators, such as live-trapping through the snow-pack or remote sensing of lemming and weasel movements in the subnivean (e.g., radio-telemetry).

Climate change is not only characterised by changes in average weather conditions, but also by increased variability which provides even greater difficulties for experiments trying to simulate future weather conditions. An experiment such as ours, ranging for up to 4 years, is suitable to measure average conditions and provide some annual variability. However, it is not long enough to account for extreme events that can have profound and lasting effects on the dynamics of animal populations and which are bound to be more frequent in the future (Callaghan et al. 2004). Examples include exceptional icing events having catastrophic impact on reindeer populations (Miller and Gunn 2003, Chan et al. 2005) or a very early onset of winter affecting the wolf-muskox-hare dynamic (Mech 2004). Future experiments similar to ours should be run over longer time periods encompassing greater climatic variability. We conclude that, although experiments aimed at manipulating climatic variables may be useful in testing hypotheses at some spatial scales, long-term, non-manipulative but spatially replicated experiments with clear hypotheses may be a better approach to address these questions at the larger spatial scales typical of population processes.

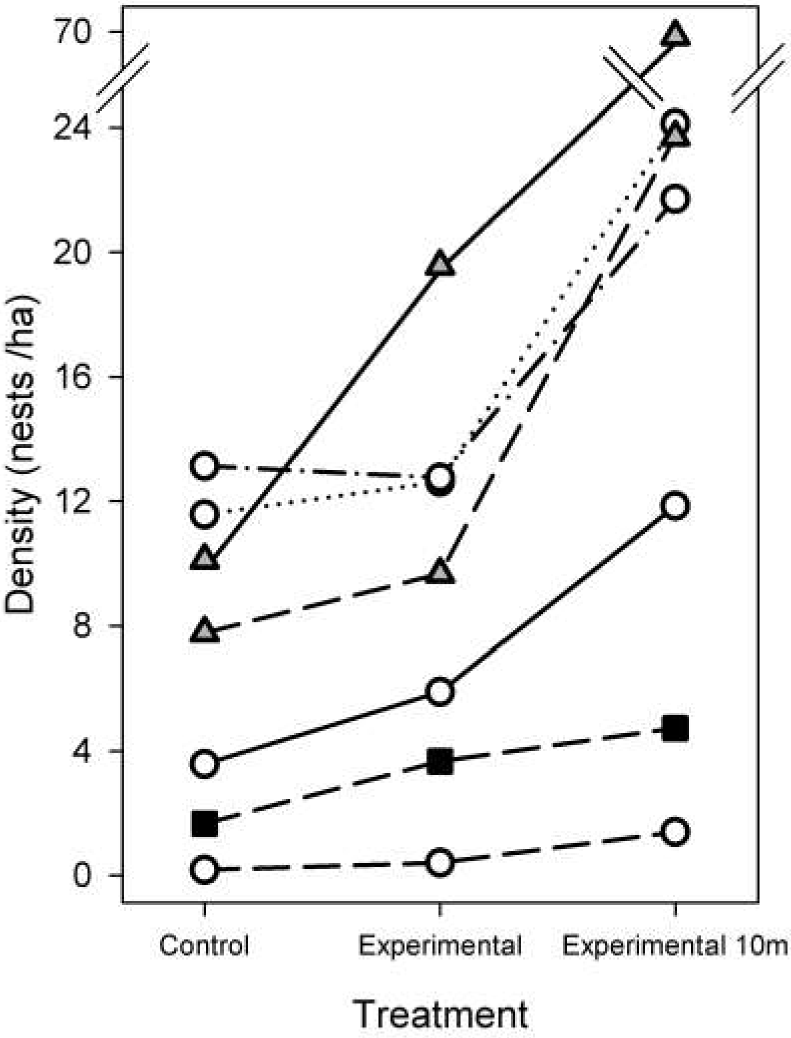

Figure 1. Small-mammal winter nests densities in our experimental and control grids at Bylot Island (white circles), Herschel Island (gray triangles) and Komakuk Beach (black squares) in 2008 (solid lines), 2009 (dashed lines), 2010 (dotted line) and 2011 (dash-dot line). "Experimental 10m" stands for the 10-m strip on either side of each fence row where snow accumulation was deepest. Species were not distinguished on the figure because all species reacted positively to our treatment (see results).

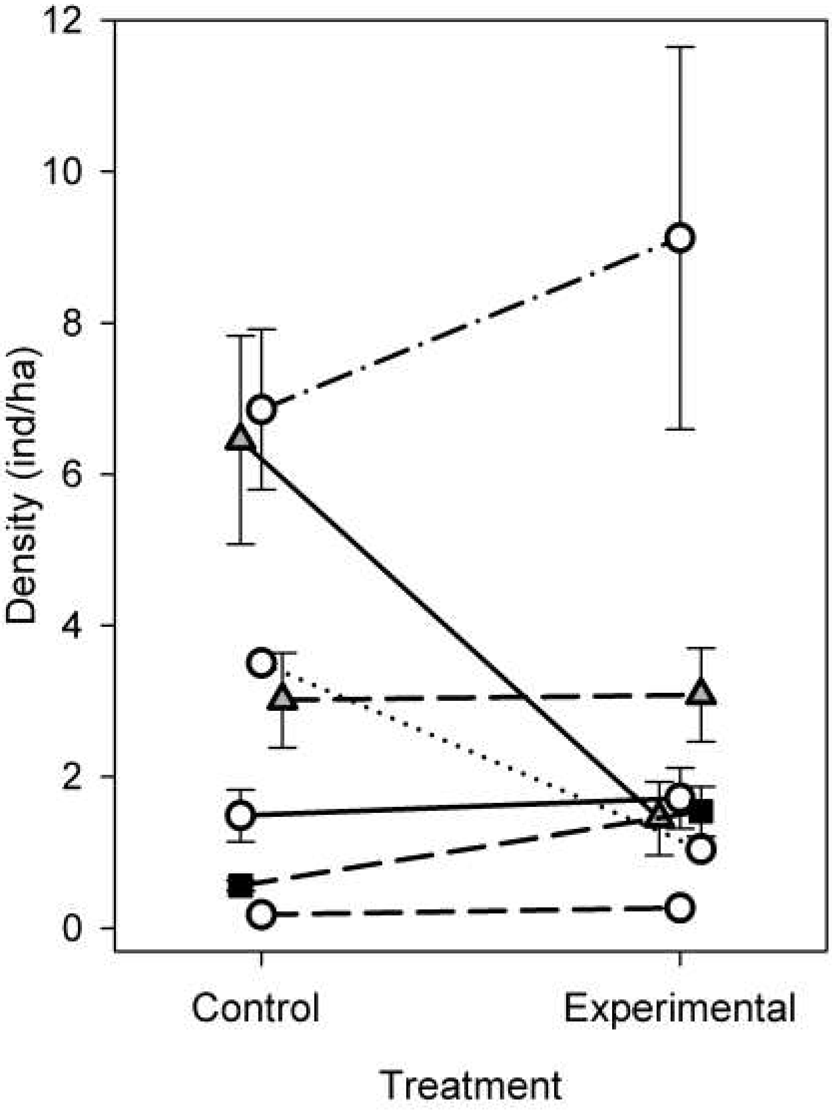

Figure 2. Small-mammal spring densities at Bylot Island (white circles), Herschel Island (gray triangles) and Komakuk Beach (black squares) from 2008 (solid lines), 2009 (dashed lines), 2010 (dotted line) and 2011 (dash-dot line). Species were not distinguished on the figure because they all responded similarly to our treatment. Error bars represent SE. Some data points were dithered horizontally to avoid superposition.

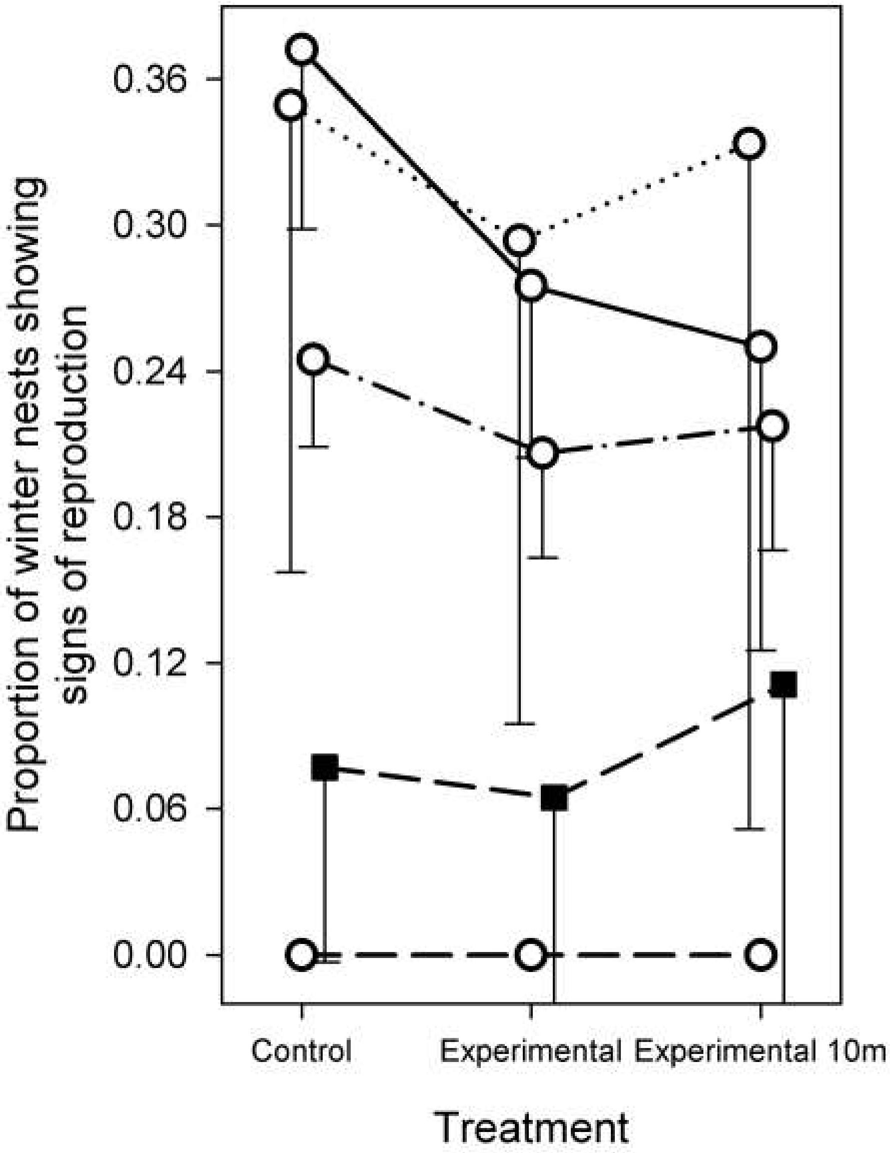

Figure 3. Proportion of small-mammal winter nests showing signs of reproduction at Bylot Island (white circles) and Komakuk Beach (black squares) from 2008 (solid lines), 2009 (dashed lines), 2010 (dotted line) and 2011 (dash-dot line). “Experimental 10m” stands for the 10-m strip on either side of each fence row where snow accumulation was deepest. Species were not distinguished on the figure because they all responded similarly to our treatment. Error bars represent SE. Some data points were dithered horizontally to avoid superposition.

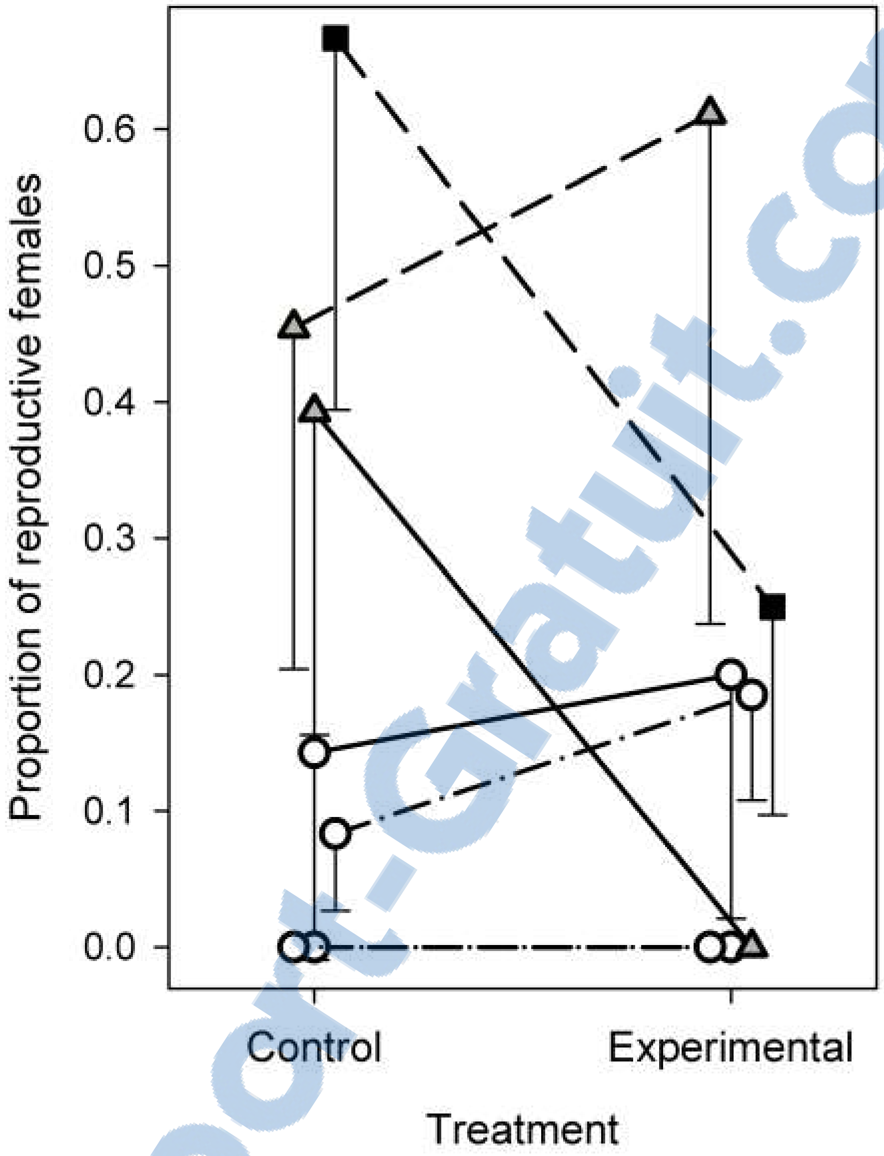

Figure 4. Proportion of small-mammal females caught in spring and showing signs of reproduction at Bylot Island (white circles), Herschel Island (gray triangles) and Komakuk Beach (black squares) from 2008 (solid lines), 2009 (dashed lines), 2010 (dotted line) and 2011 (dash-dot line). Species were not distinguished on the figure because they all responded similarly to our treatment. Error bars represent SE. Some data points were dithered horizontally to avoid superposition.

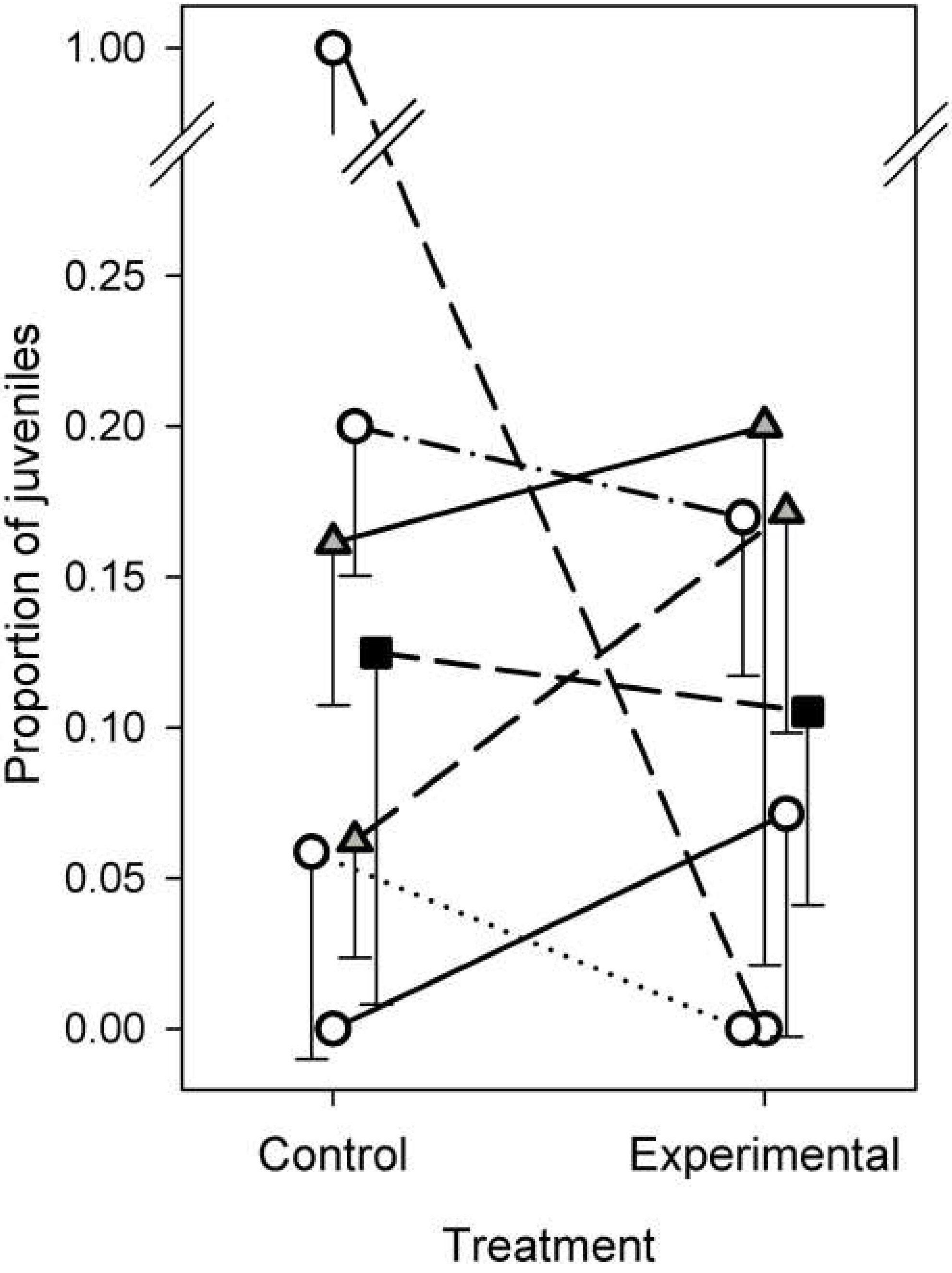

Figure 5. Proportion of small-mammal juveniles caught in spring at Bylot Island (white circles), Herschel Island (gray triangles) and Komakuk Beach (black squares) from 2008 (solid lines), 2009 (dashed lines), 2010 (dotted line) and 2011 (dash-dot line). Species were not distinguished on the figure because they all responded similarly to our treatment. Error bars represent SE. Some data points were dithered horizontally to avoid superposition.

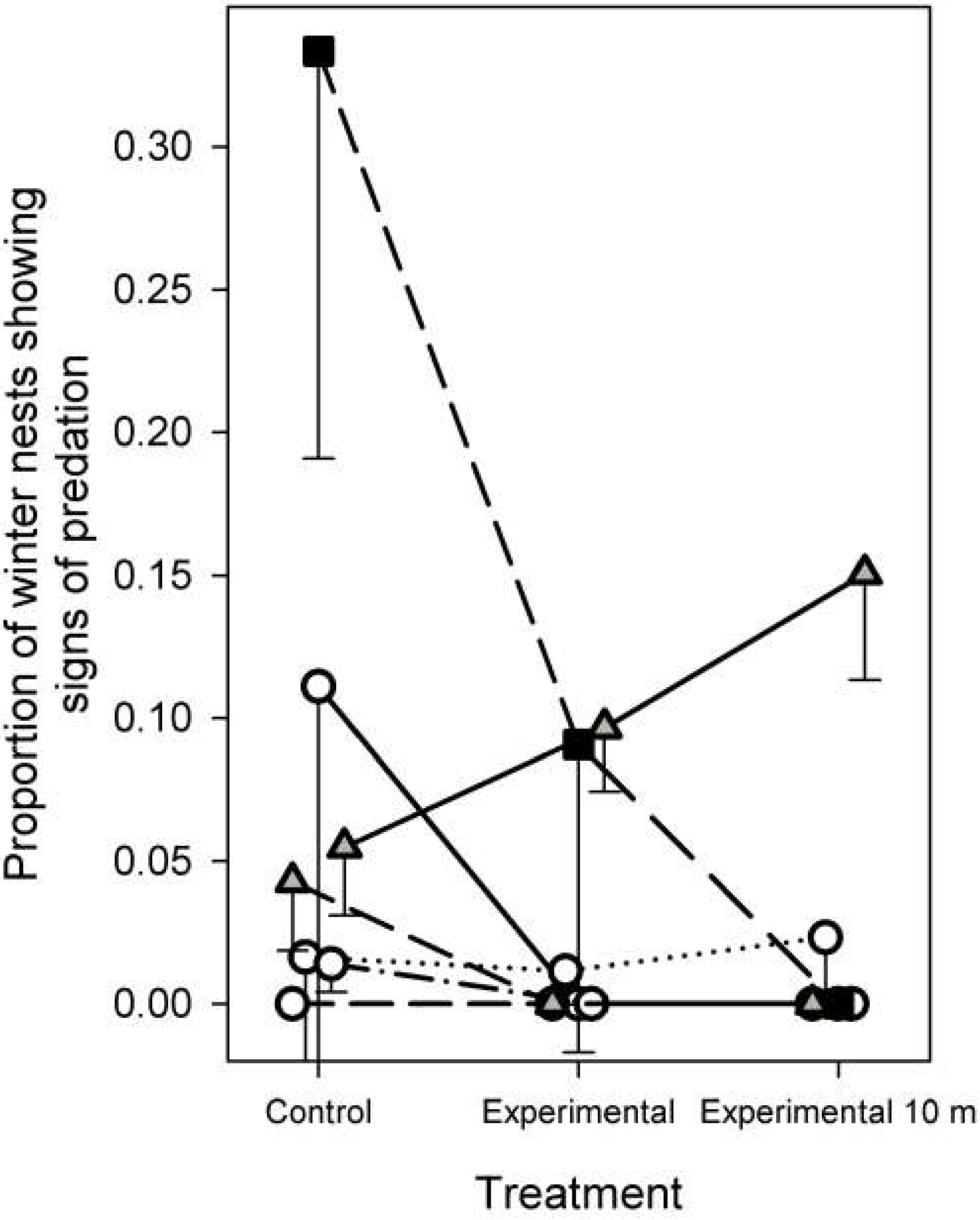

Figure 6. Proportion of small-mammal winter nests showing signs of predation by mustelids at Bylot Island (white circles), Herschel Island (gray triangles) and Komakuk Beach (black squares) from 2008 (solid lines), 2009 (dashed lines), 2010 (dotted line) and 2011 (dash-dot line). "Experimental 10m" stands for the 10 m strip on either side of each fence row where snow accumulation was deepest. Species were not distinguished on the figure because they all responded similarly to our treatment. Error bars represent SE. Some data points were dithered horizontally to avoid superposition.

Chapitre 2

The effect of snow cover on lemming population cycles in the Canadian High Arctic

Bilodeau, F., Gauthier, G. & Berteaux, D. 2013. The effect of snow cover on lemming population cycles in the Canadian High Arctic. Oecologia (in press). doi: 10.1007/s00442-012-2549-8.

Résumé

L'augmentation des températures et les changements dans le régime des précipitations vont avoir un puissant impact sur la qualité du couvert nival dans l'Arctique. Un couvert nival de bonne qualité, protégeant les lemmings des températures froides et des prédateurs serait un facteur important pour maintenir la dynamique cyclique de leurs populations dans la toundra. Nous avons examiné si les caractéristiques des fluctuations annuelles (amplitude et forme des phases) de densité du lemming brun (*Lemmus trimucronatus*) pouvaient être déterminées par l'épaisseur de neige, la densité de la neige, la température sous-nivale et la persistance de la neige. En utilisant une série temporelle s'étalant sur 18 ans d'abondance de lemming brun à l'île Bylot, dans l'Arctique Canadien, nous avons testé si les variables associées à la neige pouvaient expliquer la variation résiduelle entre les densités de lemming observées et celles prédites par des modèles où la cyclicité est expliquée. Nos analyses supportent l'hypothèse que le couvert nival peut affecter l'amplitude et possiblement la périodicité des cycles de population de lemming dans le haut Arctique. Les abondances estivales de lemming brun étaient plus élevées suivant les hivers ayant un couvert de neige épais et une couche de neige près du sol de faible densité, mais elles n'étaient pas affectées par la date d'établissement ou de fonte et la durée du couvert nival. Deux variables montraient une tendance temporelle : l'épaisseur de neige moyenne tendait à augmenter et la date d'établissement de l'épaisseur de neige critique tendait à être devancée dans le temps. Ces tendances temporelles, qui seraient favorables aux lemmings, pourraient expliquer pourquoi des cycles de population sains se sont apparemment maintenus à notre site d'étude comparativement à d'autres sites de l'Arctique.

Abstract

Rising temperatures and changes in the precipitation regime will have a strong impact on the quality of the snow cover in the Arctic. A snow cover of good quality protecting lemmings from cold temperatures and predators is thought to be an important factor for maintaining the cyclic dynamic of their populations in the tundra. We examined if the characteristics of annual fluctuations (amplitude and shape of phases) in brown lemming (*Lemmus trimucronatus*) density could be determined by snow depth, snow density, sub-nivean temperature and persistence of snow. Using an 18-year time series of brown lemming abundance on Bylot Island in the Canadian Arctic, we tested if snow variables could explain the residual variation between the observed lemming density and the one predicted by models where cyclicity had been accounted for. Our analysis provides support for the hypothesis that snow cover can affect the amplitude and possibly also the periodicity of lemming population cycles in the High Arctic. Summer abundance of brown lemmings was higher following winters with a deep snow cover and a low-density snow pack near the ground but was unaffected by the date of establishment or melting and duration of the snow cover. Two snow variables showed a temporal trend; mean winter snow depth tended to increase and date of establishment of the hiemal threshold occurred earlier over time. These temporal trends, which should be favourable to lemmings, may explain why healthy population cycles have apparently been maintained at our study site contrary to other Arctic sites.

Introduction

Small mammal population cycles have fascinated ecologists for decades and a large number of studies have tried to explain their high prevalence in northern environments (Stenseth and Ims 1993b, Korpimäki and Krebs 1996, Stenseth 1999, Hanski et al. 2001, Turchin et al. 2000, Oksanen et al. 2001, Gilg et al. 2003, Korpimäki et al. 2005, Pitelka and Batzli 2007, Krebs 2011). In recent years, population cycles in Fennoscandia and some parts of Greenland have faded out and climatic factors, especially snow cover, have been hypothesized to explain this (Hörnfeldt 2004, Hörnfeldt et al. 2005, Ims et al. 2008, Kausrud et al. 2008, Gilg et al. 2009, Ims et al. 2011). During the arctic winter, which can last up to 8 months, these rodents remain active and even reproduce under the snow (MacLean et al. 1974, Sittler 1995, Duchesne et al. 2011b). Variations in characteristics of snow cover can affect quality, and thus selection, of winter habitat (Reid et al. 2012). This in turn can influence survival, especially of young born during winter, and possibly reproduction (Yoccoz and Ims 1999, Aars and Ims 2002). Snow cover can also affect demography by reducing food availability, for instance during episodes of ground icing, or by limiting predator access to small mammals (Ims and Fuglei 2005, Kausrud et al. 2008, Gilg et al. 2009, Duchesne et al. 2011b).

A snow pack of good quality for small mammals should have several characteristics. First, it should favour the formation of a low-density depth hoar and of a sub-nivean space at its base, which facilitate tunnelling and air circulation, and provide room for small mammals to live and feed (McKay and Adam 1981, Marchand 1996, Sanecki et al. 2006). Second, it should insulate small mammals from extreme air temperature variations and protect them from the coldest meteorological events (Pomeroy and Brun 2001, Duchesne et al. 2011b, Reid et al. 2012). The thermal insulation provided by a snow layer is proportional to its depth but inversely proportional to its density (Berry 1981, Marchand 1982). Thermal insulation levels off when snow depth reaches 20-30 cm (depending on snow density), a depth referred to as the “hiemal threshold” (Pruitt 1970). Third, it should prevent ground icing due to rain or melting (Korslund and Steen 2006). This effect is maximized when a deep snowpack forms early in fall (Bergsten et al. 2001, Rixen et al. 2004). Fourth, it should persist long enough for the above effects to occur throughout the cold season.

Snow cover itself is unlikely to cause cyclic fluctuations of small mammal populations, but its high quality is believed to be an essential condition for periodic population outbreaks of arctic rodents like lemmings (MacLean et al. 1974, Ims et al. 2008, Kausrud et al. 2008). Therefore, snow cover could influence several aspects of these fluctuations, such as the stationarity of cycles (i.e. the stability of their period length), the amplitude of peaks, or the shape of individual increase-decrease phases. For instance, food or predator abundance may provide the conditions for a peak to occur, but a snow cover of poor quality may decrease its amplitude or delay its occurrence (Gilg et al. 2009). However, very few studies have tried to relate the different characteristics of the snow cover to those of small mammal fluctuations (Kausrud et al. 2008). We addressed this gap using an 18-year record of fluctuations in brown lemming (*Lemmus trimucronatus*) abundance at a Canadian high Arctic site where population cycles are still occurring (Gruyer et al. 2008). We tested the general hypothesis that a snow cover of high quality and high persistence has a positive effect on the amplitude of lemming cycles. More specifically, we examined if the characteristics of annual fluctuations (amplitude and shape of phases) in lemming density were affected by snow depth, snow pack density, temperature of the sub-nivean space, duration of the snow cover and dates at which it became established and disappeared.

Materials and methods

Study area

The study was conducted on the south plain of Bylot Island, Sirmilik National Park, Nunavut Territory, Canada (73°08’N, 80°00’W). The main study area (70 km^2) consists of tundra polygons, thaw lakes and ponds forming wetlands at the bottom of a valley and is surrounded by drier mesic habitat in the upland areas and nearby slopes and hills. Wet areas are dominated by sedges (*Carex aquatilis*, *Eriophorum sheuchzeri*) and graminoids (*Dupontia fisheri* and *Pleuropogon sabinei*) and mesic areas mainly by forbs (*Saxifraga* spp*., Potentilla* spp*., Ranunculus* spp.), graminoids (*Arctagrostis latifolia, Alopecurus alpinus, Poa* spp*., Luzula* spp.), shrubs (*Salix* spp., *Dryas integrifolia*, *Cassiope tetragona*) and mosses (Duclos 2002, Duchesne et al. 2011b). The Average air temperature from

October to June is -23.4 ± 0.4 °C and the average snow depth at the end of winter is 31.3 cm (Cadieux et al. 2008).

Two species of small mammals live in the study area, the brown and the collared lemming (*Dicrostonyx groenlandicus*). Although both species tend to fluctuate synchronously, only the brown lemming shows clear, large amplitude multiannual population cycles at our study site (Gruyer et al. 2008). Collared lemming populations are low in most years and maximum population size is always an order of magnitude lower than that of the brown lemming. For these reasons, this study focuses only on brown lemmings. In summer, brown lemmings prefer wet habitat but can also be abundant in mesic habitats (Batzli and Jung 1980, Morris et al. 2000, 2011, Ale et al. 2011). During winter, they usually prefer mesic habitat, probably because its topography is, unlike that of flat wetlands, more conducive to the accumulation of a deep snow cover in snow drifts (Batzli et al. 1983, Pitelka and Batzli 1993, Sittler 1995, Duchesne et al. 2011b). Their main predators are the snowy owl (*Bubo scandiaca*), long-tailed jaeger (*Stercorarius longicaudus*), rough-legged hawk (*Buteo lagopus*), glaucous gull (*Larus hyperboreus*), arctic fox (*Vulpes lagopus*) and ermine (*Mustela erminea*). The latter two mammals are the only winter predators.

Lemming densities

We trapped brown and collared lemmings using snap traps from 1994 to 2011 to obtain an index of abundance of each species. Trapping was conducted annually at the end of July on two sites simultaneously, one in wet habitat using four 240-m long parallel transects 100 m apart and the other in mesic habitat (since 1995) using two 500-m long parallel transects. We used Museum special traps baited with oat and peanut butter. Each transect consisted of 17 (wet) to 34 (mesic) stations spaced by 15 m. Until 2006, each station had 1 trap set near burrows or runways (when possible) within a 2-m radius and trapping lasted 10 days (for more details see Gruyer et al. 2008). From 2007 onward, we set three traps per station and trapping lasted 3 or 4 days. Both methods yielded similar results (G. Gauthier unpublished data). The total number of trap-nights varied between 500 (1994-2006) and 720-960 (2007-2011) at each site, depending on year.

From 2004 to 2011, live trapping was also conducted to obtain accurate estimates of brown lemming densities with capture-mark-recapture methods. Live trapping was conducted in mid-July for 3 or 4 consecutive days on two grids, one in the wet and one in the mesic habitat. Trapping grids were 10.9 ha and consisted of 144 traps spaced every 30 m and laid out in a Cartesian plane of 12 rows and columns. Longworth live traps were baited with apple and were checked every 12 h (see Gruyer et al. 2010). Lemming populations during trapping sessions were considered closed for the analysis. The number of individuals trapped annually varied from two to 187, and the recapture rate was relatively high. All density estimates were carried out in DENSITY 4.4 (http://www.otago.ac.nz/density) using Efford's maximum likelihood spatial model (Efford et al. 2004, Borchers and Efford 2008, see also Krebs et al. 2011).

Because snap trapping provides only an index of abundance, we used the more precise density estimate obtained by live trapping. We transformed the abundance index for years prior to 2004 into density estimates using results from the linear relationship between live trapping and snap trapping data from 2004 to 2011, using each trapping grid as a sampling unit ($F_{1,13} = 65.2$, $P < 0.001$, $R^2 = 0.82$).

Snow cover

An automated weather station installed at our field site provided the following hourly, year-round data since 1993: air (2 m above ground) and ground (2 cm below ground) temperatures, air humidity, wind velocity and direction, incoming and reflected radiation, and snow depth (since 2001). To fill in periods when information was missing (primarily snow depth prior to 2001; occasionally other variables due to sensor breakdown), we retrieved data from the Pond Inlet airport weather station situated at 80 km from our site (for snow depth in April and May 1994, we had to use data from the Nanisivik weather station situated 150 km from our site). All climatic data including snow depth were recorded daily at those weather stations. Following Dickey et al. (2008), we used linear models to relate the data from our weather station to those from Pond Inlet (or Nanisivik) during periods of overlap. Strong relationships were found for most variables (e.g. daily snow depth values: $F_{1,464} = 959.2$, $P < 0.001$, $R^2 = 0.67$ for Pond Inlet; $F_{1,719} = 139.5$, $P <$

0.001 $R^2 = 0.14$ for Nanisivik). We used these relationships to predict missing values in our weather data. For winter 2009-2010, no snow depth data were available from any weather station; mean winter snow depth had to be estimated from a relationship between mean snow depth determined at our weather station and that obtained from our snow-melt transects in early spring during years of overlap ($F_{1,7} = 4.04$, $P = 0.084$, $R^2 = 0.37$). Since 1995, snow depth has been measured manually every other day from ca. 1 to 20 June on 50 stations along two 250-m transects located 100 m apart. This information was also used to determine the timing of snow melt (i.e. when snow had completely disappeared).

Prior to snow melt, we dug snow pits at 60 random locations throughout our study site in 2010 (19- 30 May) and 2011 (19- 26 May). At each site, a temperature logger (I-button) had been set at ground level the previous fall to record sub-nivean temperatures at 5-h intervals during winter. We measured snow depth, the number of recognizable layers and their respective thickness, hardness, density, snow grain size and type, following the protocol developed by M. Bernier and Y. Gauthier (personal communication) and the snow classification by Fierz et al. (2009). We also measured the temperature gradient of each snow profile by taking from five to six measurements at varying depth.

We modelled the snow conditions with the SNOWPACK software using our meteorological data as input variables (see Bartelt and Lehning 2002, Lehning et al. 2002a, b for detailed information and methods; Annexe 2). This allowed us to estimate the evolution of the snowpack on a daily basis throughout the winter and especially to estimate snow density at ground level, a key parameter that we could not directly measure during winter. We used the data from our snow profiles made in May 2011 to test SNOWPACK predictions for density of the ground-level snow layer. The weighted-average of snow density of the bottom 5 cm estimated from the snow profiles was 281.2 kg m^{-3} (95% confidence interval: 267.6-294.7 kg m^{-3}). The SNOWPACK estimate for that layer on the same dates (278.8 kg m^{-3}) was very close and well within the confidence interval, which suggests that SNOWPACK performed well.

We could not estimate snow density with SNOWPACK for winter 2009-2010 due to lack of daily snow depth data. As a substitute, we used the average snow density measured at ground level in our snow pits that year (146.8 kg m^{-3}). Density measured before the onset of snowmelt should be representative of the mean winter density because major changes in density usually do not occur prior to that (McKay and Gray 1981).

Statistical analyses

Our premise was that snow cover did not generate the lemming cycle but could modulate some of its parameters. Therefore, we worked in three steps to examine if some descriptive variables of snow cover explained variations in the amplitude and periodicity of annual fluctuations in lemming density: we generated cycles using three different models, we extracted residuals from the relations between these modelled cycles and our observed annual lemming densities, we regressed the obtained residuals with the snow variables that we thought could affect lemming populations. We reasoned that these analytical steps would allow us to assess directly the effects of individual snow cover variables on lemming abundance while removing the potential effects of the other (unknown) variables generating the cycles.

Generation of cycles

We first generated a sinusoidal model with a 4-year periodicity, the average periodicity of brown lemming cycles at our site (Gruyer et al. 2008) using the following equation:

$$(1)\ x_t = 2\sin(2\,t\,\pi)$$

where x_t stands for the ln (brown lemming summer density + 0.01) in year t.

We then modelled the observed lemming cycle by adjusting first- and second-order autoregressive models (Stenseth et al. 1996, Stenseth 1999) using the following equations:

$$(2)\ x_t = \beta_0 + \beta_1 x_{t\text{-}1} + \varepsilon_t$$

$$(3)\ x_t = \beta_0 + \beta_1 x_{t\text{-}1} + \beta_2 x_{t\text{-}2} + \varepsilon_t,$$

where β_0 is the coefficient of the intercept, β_1 and β_2 represent the first- and second-order autoregressive coefficients and ε_t is the error term.

Extraction of residuals

To obtain residuals, we calculated the differences between the annual densities predicted by the three above models ($\hat{x}_t$) and our annual observed values of lemming densities.

Regression of residuals with snow variables

We used seven variables descriptive of snow cover: mean daily snow depth, mean daily density of the bottom 5 cm of the snow pack, mean daily temperature of the sub-nivean space, date at which the snow cover became established, date at which the hiemal threshold (defined as 20 cm snow depth; Pruitt 1970) was reached, date when snow had completely melted, and duration (in days) of the snow cover. We also added year as a continuous variable in our model to test for any temporal trend in population densities. We tested for multicollinearity among snow variables. Duration of snow cover and time of snow establishment were highly correlated ($r = -0.87$, $t = -7.09$, $df = 16$, $P < 0.001$) and these two variables were thus never used in the same model. Correlations among the remaining independent variables (all, ≤ 0.61) were considered acceptable (Grewal et al. 2004).

To avoid model saturation due to our relatively short time series (17 and 18 years according to habitat), a maximum of three variables were used at the same time in each model. All models were compared using second-order Akaike's information criterion adjusted for small sample size (AICc) and AICc weight (Burnham and Anderson 2002). All analyses were conducted in R 2.11 (R Development Core Team 2010). Mean values are presented with SE throughout.

Results

Lemming cycles

Throughout the study period, brown lemmings showed a fairly regular population cycle (Fig. 1) of high amplitude with peaks occurring every 3-4 years. During peak years, densities reached up to 41.4 lemmings ha^{-1} in the wet grid and 20.4 lemmings ha^{-1} in the mesic grid. During the low phases, densities were as low as 0.07 lemmings ha^{-1} in both habitats. Based on the mean densities for peak and low years obtained with live trapping, this represents 37-fold and 94-fold variations in the wet and mesic grids, respectively.

Snow variables

Most of the seven snow variables examined showed moderate to large fluctuations over the 18-year period (coefficient of variation ranging from 3.9 to 27.8 %) and only two of them showed a temporal trend (Fig. 2). Mean winter snow depth tended to increase ($F_{1,16} = 4.31$, $P = 0.054$) and date of establishment of the hiemal threshold occurred earlier over time ($F_{1,16} = 8.69$, $P = 0.009$). These trends are consistent with those reported elsewhere in the Arctic (SWIPA 2011).

Modelling of cycles

Whereas the sinusoidal approach always generated a cycle and thus allowed extraction of residuals between the generated cycle and the observed values, the same was not necessarily true with the autoregressive approach. Only the first-order autoregressive model yielded a discernible cyclic pattern of fluctuations in the mesic grid, though the fit was not as good as with the sinusoidal model. None of the autoregressive (i.e. first- and second-order) models yielded a cycle in the wet grid, and thus the effect of snow variables was not tested on those residuals.

Effect of snow variables on lemming abundance

Mesic habitat

Model selection for residuals of brown lemming summer density from the sinusoidal model indicated that some snow variables affected lemming density in the mesic grid (Table 1). One variable appeared most influential, mean winter snow depth (cumulative AICc weight across models = 0.99). Models including ground temperature and mean winter density of the bottom snow layer were close competitors (ΔAICc = 0.61 and 0.94, respectively). However, across models snow density had more weight than ground temperature (cumulative AICc weight = 0.32 and 0.22, respectively). Snow depth was positively related to lemming densities ($F_{1,15} = 6.83$, $P = 0.020$, $R^2 = 0.31$; $\beta = 28.2 \pm 10.8$; Fig. 3) whereas snow density was negatively related ($F_{1,15} = 4.58$, $P = 0.049$, $R^2 = 0.23$; $\beta = -0.017 \pm 0.008$; Fig. 3). There was a positive, though non-significant, trend between lemming density and ground temperature ($F_{1,15} = 2.56$, $P = 0.131$, $R^2 = 0.15$; $\beta = 0.44 \pm 0.28$). Adding snow depth and density to the sinusoidal model improved its fit with the observed data (Fig. 4). For instance, the model with snow variables predicted well the low lemming density observed in summer 1999 and the increase that started in 2010 and lead to a peak in 2011, 3 years after the previous peak instead of 4 years as in the preceding ones. This suggests that snow characteristics may not only affect the amplitude of lemming fluctuations but possibly also their periodicity. However, the sharp 2005 decline remained unpredicted.

The same analysis based on the residuals from the first-order autoregressive model also suggested that brown lemming density was affected by mean snow depth (cumulative AICc weight = 0.76; Table 2) as it was positively related to it ($F_{1,15} = 4.68$, $P = 0.047$, $R^2 = 0.24$; $\beta = 26.5 \pm 12.3$). Even though ground temperature and snow density in the bottom layer were not retained in the model selections, lemming density also showed a positive trend with ground temperature ($F_{1,15} = 2.43$, $P = 0.140$, $R^2 = 0.14$; $\beta = 0.47 \pm 0.30$) and a negative one with snow density ($F_{1,15} = 2.45$, $P = 0.139$, $R^2 = 0.14$; $\beta = -0.014 \pm 0.009$).

Wet habitat

In the wet grid, model selection for residuals of brown lemming summer density from the sinusoidal model indicated that the null model was preferred (Table 3). Although a model with density of the bottom snow layer was a close competitor (ΔAICc = 0.32), overall the evidence for this effect was moderate (cumulative AICc weight = 0.42). There was a weak trend for a negative relationship between lemming abundance and snow density ($F_{1,16} = 2.48$, $P = 0.135$, $R^2 = 0.13$; $\beta = -0.012 \pm 0.008$). Adding snow density to the sinusoidal model slightly improved the fit of the model to the observed data as the low abundance in 1995, as well as the high abundance in 2010 were better predicted (Fig. 5).

Discussion

The logic of our approach was to remove analytically the cyclicity in lemming population fluctuations in order to better assess the effect of snow parameters on their abundance. This approach is analogous to detrending a time series before evaluating the effects of covariates (Votier et al. 2009). Autoregressive models were not always successful in generating cyclic oscillations with our data. Nonetheless, it is reassuring to find that, whether we detrended the data with a sinusoidal or an autoregressive model, the effect of snow variables on residual variations in lemming abundance remained qualitatively the same. This suggests that our analysis was not highly sensitive to the model used to control for the cyclic pattern of fluctuations.

Our analysis provides support for the hypothesis that winter snow cover can affect the amplitude and even possibly the periodicity of lemming population cycles in the High Arctic. Based on the relationships presented in Fig. 3, a twofold increase in snow depth could increase summer density of brown lemmings by a factor of 17 in mesic habitat whereas a twofold increase in snow density could decrease their density by a factor of 27. Evidence for an effect of snow cover in the wet habitat was weaker, with only a possible negative effect of snow density on brown lemming abundance. Although brown lemmings tend to prefer wet habitats in summer, when our trapping occurred, they can use both habitats (Morris et al. 2000, Gruyer et al. 2010) and during winter they actually tend to avoid wet habitats where snow accumulation is shallower (Duchesne et al. 2011b). If brown lemmings concentrate in wet habitat during the summer, especially when densities are low, this may distort the amplitude locally, and possibly weaken our ability to detect an effect of snow cover. However, considering that the mesic habitat composes the majority of the landscape of our study area (85 %), patterns observed in this habitat may be more representative of the population at large.

Depth is a key component of the snow cover, influencing most other snow-related parameters (Pomeroy and Brun 2001). For instance, greater snow depth will permit higher sub-nivean temperatures and lower snow layers will be less subject to compaction (by wind for example) and thus have lower densities. Higher sub-nivean temperatures will reduce the physiological stress that lemmings undergo during winter (Chappell 1980, Casey 1981). As deeper snow will provide a more favourable thermal environment (Duchesne et al. 2011b, Reid et al. 2012) and potentially reduced predation (Duchesne et al. 2011b), survival should be higher. Although we found only weak positive trends of sub-nivean temperature on density, ground temperature was not measured in the areas of deepest snow but at standard weather stations. When snow accumulation is high, this measurement bias could have a disproportional effect in areas conducive to high snow accumulation (i.e. depressions) and thus lead to an improvement in sub-nivean temperature in areas of deepest snow. Lemming winter habitat selection is also greatly influenced by topography, with preferred habitat being under greater snow depth (Sittler 1995, Duchesne et al. 2011b, Reid et al. 2012).

Deeper snow could also improve winter reproduction, a condition believed to be essential for summer outbreaks in lemmings (Ims and Fuglei 2005, Ims et al. 2011). By providing a better thermal environment, it could enhance winter survival of young after weaning. In contrast, Bilodeau et al. (2013d) found no effect of experimentally increased snow on reproductive effort based on proportion of winter nests with reproduction. However, they could not measure other parameters such as litter size or early survival of weaned young.

Snow density is a difficult parameter to monitor in the field throughout the winter and this is why we had to resort to a modelling approach (SNOWPACK) based on weather data collected at the study site. SNOWPACK has been validated in multiple studies (Lundy et al. 2001, Hirashima et al. 2004, Nishimura et al. 2005, Rasmus et al. 2007) and improved over the years (Schweizer et al. 2006) although it has been mostly used in alpine environments to forecast avalanche risks. In the one year where we could validate the predictions of the model with field density measurements, predicted and observed values were in good agreement, but more validations of this model under arctic conditions are desirable.

Snow density at the base of the snowpack is important for lemmings because this is where they live during the winter. A dense, hard snow pack may be less conducive to the formation of a sub-nivean space and less suitable for digging and tunnelling (Sanecki et al.

2006). Lemmings may need to expend more energy to dig in dense snow or, in the worst case, dense snow could prevent them from moving to new or better feeding sites, thereby reducing food availability. Both situations could lead to increased winter mortality, and thus it was not surprising to find that dense snow had a negative effect on lemming abundance.

Contrary to what Gilg et al. (2009) found in Greenland, temporal variations in the establishment, duration or melting of the snow cover did not seem to play any major role in modulating lemming abundance even though we found a significant temporal trend in the hiemal threshold date, which is now reached earlier in fall than in the past. Because our study site is located in the High Arctic where the winter is very long (~ 8 months), inter-annual variability in winter length is perhaps too low to have significant effects. To modulate peaks, reproduction and survival of young under the snow may be more important than adult survival (Aars and Ims 2002). Therefore, what happens in fall (i.e. faster establishment of the hiemal threshold) could be less important, especially if reproduction occurs mostly in late winter or early spring. Unfortunately, we have no information on timing of reproduction under the snow.

At our study site, temperature has increased, mostly in fall and somewhat in summer, but not in winter (Gauthier et al. 2011), which remains very cold. At other sites where annual temperature is warmer and where small mammal cycles have collapsed, such as East Greenland and Fennoscandia, researchers have linked the latter phenomenon with climatic changes that occurred mostly in winter, such as freeze-thaw cycles, freezing rain and ground-icing events (Hörnfeldt 2004, Hörnfeldt et al. 2005, Kausrud et al. 2008). Winter ground-icing events in the Canadian High Arctic are relatively rare and no ice was found at the bottom of the snow profiles that we dug. Furthermore, as the SNOWPACK model provides estimates of the density of every snow layer, it can help in detecting the occurrence of icing events. No such events were detected based on the long-term climatic record at our study site.

The temporal trend towards greater snow depth that we detected, which should have a positive effect on lemming population growth based on our results, and the faster establishment of the hiemal threshold, may both result from the recent increase in fall air temperature (Gauthier et al. 2011, SWIPA 2011). Indeed, higher temperatures may have increased air humidity, which in turn may have accentuated precipitation. In this context, it is not surprising that lemming cycles have not collapsed in our region of the Arctic.

Although our analysis provided some insights on the role of snow cover in brown lemming population dynamics, it was somewhat limited by the climatic data available. A first problem is that those data came from standard weather stations, which may not always accurately represent conditions experienced by lemmings in their micro-habitat. A second problem was that some of the variables that we used were not directly measured but had to be indirectly derived (e.g. snow density). A third problem is that several measurements were taken at a single site (e.g. sub-nivean temperature, snow depth) and thus did not take into account spatial variability. More accurate field measurements of snow properties and of its persistence taken during the entire course of the winter and in the different habitats occupied by lemmings would be important to validate and strengthen our findings. However, accessing study sites in winter, particularly in the Canadian Arctic, is logistically difficult and very costly. Improvements in automated recording systems could alleviate some of these problems. For instance, systems recently developed to automatically record snow conductivity and density (Morin et al. 2010) could vastly improve our abilities to monitor changes in the thermal properties of the snow over the winter. Nonetheless, finding the most relevant climatic variables at the scale experienced by small mammals will remain a challenge.

Table 1. Model selection for the effect of snow variables on residuals of summer brown lemming density in the mesic habitat from the sinusoidal model. Dens = mean snow density of the bottom 5-cm of the snow pack over the winter, Depth = mean daily snow depth over the winter, Snowdate = date at which the snow cover became established, Hiemal = date of establishment of the hiemal threshold, Melt = date when snow has completely melted, Snowperiod = length of the snowperiod, Temp = mean daily temperature of the sub-nivean space over the winter, Year = continuous variable (temporal trend), K = number of parameters.

Rank	Model	Δ AICc	AICc Weight	K
1	Depth	0.00	0.22	1
2	Depth + Temp	0.61	0.16	2
3	Depth + Dens	0.94	0.14	2
4	Depth + Snowperiod	1.84	0.09	2
5	Depth + Snowdate	2.12	0.08	2
6	Depth + Dens + Snowperiod	2.21	0.07	3
7	Depth + Dens + Temp	2.60	0.06	3
8	Depth + Dens + Snowdate	2.85	0.05	3
9	Depth + Hiemal	3.45	0.04	2
10	Depth + Melt	3.49	0.04	2
11	Depth + Year	3.49	0.04	2
12	Null	6.27	0.01	0

Table 2. Model selection for the effect of snow variables on residuals of summer brown lemming density in the mesic habitat from the 1st order autoregressive model. See Table 1 for definition of variables.

Rank	Model	Δ AICc	AICc Weight	K
1	Depth	0.00	0.27	1
2	Depth + Temp	1.12	0.15	2
3	Null	2.17	0.09	0
4	Temp	2.60	0.07	1
5	Depth + Snowdate	2.88	0.06	2
6	Depth + Dens	2.92	0.06	2
7	Depth + Snowperiod	3.00	0.06	2
8	Depth + Hiemal	3.02	0.06	2
9	Depth + Melt	3.42	0.05	2
10	Depth + Year	3.48	0.05	2

Table 3. Model selection for the effect of snow variables on residuals of summer brown lemming density in the wet habitat from the sinusoidal model. See Table 1 for definition of variables.

Rank	Model	Δ AICc	AICc Weight	K
1	Null	0.00	0.22	0
2	Dens	0.32	0.19	1
3	Depth	2.02	0.08	1
4	Depth + Hiemal	2.16	0.08	2
5	Dens + Hiemal	2.23	0.07	2
6	Temp	2.67	0.06	1
7	Depth + Dens	2.92	0.05	2
8	Depth + Year	2.96	0.05	2
9	Dens + Temp	3.15	0.05	2
10	Depth + Snowperiod	3.81	0.03	2

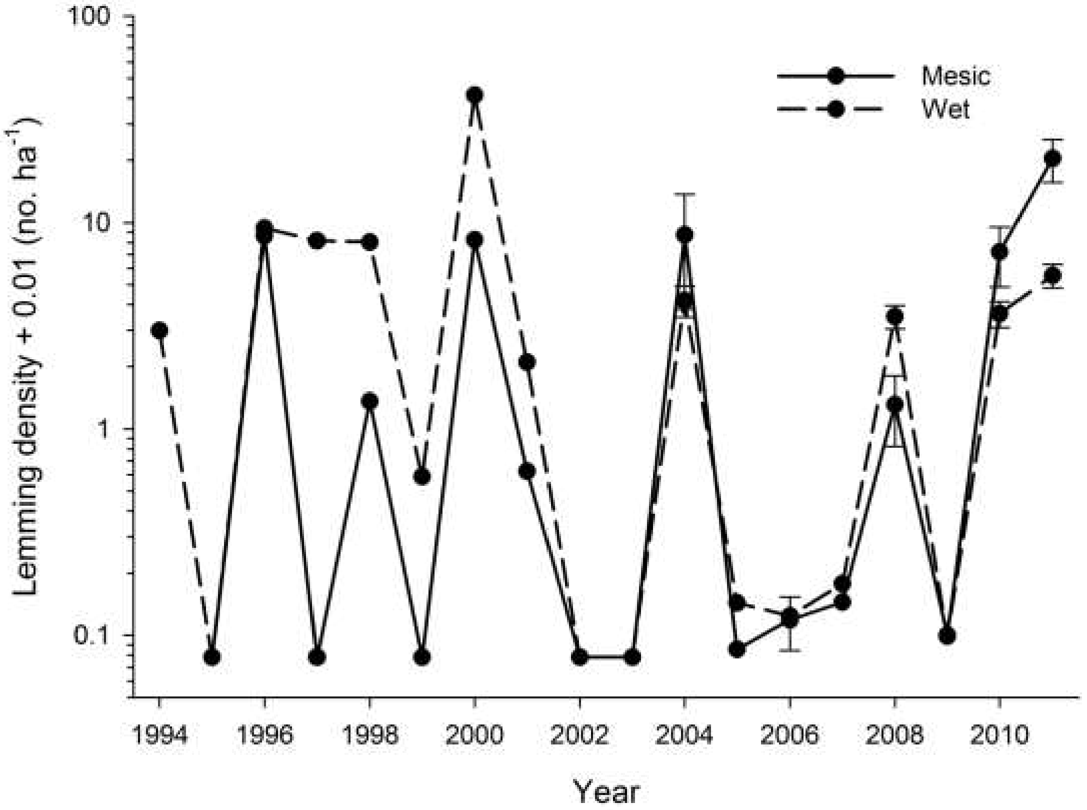

Figure 1. Time series of summer brown lemming densities (no. ha^{-1}) in the mesic and wet grid from 1994 to 2011. Error bars represent SE (only available for the period where data were from live trapping).

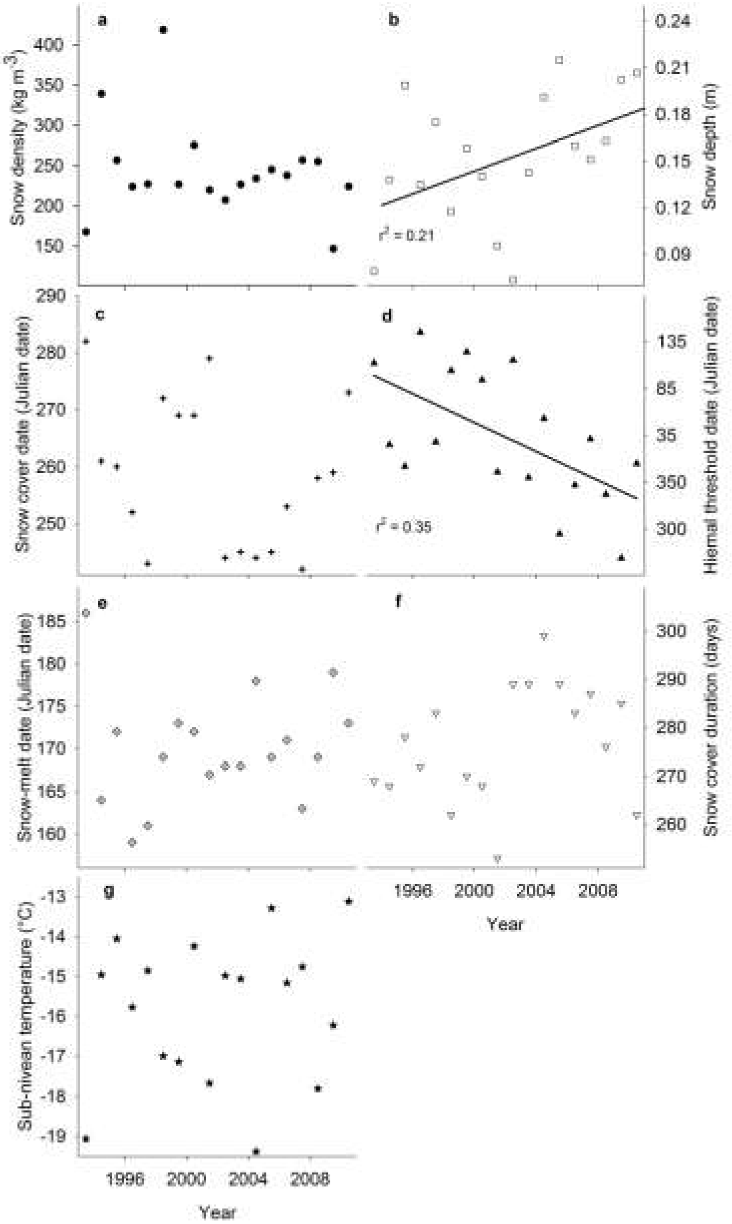

Figure 2. Time series of mean density of the bottom 5 cm of the snow pack over the winter (**a**; *black circles*), mean daily snow depth over the winter (**b**; *white squares*), date at which the snow cover became established (**c**; *black crosses*), date of establishment of the hiemal threshold (**d**; *upward black triangles*), date when snow has completely melted (**e**; *grey diamonds*), duration of the snow cover (**f**; *downward white triangles*), and mean daily temperature of the sub-nivean space over the winter (**g**; *black stars*), from winter 1993-1994 to 2010-2011 on Bylot Island, Nunavut. Solid lines represent temporal trends ($P \leq 0.05$).

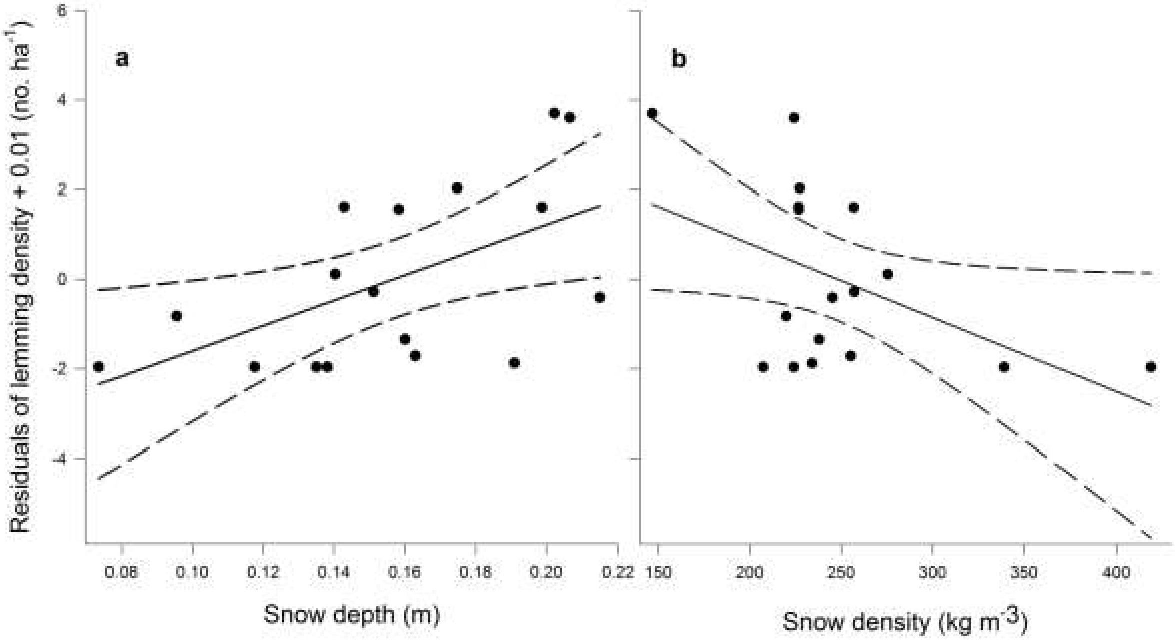

Figure 3. Plot of the residuals of brown lemming summer density [ln(density+0.01)] from the sinusoidal model in relation to the mean daily snow depth (**a**) and the mean density of the bottom 5 cm of the snowpack (**b**) from 1995 to 2011. Solid line is the regression line and dashed lines show 95% confidence interval.

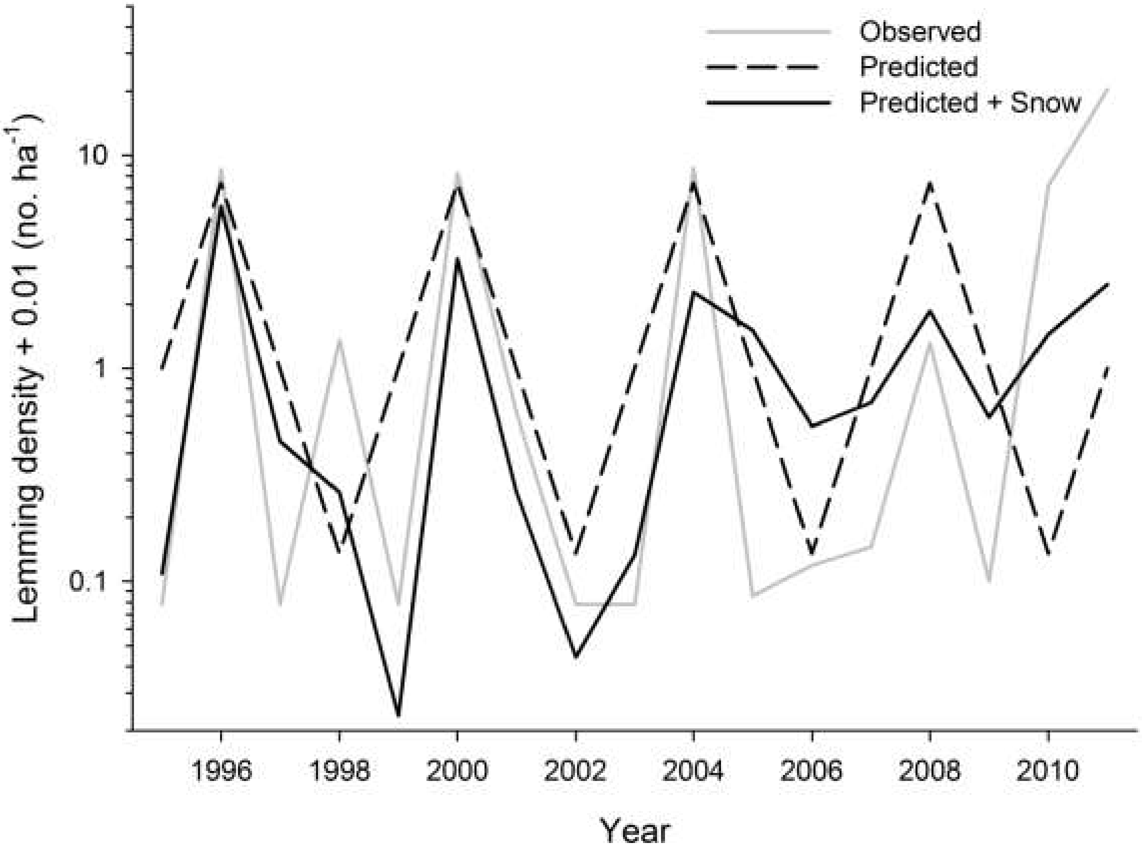

Figure 4. Time series of brown lemming summer densities (no. ha^{-1}) in the mesic grid from 1995 to 2011. Observed values (*Observed*), values predicted from the sinusoidal model (*Predicted*) and values predicted from the sinusoidal model with snow depth and snow density (*Predicted + Snow*) values are shown.

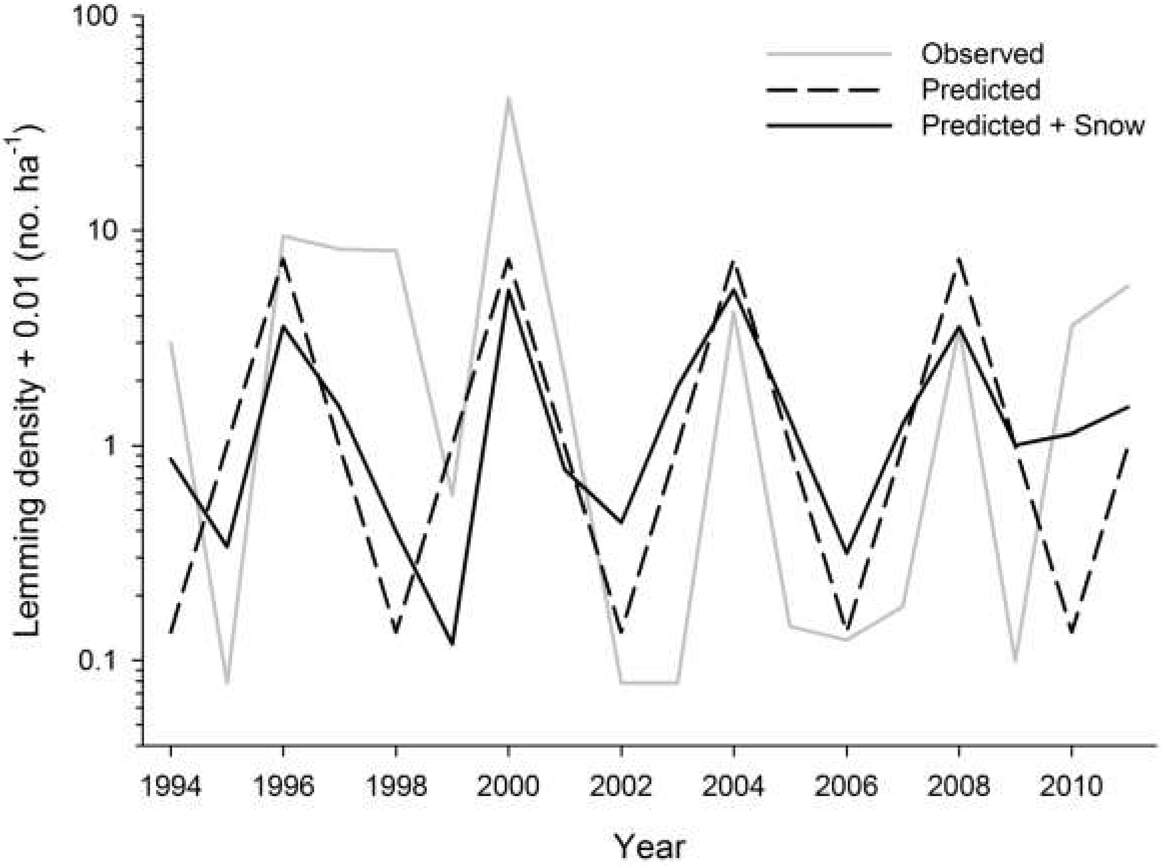

Figure 5. Time series of brown lemming summer densities (no. ha^{-1}) in the wet grid from 1994 to 2011. Observed values (*Observed*), values predicted from the sinusoidal model (*Predicted*) and values predicted from the sinusoidal model with snow density (*Predicted + Snow*) are shown.

Chapitre 3

Evaluation of a technique to trap lemmings under the snow

Bilodeau, F., Kenney, A., Gilbert, B.S., Hofer, E., Gauthier, G., Reid, D.G., Berteaux, D. & Krebs, C.J. 2013. Evaluation of a technique to trap lemmings under the snow. Arctic 66: 32-36.

Résumé

Nous avons tenté de capturer des lemmings sous la neige dans leur habitat hivernal préféré en utilisant des boîtes en forme de cheminée à deux sites situés dans l'Arctique Canadien. Les boîtes ont été utilisées par les lemmings durant l'hiver mais nous avons eu un très faible succès de capture en avril et mai. Contrairement à la majorité de l'hiver, les températures sous-nivales étaient plus froides que les températures de l'air pendant que nous avons trappé au printemps. Nous émettons l'hypothèse que notre faible succès est dû au déplacement des lemmings des sites de fort enneigement, où nos boîtes étaient installées, vers ceux de faible enneigement ou vers la toundra exposée. Nous suggérons que les boîtes de trappage pourraient être plus utiles si le trappage se faisait plus tôt au courant de l'hiver.

Abstract

We attempted to live trap lemmings under the snow in their preferred winter habitat at two sites in the Canadian Arctic using chimney-like boxes. Boxes were used by lemmings during winter, but we had very low trapping success in April and May. In contrast to most of the winter, sub-nivean temperatures became colder than ambient air temperatures in spring when we trapped. We hypothesize that our low success resulted from lemmings leaving the deeper snow areas where our boxes were located and moving to shallower snow or exposed tundra. We suggest that the trapping boxes could be successful if trapping occurred earlier during winter.

Introduction

Our understanding of the winter ecology of Arctic lemmings (*Dicrostonyx* and *Lemmus* spp.) remains poor despite almost a hundred years of study (Elton 1924). In recent decades, new information has been acquired (MacLean et al. 1974, Sittler 1995, Korslund and Steen 2006, Kausrud et al. 2008, Gilg et al. 2009, Ims et al. 2011, Duchesne et al. 2011b, Reid et al. 2012), but much has been indirect. Lemmings live under the snow for up to eight months in the Arctic and build nests of vegetation as insulation from the cold. Much of our understanding of their winter ecology comes from sampling and analysing these nests at snow-melt (MacLean et al. 1974, Sittler, 1995).

Our understanding would increase dramatically if we could live-trap lemmings through the snow, and employ mark-recapture, radio-telemetry and repeated tissue sampling. Some early attempts to trap small rodents through the snow had some success. For instance, in Russia, Denisenko (1986) dug chimney-like shafts through the snow, installed snap traps near active sub-nivean lemming burrows, covered the traps and then added back the snow. Though successful, such methods are time-consuming and result in repeated disturbance of the snow pack and subnivean space, altering the habitat significantly (Fay 1960, Iverson and Turner 1969). Therefore, we tested a less disruptive technique using trapping boxes that necessitate very little or no digging to access traps and allowed repeated access, as required by live-trapping techniques. These boxes were based on the design of Pruitt (1959), and have been used by Korslund and Steen (2006) to trap voles through the snowpack. In this paper, we describe the use of trapping boxes, and a test of their effectiveness in trapping lemmings in winter at two sites in the Canadian High Arctic. Because the technique was not very effective during the time periods we tested it, so we provide some testable hypotheses to explain this failure and recommendations on potential improvements.

Methods

Study area

The study was conducted on the south plain of Bylot Island, Sirmilik National Park, Nunavut (73° 08 'N, 80°00' W) and on Herschel Island, Yukon (69° 34'N, 138° 55'W). On Bylot, the study area (70 km^2) was comprised of upland plateaus and rolling hills dominated by mesic tundra and wetter lowland areas with tundra polygons, thaw lakes and ponds. Small, intermittent streams running through upland areas supported riparian wetland vegetation (Duchesne et al. 2011b). On eastern Herschel Island (50 km^2), two types of drier upland plant community, - tussock tundra and prostrate-shrub heath, - were dominant, with infrequent small wetlands (Reid et al. 2012). Both study areas supported cyclic populations of collared lemming (*Dicrostonyx groenlandicus*) and brown lemming (*Lemmus trimucronatus*; Gruyer et al. 2008, Krebs et al. 2011). On Herschel Island, lemmings were in their low phase in spring 2009 (Krebs et al. 2011). On Bylot Island, both species were in their increase phase in spring 2010 and brown lemmings increased further to reach a peak in spring 2011 though collared lemming populations had crashed before spring (Gauthier, G. and Bilodeau, F. unpublished data).

Selecting trapping sites

Trapping occurred in springs 2010 and 2011 on Bylot Island and spring 2009 on Herschel Island. We selected trapping sites with a high probability of winter use by lemmings. Wintering lemmings prefer heterogeneous micro-topography and deep snow cover (≥60 cm), conditions that are typically found in hilly mesic tundra and along gullies bordering streams (Duchesne et al. 2011b). During early June 2009 on Bylot, we measured snow depth at 100 sites and pre-selected those with depth >60 cm. After snow-melt, we checked these sites for evidence of lemming use during winter, and then selected 40 sites with the highest density of sign to install the trapping boxes. Boxes were spread over 980 ha and the distance between boxes ranged from 42 to 155 m. On Herschel, we mapped lemming winter nests after snow-melt in June 2007 and June 2008. In September 2008 we chose trapping sites where there had been clusters of winter nests the previous two winters, and placed 27 trapping boxes on one 9 ha area, and four trapping boxes on another 2.5 ha area.

Trapping boxes

To allow placement of live traps at ground level and allow access to traps through the snow pack, we built chimney-like boxes (60 cm high, 40 cm long and 20 cm wide) of 1.3 cm plywood with a removable lid insulated with 5 cm of foam (Fig. 1). Once installed, trapping boxes were secured to the ground with two 2 m metal stakes to resist wind and disturbance by caribou. The interior floor of a box was large enough for a Longworth® live trap with extra space for lemmings to move around. Lemmings could enter the boxes through two 5 cm diameter, 20 cm long, plastic tubes located on opposite sides at ground level. At both study areas, a trap with cotton bedding was locked open and placed inside each box at the end of summer. At Herschel, just before snow-melt in April 2009, we opened the boxes, examined them for signs of lemming use, and baited the traps with apple. The traps were set for two days, checking every two hours. At Bylot Island, we opened the boxes in early May, and set traps with cotton bedding, and apples and peanut butter as bait. We visited traps every six hours for 10 days in May 2010 and 5 days in May 2011. We inferred lemming use of boxes during winter based on sign (faeces or nests) left in the boxes. We judged lemming species, and determined whether reproduction had occurred, based on faeces size, shape and colour according to Duchesne et al. (2011a).

Temperature loggers (i-buttons®) were installed on the floor of some boxes on Bylot in late August (16 in 2009 and four in 2010) and outside boxes at ground level (33 and 22 at sites under ≥ 60 cm of snow during winter, and 27 and 38 at random sites under < 60 cm of snow in 2009 and 2010, respectively) to compare temperatures inside the boxes with those in the surrounding sub-nivean space.

Snowmelt

We monitored snowmelt by measuring snow depth along two 250 m long transects every two days until all snow had disappeared. This started on 19 May each year on Bylot, and 21 May on Herschel.

Results

At Herschel Island, on the 2.5 ha area, all four boxes, when checked in late winter, contained winter nests built by brown lemmings but later taken over by weasels (likely *Mustela nivalis* judging by faeces size). Each box had remains of one or two lemmings. On the 9 ha area, only one box had a winter nest (built by a collared lemming) while 12/27 had sign (faeces) that the boxes had been visited at some time by collared lemmings. Winter nests were also found in the vicinity (< 5 m) of 4 boxes. Two days after baiting, the apple had disappeared from four boxes but only one juvenile male collared lemming (28.5g) was captured.

At Bylot Island, lemmings left sign indicating use or visitation at 13 of 40 boxes in 2010 and 31 of 40 boxes in 2011. They had built nests in some boxes (0/40 in 2010 and 10/40 in 2011). In 2010, boxes were used by collared lemmings (7/40), brown lemmings (2/40), or by both species (4/40), but only brown lemmings used the boxes in 2011. Signs of reproduction were found in one box in 2011 and none in 2010. Winter nests were also found in the vicinity of 15 boxes in 2010 and 19 in 2011. Stoats (*Mustela erminea*) used some boxes (1/40 in 2010 and 4/40 in 2011) to store lemmings they had killed in the surrounding area or, in one case, the lemmings occupying a nest built inside a box. No lemmings were caught in the boxes in spring, despite all the sign of winter use and even though lemmings were at high densities during both winters (Gauthier, G. and Bilodeau, F. unpublished data).

Snow depth at the end of winter on Bylot Island was near average in 2011 but much deeper in 2010 (Fig. 2). Our trapping occurred during early snowmelt in both years. Snowmelt was faster during trapping in 2011 (6.2 cm loss in five days) compared with 2010 (3.5 cm loss in ten days). Tunnels leading into the boxes were not blocked by hard snow or ice, suggesting that our traps could have been accessed easily by lemmings during the trapping period.

From early December to late April on Bylot, sub-nivean temperatures were higher than ambient air temperatures, whereas temperatures inside boxes were slightly higher than those at random sub-nivean sites with <60 cm of snow but lower than those at sites with ≥60 cm of snow (Fig. 3). However, the situation was reversed during May, when trapping occurred. In 2010 and 2011, respectively, average temperatures in boxes were 6.6 °C and 6.3 °C lower than ambient, 0.4 °C and 1.4 °C lower than random sites, but 1.0 °C higher than sites with ≥60 cm of snow in 2010 and 1.1°C lower in 2011.

Discussion

Contrary to previous studies that used boxes similar to ours to trap voles under the snow (Sullivan et al. 2004, Korslund and Steen 2006), we had poor success trapping lemmings under the snow during late winter in the Canadian Arctic. Yet, lemmings used our trapping boxes extensively sometime during winter. On Herschel Island, where we were able to trap before snow melt, we caught one lemming and bait was eaten from several boxes. Lemming population density on Herschel was relatively low by spring that year (Krebs et al. 2011) and would have contributed to our low trapping success.

Snow is a good insulating material, as shown by the higher sub-nivean compared to ambient air temperatures we recorded during winter. Temperatures were also higher inside our boxes than at random sub-nivean sites in winter, so the boxes provided a suitable temperature regime for lemmings. Lemmings are attracted to warmer sub-nivean sites in winter (Duchesne et al. 2011b, Reid et al. 2012), so we presume that lemmings mostly used the boxes in winter However, in late winter or early spring, the temperature profile in the snow pack changes such that ambient air is generally warmer than the sub-nivean space. In May of both years, temperatures inside our trapping boxes were actually colder than those at all other sites available to lemmings. Therefore, lemmings had a clear thermal advantage in moving to exposed tundra without snow or sites with shallow snow, after this thermal inversion. We hypothesize that the colder temperatures inside boxes in May explain why we caught no lemmings on Bylot in that month.

When we were trapping on Bylot Island, snow had started to melt and snow depth was continually decreasing (Fig. 2). During melt, ice can form in the subnivean space potentially restricting access to food plants, and melt-water may flood low-lying areas. Lemmings may have moved out of areas with deeper snow pack in anticipation of these spring events and to gain better access to early growing plants on exposed tundra.

There is a concern that use of the boxes by weasels and stoats may have deterred lemmings from using the same boxes. However, brown lemmings readily go into live traps, even those baited to catch stoats (F. Bilodeau personal observations), so the past use of boxes and their traps by stoats is unlikely to be a factor reducing lemming trappability.

Conclusion

We hypothesize that trapping with our boxes would be more successful if conducted during winter and before the spring overturn of the temperature gradient in the snow pack. This could be tested at field sites with easier winter access than ours. To improve the insulative capacity of the boxes, especially before snow depth accumulates to 40 or 50 cm, we recommend increasing the thickness of foam insulation in the lid. Based on prior studies which successfully trapped small mammals during winter (Schweiger and Boutin 1995, Sullivan et al. 2004, Korslund and Steen 2006), trappability could also be improved by (i) deploying the boxes with baited traps prior to snow-fall so that the traps become an established feature of the environment for the target animals, and (ii) maintaining a fairly frequent live-trapping regime, including pre-baiting, within the boxes so that the bait provides fairly consistent and frequent positive reinforcement for rodents during the source of the winter. Differences in capture rates between boxes submitted to such trapping protocols compared to boxes without them should be tested to determine if the protocols improve capture success.

Figure 1. Picture of a trapping box at Herschel Island.

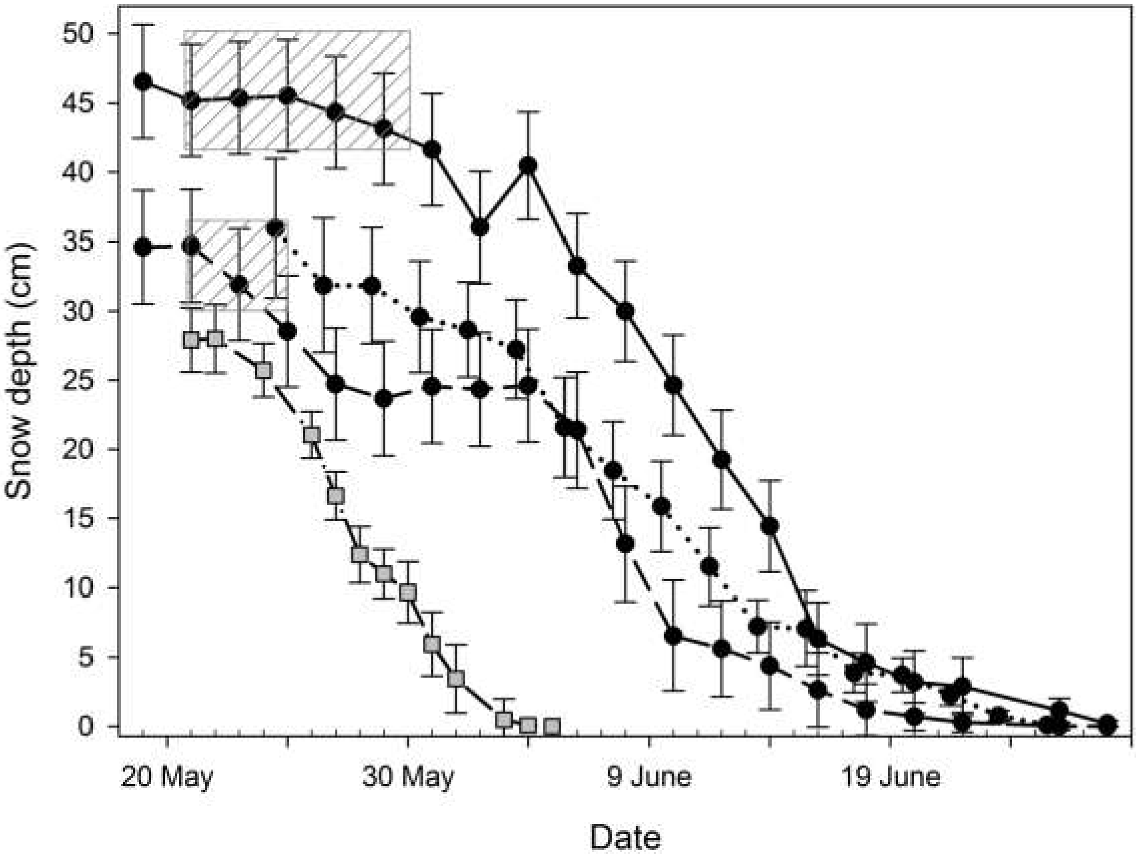

Figure 2. Change in snow depth along transects during snowmelt in spring 2009 on Herschel Island (gray boxes, dash-dot line) and in spring 2010 (solid line), 2011 (dashed line) and long-term average (dotted line) on Bylot Island (black circles). Error bars represent SE. Hatched areas represent when trapping occurred on Bylot each year.

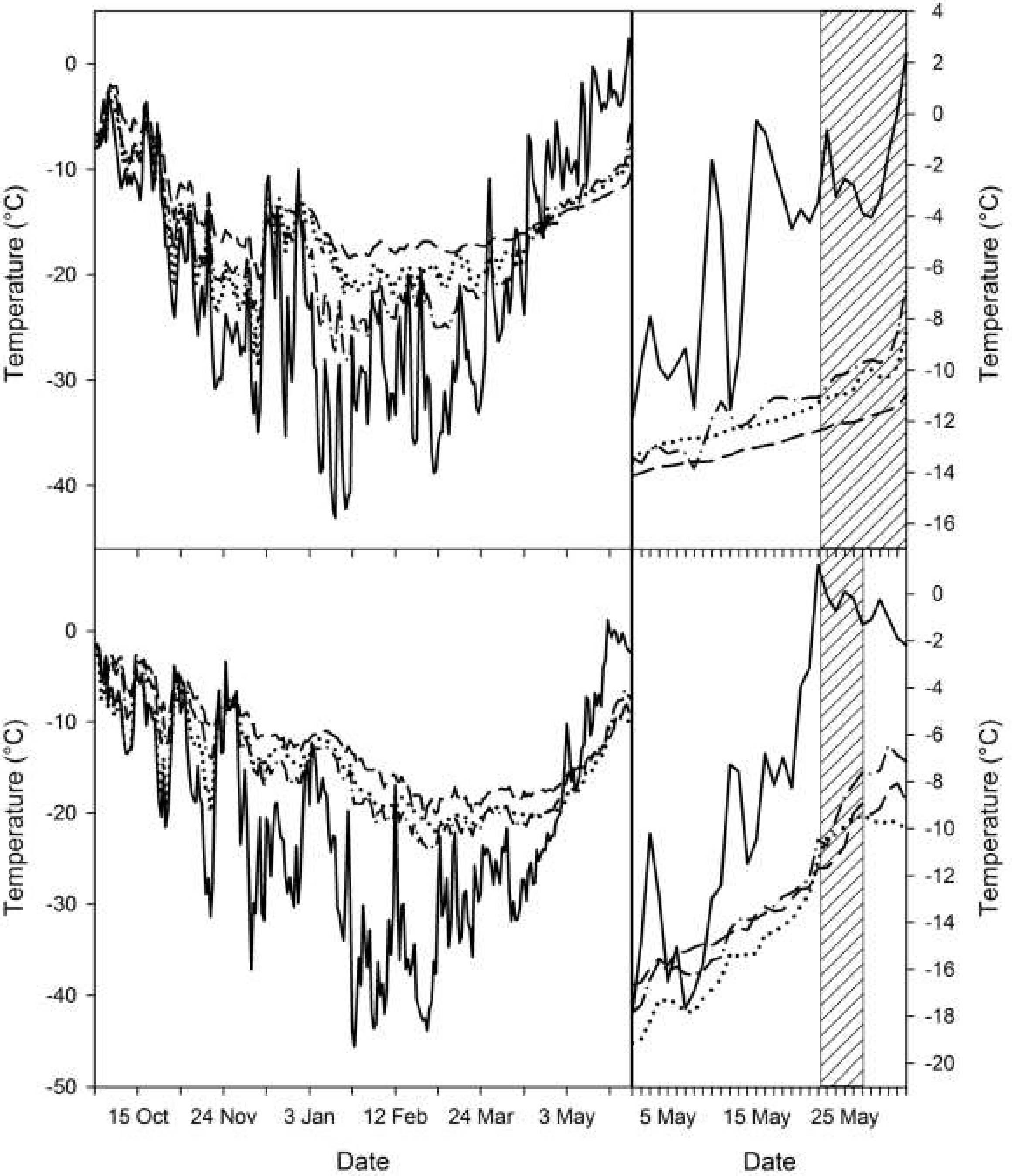

Figure 3. Daily temperature of ambient air (solid line), sub-nivean space under ≥60 cm of snow (dashed lines), subnivean space under <60 cm of snow (dashed-dotted lines) and trapping boxes (dotted lines) on Bylot Island during winters 2009-2010 (upper panel) and 2010-2011 (lower panel). Hatched area represents when trapping occurred.

Chapitre 4

Does lemming winter grazing impact vegetation in the Canadian Arctic?

Bilodeau, F., Gauthier, G. & Berteaux, D. Ce manuscrit sera soumis pour publication au journal Polar Biology

Résumé

Dans les environnements comme la toundra, où la productivité est faible, il a été proposé que les cycles de population multi-annuels des lemmings soient causés par l'épuisement des ressources alimentaires pendant l'hiver lors des années de pics d'abondance. Si la dynamique de population de lemming est contrôlée par les ressources alimentaires, nous prédisons (1) que le broutement hivernal devrait avoir un impact négatif sur l'abondance des plantes consommées, (2) que cet impact devrait être proportionnel à la densité de lemming et (3) que la forte pression exercée par un broutement hivernal élevé devrait se traduire dans une réduction de la croissance des plantes lors de l'été subséquent. Nous avons testé ces prédictions à l'île Bylot, Nunavut, Canada, où deux espèces de lemming sont présentes, le lemming brun (*Lemmus trimucronatus*) et le variable (*Dicrostonyx groenlandicus*). Nous avons installé 16 exclos dans leurs habitats hivernaux préférés (combes à neige) et échantillonné annuellement la biomasse des plantes vasculaires et des mousses à l'intérieur et à l'extérieur des exclos directement après la fonte de la neige et à la fin de la saison de croissance durant les étés 2009-2012, couvrant un cycle de population complet. Les plantes ont été exposées aux densités de lemming les plus élevées au cours des hivers 2009-2010 et 2010-2011, d'après l'abondance de nids d'hiver; les populations avaient chuté à l'hiver 2011-2012. Le broutement hivernal n'a eu aucun impact sur la biomasse totale de plantes vasculaires ou de mousses à la fonte de la neige. Seulement deux familles de plantes, les Polygonacées et les Caryophyllacées, deux plantes peu communes, ont montré un déclin. Aucun effet n'a été détecté sur les Salicacées, Poacées et Juncacées. Pour les mousses, un effet négatif a été détecté sur les *Polytrichum* mais seulement une année sur trois. Dans l'ensemble, la croissance des plantes durant l'été a montré peu de variation annuelle et n'a pas été réduite lors des années de fortes abondances de lemmings. Seulement la croissance des Polygonacées et des Caryophyllacées semble avoir été réduite par le broutement des lemmings. Nos résultats suggèrent qu'il est peu probable que l'épuisement de la nourriture durant l'hiver soit la cause du déclin des populations de lemming suite au pic d'abondance. D'autres facteurs limitent probablement les populations de lemmings et les empêchent d'atteindre des densités assez élevées pour épuiser leurs ressources alimentaires.

Abstract

In low productivity environments such as the tundra, it has been proposed that regular multi-annual population cycles of lemmings are driven by winter food depletion in years of peak abundance. If lemming population dynamics is controlled by food resources, we predict that (1) winter grazing should negatively impact the abundance of food plants, (2) this impact should be proportional to lemming density and (3) high lemming winter grazing pressure should result in a reduction of plant growth in the subsequent summer. We tested these predictions on Bylot Island, Nunavut, Canada, where two species of lemmings are present, the brown (*Lemmus trimucronatus*) and collared lemming (*Dicrostonyx groenlandicus*). We installed 16 exclosures in their preferred wintering habitat (snow beds) and sampled annually vascular and moss plant biomass inside and outside exclosures at snow-melt and at peak growth during the summer from 2009-2012, covering a full population cycle. Plants were exposed to the highest lemming densities during winter 2009-10 and 2010-11, as judged by winter nest abundance; populations had crashed by winter 2011-2012. Winter grazing had no impact on total vascular plant or moss biomass at snow-melt. Among plant families, only Caryophyllaceae, an uncommon plant, showed a decline. No effect was found on Salicaceae, Poaceae and Juncaceae. In moss taxa, a negative effect was found on *Polythichum* in only one year out of three. Overall, plant regrowth during the summer showed little annual variation and was not reduced in years of high lemming abundance. Only the summer regrowth of Polygonaceae and Caryophyllaceae appeared to be reduced by lemming grazing. Our results suggest that it is unlikely that food depletion during winter was the cause of the decline in lemming abundance following peak abundance. Other factors probably limit lemming populations and may prevent them from reaching densities high enough to exhaust their food resources.

Introduction

The relative importance of bottom-up (i.e. resources) vs top-down (i.e. predators) forces in controlling small mammal populations in northern ecosystems is still debated (Stenseth 1999, Oksanen et al. 2008, Gauthier et al. 2009, Oksanen et al. 2009). According to the bottom-up hypothesis, herbivore abundance is primarily influenced by the abundance and availability of their food resources (i.e. plants) (Polis and Strong 1996, Polis 1999). The exploitation ecosystem hypothesis (EEH) attempts to reconcile the latter view with a top-down control by stating that, although primary production determines the length of food chains and thus ultimately the abundance of higher trophic levels, in the absence of predators, herbivore populations can be high enough to negatively impact plant abundance (Oksanen et al. 1981, Oksanen and Oksanen 2000). In temperate and desert areas, small mammals can sometimes exert a significant impact on plant production and species composition (Bowers 1993, Hulme 1996, Howe and Brown 1999, Curtin et al. 2000, Howe et al. 2006, Fraser and Madson 2008), though not always (Báez et al. 2006; see also Moen 1990).

According to the EEH, in low productivity environments such as the Arctic, predator abundance should be too low to control herbivores and thus food webs should be dominated by plant-herbivore interactions (Oksanen 1983, Oksanen and Oksanen 2000). Support for this view comes from Fennoscandia and Alaska where small mammals can have a strong impact on plant production (Moen et al. 1993, Moen and Oksanen 1998, Huitu et al. 2003, Pitelka and Batzli 2007, Olofsson et al. 2012). Therefore, it has been proposed that regular, multi-annual population cycles of lemmings, the dominant small mammals of the tundra, are driven by food limitation in years of peak abundance in those areas (Oksanen and Oksanen 1992, Turchin et al. 2000, Turchin and Batzli 2001, Pitelka and Batzli 2007, Oksanen et al. 2008).

Lemming populations often reach their highest densities during late winter (Henttonen and Kaikusalo 1993, Reid et al. 1997, Gilg 2002, Kausrud et al. 2008) because reproduction starts under the snow (MacLean et al. 1974, Negus and Berger 1998, Duchesne et al. 2011b). However, lemmings have access to low-quality food during winter because photosynthetic activity and plant growth stops under the snow, a period that can last for up to 9 months in the High Arctic (Hansson 2002). Wintering lemmings show a strong selection for areas with deep snow and a heterogeneous micro-topography (Duchesne et al. 2011b), and thus will concentrate their foraging activity in those areas. Access to plants may sometimes be limited by snow conditions, for instance when their food becomes encapsulated in ice during melt-freeze or freezing-rain events (Callaghan et al. 2004, Korslund and Steen 2006). Therefore, it is during winter that food limitation should be most severe for lemmings.

If bottom up forces are the main factors controlling lemming population cycles, it is then during winter that the impact of lemming grazing on plants should be greatest, especially when densities are at their highest. A strong impact of lemmings on their winter food may not be sufficient to conclude that lemming population dynamic is controlled by resources, but it is a necessary condition to accept the hypothesis of a bottom-up control. Thus, according to the latter hypothesis, we predicted that (1) winter grazing by lemmings should negatively impact the abundance of food plants in their preferred habitats, (2) this impact should be proportional to lemming density and (3) high lemming winter grazing pressure should result in a reduction of plant growth in the subsequent summer. We tested these predictions in the Canadian High Arctic where two species of lemmings coexist, the brown (*Lemmus trimucronatus*) and collared lemming (*Dicrostonyx groenlandicus*). When they occur in sympatry, both species have relatively synchronous multiannual population cycles, with the brown lemming showing cyclic fluctuations of abundance of much greater amplitude than the collared (Batzli et al. 1983, Negus and Berger 1998, Gruyer et al. 2008).

Methods

The study site was located in the Qarlikturvik glacial valley (73° 08 'N, 80°00' W) on Bylot Island, Sirmilik National Park, Nunavut Territory. The study area (70 km^2) consisted of tundra polygons, thaw lakes and ponds forming wetlands at the bottom of the valley and is surrounded by drier mesic tundra on the nearby slopes and hills, which account for 90% of the landscape on the south plain of Bylot Island. The wetlands form grass/sedge meadows dominated by mosses and graminoids (*Dupontia fisheri*, *Eriophorum scheuchzeri* and *Carex aquatilis*; Gauthier et al. 1996). The mesic tundra is dominated by prostrate shrubs (*Salix* spp., *Dryas integrifolia*, *Cassiope tetragona*) with a sparse cover of forbs (*Saxifraga* spp., *Potentilla* spp., *Ranunculus* spp., *Pedicularis* spp.), graminoids (*Arctagrostis latifolia*, *Alopecurus alpinus*, *Poa* spp., *Luzula* spp.), mosses and lichens. Small, intermittent streams running through upland areas were also often located at the bottom of small gullies and were characterized by a thin band of wetland vegetation surrounded by mesic tundra. These sites were especially important for lemmings during winter.

The most important herbivores present on the island are the two lemming species, which are present throughout the year, and the greater snow goose (*Chen caerulescens atlantica*), which is present only in summer. No other small mammal species are present and large mammalian herbivores are absent. Other herbivores such as the rock ptarmigan (*Lagopus mutus*) and arctic hare (*Lepus arcticus*) are present at low densities. The two lemming species show some segregation in their summer habitat, with brown lemmings preferring wetter and collared drier habitats (MacLean et al. 1974, Batzli et al. 1983, Morris et al. 2011). During winter, both species share the same habitats and concentrate in mesic tundra and especially in small gullies along streams which are conducive to deep snow accumulation (Duchesne et al. 2011b, Reid et al. 2012). According to the literature, the two species have divergent diets, with brown lemmings preferring monocotyledons and mosses and collared lemmings preferring dicotyledons (Batzli and Jung 1980, Rodgers and Lewis 1985, 1986, Negus and Berger 1998). However, recent data based on DNA barcoding (Soininen et al. 2009) suggests that brown lemmings may actually be concentrating on dicotyledons (primarily *Salix* spp.) and mosses and eat little monocotyledons during winter at our study site (E. Soininen and G. Gauthier, unpublished data).

Lemming exclosures

In late May and early June 2009, before snow-melt, we systematically measured snow depth in 95 sites of high snow accumulation, mostly snow drifts caused by topography. We retained sites showing snow depth >60 cm, which are preferred by lemmings during winter at our study site (Duchesne et al. 2011b). These sites were visited after snowmelt and those showing signs of lemming use (winter nests or piles of faeces) were noted. We randomly selected 16 of those sites (8 in mesic tundra and 8 in stream gullies) to set lemming exclosures in August 2009. Exclosures consisted of galvanized, welded wire fence (1.25-cm mesh size) attached to wooden stakes in each corner and were separated by at least 50 m. Each exclosure was 0.75 x 0.75 m, 1 m high, and the fence was driven 15 cm into the ground to prevent lemmings from digging under. In subsequent years, at the same time that vegetation was sampled in August (see below), exclosures were moved by at least 10 m to a new site showing signs of winter use by lemmings to avoid sampling the same site twice.

Plant biomass was sampled in quadrats twice a year: at the end of the growing season in early August and at snow melt in June (or early July in a few sites where snow persisted late). In August, a vegetation sample was taken at ~2 m from where the exclosure was set. At snow-melt, a first sample was taken inside the exclosure and a second one outside, again within 2 m of the exclosure. If the sample collected outside did not show any sign of lemming activity (e.g. shoot clipping, pile of faeces, etc.), we searched for these signs within a 5 m radius around the exclosure and collected a third sample at such site. Positions of quadrats outside exclosures were chosen randomly except for the third sample at snow-melt, when no signs of lemming activity had been found in the random quadrat. For the third quadrat, we sampled the first area where signs of lemming activity were detected. Vascular plants were sampled in 20x50 cm quadrats and mosses in a 10x10 cm sub-quadrat inside the previous one. All above ground vascular plants were clipped at the ground level. Dead material was removed and the remaining live material was sorted by family, genus or species, dried to constant mass at 45^{o} C, and weighed. *Salix* were sorted into two categories, woody parts and leaves. Buds were included with leaves. Mosses were identified by genus or species on the 10x10 cm quadrat. Proportion cover of each genus or species was visually estimated in the field to the nearest 5 % before all above ground live (i.e. green) material was clipped (Pouliot et al. 2009). Clipped material was dried to constant mass at 45°C and weighed. Total weight was then divided by the proportion estimated for all genus or species.

We analysed the standing crop of each taxa (family, genus or species) of vascular plants and mosses using generalised linear models to test if we could detect a difference between (1) ungrazed (i.e. inside exclosure) and random plots outside exclosures and (2) ungrazed and grazed plots (i.e. those showing signs of lemming use outside exclosure) at snow-melt. We ran these two analyses separately because not all sites had both a random and a grazed plot. We hereafter refer to grazed and random plots as the treatment effects as both were potentially exposed to lemmings. Habitat (mesic tundra and stream gullies) and year were additional factors entered into the analysis and two-way interactions between those variables and the treatment effect were also examined (interactions are only reported when significant, i.e. $P < 0.05$). We further tested if biomass of each taxa at the end of the growing season remained stable throughout the study years, including habitat and its interaction with year, using a generalised linear model. All plant biomass data was transformed using natural logarithm to respect normality for analyses. We used Tukey's test to compare individual means (or Least Square Means, LSM when there was a significant interaction). Statistical analyses were performed with R statistical software (http://cran.r-project.org/).

Lemming density

Lemming density was estimated each summer. We live trapped rodents on two 11-ha grids (330 x 330 m), one set out in wetlands and one in mesic tundra, to obtain mark-recapture estimation of abundance. The trapping grids were laid out in a Cartesian plane of rows and columns, with numbered stakes spaced every 30 m. At each stake, we set out a Longworth trap baited with apple near signs of lemming use or active burrows. Trapping occurred over 3 consecutive days 3 times during the summer (mid-June, mid-July and mid-August) and traps were checked twice a day. All individuals captured were identified to the species, marked with PIT tags (when unmarked) and released. We considered the lemming population closed within our trapping sessions. All density estimates were carried out in DENSITY 4.4 (http://www.otago.ac.nz/density) using Efford's maximum likelihood method (Efford et al. 2004, Borchers and Efford 2008; see Bilodeau et al. 2013d for details).

Lemming winter nests provided us with an index of winter density (Krebs et al. 2012). We estimated nest density each spring, shortly after snow-melt, on 60 transects distributed randomly across the study area and equally in our 3 habitats (20 each in wetlands, mesic tundra and stream gullies). Transects were 500 m long and the same transects were used each year. All winter nests found while walking along the transect line were removed, their exact position and perpendicular distance to the transect noted, and the species using it identified (see Duchesne et al. 2011b for details). Nest density was estimated using line transect method (Buckland et al. 2001) and was carried out in Distance 6.0 (http://www.ruwpa.st-and.ac.uk/distance/), a software for distance sampling analysis (Thomas et al. 2009).

Results

Lemming population dynamic

The combination of winter nest and summer density data (Figs. 1 and 2) indicates that both species of lemmings had declined from high densities in summer 2008 to a near absence during the winter 2008-2009. Populations were extremely low during the summer 2009 but both species increased during winter 2009-2010 to reach high densities during summer 2010. Populations of both species remained high during the winter 2010-2011 but showed a divergent dynamic during summer 2011. Whereas brown lemmings reached very high densities during that summer, the collared lemming population had apparently crashed by the time snow had disappeared. By winter 2011-2012, brown lemmings had also declined to low numbers and densities of both species were low during summer 2012.

Impact of lemmings on plants during winter

The dominant vascular plants were the same in both habitats (Table 1), with Ericaceae and Salicaceae being the most abundant, followed by Juncaceae and Poaceae. In spring 2010, 12 out of 16 random quadrats had signs of lemming use, 14 out of 16 in spring 2011, but none in spring 2012. We found no differences in total vascular plant biomass between random sites outside the exclosures and ungrazed sites inside ($F_{1,86} = 0.34$, $P = 0.561$) nor between sites showing signs of lemming grazing and ungrazed sites ($F_{1,86} = 0.92$, $P = 0.339$; Fig. 3). There was more biomass in 2012 compared to 2010 and 2011 (random vs ungrazed: $F_{2,86} = 4.25$, $P = 0.017$; grazed vs ungrazed: $F_{2,86} = 7.19$, $P = 0.001$). This effect is mostly due to the high biomass of *Cassiope tetragona* (an Ericaceae) in and around our exclosures in spring 2012 (Fig. 4). Grazed sites tended to have less *Cassiope* in 2012 compared to ungrazed sites ($P = 0.084$), probably because these plants tend to overgrow other plants when present and are not eaten by lemmings.

Among 17 individual plant families, only four showed some evidence of an effect of lemmings' winter grazing (for the others, $P > 0.32$ in all comparisons; see Annexe 3). There was no treatment effect on Salicaceae woody parts (random vs ungrazed: $F_{1,86} = 0.23$, $P = 0.629$; grazed vs ungrazed: $F_{1,86} = 0.43$, $P = 0.515$; Fig. 4) but biomass was higher in 2012 than in other years ($F_{2,86} = 6.17$, $P = 0.003$). Similarly, no treatment effect was detected on Salicaceae leaves (random vs ungrazed: $F_{1,86} = 0.83$, $P = 0.364$; grazed vs ungrazed: $F_{1,86} = 0.10$, $P = 0.749$) although leaf biomass was lower in 2011 than in the other 2 years ($F_{2,86} = 13.5$, $P < 0.001$; Fig. 4). The large annual difference is possibly due to later sampling dates in 2010 and 2012 when *Salix* had already started to grow before snow on quadrats had completely melted. Biomass of Juncacea did not differ between inside and outside exclosures (random vs ungrazed: $F_{1,86} = 0.07$, $P = 0.799$; grazed vs ungrazed: $F_{1,86} = 0.51$, $P = 0.476$) nor that of Poaceae (random vs ungrazed: $F_{1,86} = 0.75$, $P = 0.390$; grazed vs ungrazed: $F_{1,86} = 0.80$, $P = 0.375$ Fig. 4). Caryophyllaceae biomass was reduced by 33 % in grazed sites compared to ungrazed sites ($F_{1,86} = 5.97$, $P = 0.017$; Fig. 4) but not in random sites ($F_{1,86} = 0.73$, $P = 0.395$). Papaveraceae, a rare family, showed inconsistent trends, its biomass being significantly lower in random compared to ungrazed sites but higher in grazed sites.

Dominant mosses were similar in both habitats (Table 2), with the genus *Drepanocladus*, *Hylocomium*, *Polytrichum* and *Scapania* being the most abundant. We found no differences in total live moss biomass between random sites and ungrazed sites within exclosures ($F_{1,86} < 0.001$, $P = 0.984$), nor between sites showing signs of lemming grazing and ungrazed sites ($F_{1,86} < 0.001$, $P = 0.989$; Fig. 3). The apparent decline in spring moss biomass over the years ($F_{2,86} = 4.34$, P = 0.016) is probably related to the high prevalence of Ericaceae in 2012, as explained above, because this decline was not apparent at the end of the growing season (see below). Evidence for an effect of lemming grazing was detected for 3 out of 32 individual moss species or genus. The effect on *Polytrichum* tended to vary among years with random plots (treatment x year: $F_{2,86} = 2.48$, P = 0.089). In grazed plots, biomass varied according to year ($F_{2,86} = 3.59$, P = 0.032) and tended to differ among treatments ($F_{2,86} = 3.10$, P = 0.082). *Polytrichum* biomass in random and grazed sites was about 57% lower than in ungrazed sites in 2010 but not in 2011 and 2012 (Fig. 4). The effect of grazing on *Drepanocladus* biomass varied with habitat but was inconsistent. Biomass was 9% lower in random than in ungrazed sites in mesic tundra but not in stream gullies (treatment x habitat; $F_{2,86} = 3.33$, P = 0.072) whereas biomass was 51% higher in grazed than in ungrazed sites in the stream gullies but not in the mesic tundra (treatment x habitat: $F_{2,86} = 4.50$, P = 0.037). Finally, *Ptilidium* biomass was also 56 % lower in grazed than in ungrazed sites but this time only in the stream gullies (treatment x habitat: $F_{2,86} = 6.49$, P = 0.013).

Annual variation in plant growth

Aboveground live vascular plant biomass at the end of the growing season tended to increase over the years ($F_{3,56} = 2.07$, P = 0.114) and was significantly higher in 2012 than in 2010 (Fig. 5). For individual vascular plant families, there were few differences among years, and trends were not always consistent (see Annexe 3 for details). The biomass of Salicaceae did not vary significantly among years (leaves: $F_{3,55} = 0.76$, P = 0.523; wood: $F_{3,55} = 0.78$, P = 0.509) although biomass appeared much higher in 2012 than in other years (Fig. 6). This was partly due to one exclosure showing an extremely high biomass (leaves: 101.5 g/m^2; wood: 177.2 g/m^2). Excluding this outlier, Salicaceae biomass in 2012 was 27.7 ± 6.3 g/m^2 for leaves and 30.5 ± 6.3 g/m^2 for wood. Poaceae biomass tended to differ among years ($F_{3,56} = 2.71$, P = 0.054; Fig. 6) as there was more biomass in 2012 compared to 2010 (Fig. 6). The biomass of Juncaceae did not vary among years ($F_{3,56} = 0.21$, P = 0.888). The biomass of Caryophyllaceae and Polygonaceae varied among years ($F_{3,56} = 4.03$, P = 0.012 and $F_{3,56} = 4.17$, P = 0.010; respectively) as the biomass was higher in 2009 than in 2010, 2011 (both species) and 2012 (Polygonaceae only; Fig. 6).

Total moss biomass at the end of the growing season did not vary significantly among years ($F_{3,56} = 0.97$, $P = 0.415$; Fig. 5). Analysis of individual taxa revealed variable effects across species and sometimes also habitats. *Aulacomnium* tended to have higher biomass in 2012 than in other years ($F_{3,56} = 2.23$, $P = 0.095$), *Cinclidium* had higher biomass in 2009 than in other years ($F_{3,56} = 3.50$, $P = 0.021$) and *Scapania* had lower biomass in 2009 than in other years ($F_{3,56} = 7.86$, $P < 0.001$). Finally, annual change in biomass of *Ditrichum flexicaule* and *Hylocomnium* varied among habitats (interaction year x habitat: $F_{3,56} = 3.30$, $P = 0.027$ and $F_{3,56} = 2.66$, $P = 0.057$, respectively).

Discussion

During winter, plant growth stops under the snow and a large proportion of plant biomass is lost to senescence (Hansson 2002). Therefore, if small mammal populations are controlled by their resources, they should be particularly vulnerable to food shortage during winter, and years of high population densities should result in detectable signs of food depletion at snow melt. This is especially true for lemmings that can breed and show population growth under the snow, which would put even more pressure on their winter food supply.

We found weak evidence to support the hypothesis that winter grazing by lemmings reduced plant biomass in their preferred habitat and no support for the hypothesis that this impact should be highest during the winter of peak abundance (2010-2011 at our study site). Even when we selected sites with signs of lemming grazing, differences in biomass between these sites and those protected from grazing were small or absent. A significant but slight impact of winter grazing was detected on a few mosses known to be important food items for brown lemmings (Batzli et al. 1983), the most abundant lemming species at our site, and no effect was detected on Poaceae and Juncaceae. Similarly, no effect on Salicaceae and Rosaceae was detected, two plants known to be preferred by collared lemmings (Batzli et al. 1983, Rodgers and Lewis 1985). The only dicotyledon plants showing a substantial impact were the Caryophyllaceae, which compose a very small proportion of total plant biomass at our site. We must point out that, contrarily to what was reported elsewhere (Batzli and Jung 1980, Rodgers and Lewis 1985, 1986), Soininen and Gauthier (unpublished data) recently found that Salicaceae was the dominant vascular plant eaten by brown lemmings during winter at our study site (up to 55% of their diet), though data came from only one year (2011). These results were based on DNA barcoding analysis of fecal material (Soininen et al. 2009). Thus, even though *Salix* may be the most important food item for both lemming species, the impact of grazing was non-detectable, probably because this plant is extremely abundant at our study site. It could be argued that brown lemmings used *Salix* because their putative preferred food resources (graminoids and mosses) were depleted, but we found no evidence for that. Moreover, we stress that we measured grazing impact in their preferred winter habitat (i.e. areas with the deepest snow pack; Duchesne et al. 2011b, Reid et al. 2012) where lemming densities are highest. Lemmings also use areas outside snowdrifts, which compose the majority of the study area and where densities are generally lower. Even less impact on vegetation should be expected in those areas.

Plants were exposed to the highest lemming densities during winter 2009-10 and 2010-11 as judged by winter nest abundance. If lemming grazing has a negative impact on plant growth, we should have observed a marked decline in plant and moss biomass in summer 2010 and 2011 compared to 2009. We did not observe such pattern in total vascular and moss biomass in late summer as vascular biomass was generally higher in 2011 and 2012 than in 2009 and 2010, and moss biomass did not show annual variations. Annual variation in vascular plant biomass may be best explained by climatic factors, which are a strong driver of plant growth (Gauthier et al. 2011). At individual taxa level, we did find evidence for a reduction in the biomass of some species at the end of the summer in the two years of high lemming abundance. Caryophyllaceae, Polygonaceae and to a lesser extent Salicaceae and Poaceae biomass were lower in the two years of high lemming abundances. However, considering that the reduction in biomass during the winter was generally weak or absent, especially for important families such as Salicaceae and Poaceae, it is possible that the reduction in biomass observed in late summer was partly a consequence of summer grazing as the plots sampled in August had not been protected from grazing. If food resources were controlling lemming populations, plant biomass should have been lowest by the end of the

2011 growing season, after two winters of high densities, which was not the case. If high grazing pressure during the lemming peak years had damaged these plants, we would have expected a carry-over effect during the following growth season. However, in 2012, Salicaceae, Poaceae and Caryophyllaceae growth was high and comparable to 2009. Therefore, the Polygonaceae appears to be the only plant family that consistently suffered from lemming grazing.

At our study site, lemmings show regular 3 to 4 years cycles of high amplitude (Gruyer er al. 2008, Legagneux et al. 2012) and 2010 and 2011 were two consecutive years of high lemming abundance. Both lemming species increased in densities from 2009 to 2010, but while brown lemmings, the most abundant species, continued to increase during the following winter to reach peak densities in 2011, collared lemmings started decreasing in late summer 2010 and had crashed by spring 2011. Considering that the two species can eat the same food plants during winter (E. Soininen and G. Gauthier, unpublished data), it appears unlikely that food depletion during winter was the cause of the decline in collared lemmings.

Our results do not provide evidence that a lack of plant food during winter may have caused the crash of lemming populations on Bylot Island. Nonetheless, it is still possible that exceptional environmental conditions such as the extensive formation of ground ice or an extremely hard and compacted snowpack, could severely limit food availability for lemmings during some winters. Episodes of ground icing have been reported in Fennoscandia and Svalbard and appear to be relatively common in those areas (Callaghan et al. 2004, Korslund and Steen 2006, Stien et al. 2012). Moreover, changes in the quality of the snow cover have been invoked as a possible cause of the collapse of lemming cycles in some areas (Kausrud et al. 2008, Gilg et al. 2009). Snow cover in the Canadian Arctic is generally much drier than in Fennoscandia and is subject to more consistent cold temperatures, allowing the formation of a stable subnivean space for lemmings to move under the snow (Reid et al. 2012, Bilodeau et al. 2013b). Signs of lemming use (e.g. travel paths in the moss, piles of faeces, winter nests) were easy to find and were common around our exclosures and throughout the study area in peak years, suggesting that lemmings were not restricted in their movements and had easy access to their preferred winter habitats.

It has been suggested that plant quality, mostly through the presence of secondary compounds, could limit population growth of small mammals more than does available biomass (Seldal et al. 1994, Berg 2003, Hogstedt et al. 2005). Because we did not look at plant nutritive quality during this study, we cannot rule out a possible role of this factor in the population dynamic of lemmings at our study site. However, since we investigated winter grazing when plants are metabolically inactive, we believe that it is unlikely that secondary compounds played a major role, especially for fast growing plants such as graminoids, which allocate a very small proportion of their resources to defences (Coley et al. 1985).

Even though we found some impact of winter grazing on a few vascular plant and moss taxa in preferred lemming habitat, these effects were relatively modest and short-lived. In order to reduce the carrying capacity and maintain a cyclic dynamic, the impact on food resources must be sufficiently strong and sustained to have a long-lasting effect on plants, i.e. plants must take more than one year to recover (Turchin and Batzli 2001, Ims and Fuglei 2005). Our results show that these conditions were not met in our system, which suggests that resources are unlikely to control the population dynamic. It appears that other factors may be limiting lemming populations and prevent them from reaching densities high enough to deplete their food resources and cause a crash. On Bylot Island, recent evidence suggests that predators could play that role and perhaps regulate lemming populations (Legagneux et al. 2012, Therrien 2012).

Table 1. Percentage of aboveground biomass of the different vascular plant families found at the peak of growth in the two lemming winter habitats in late summer.

Vascular plant family or group	Mesic tundra	Stream gullies
Ericacea [a]	47.2	59.8
Salicaceae [b]	38.2 (18.2) [k]	31.7 (15.2) [k]
Juncaceae [c]	6.0	3.7
Poaceae [d]	4.0	2.5
Fabaceae [e]	0.8	1.0
Caryophyllaceae [f]	0.8	0.3
Pyrolaceae [g]	1.0	0.1
Rosaceae [h]	0.4	0.6
Polygonaceae [i]	0.4	0.1
Others [j]	1.2	0.2

[a] *Cassiope tetragona*

[b] Mostly *Salix arctica*

[c] Mostly *Luzula confusa* and *Luzula nivalis*

[d] Mostly *Arctagrostis latifolia* and *Poa arctica*

[e] Mostly *Astragalus alpinus*

[f] Mostly *Stellaria longipes* and *Cerastium regelii*

[g] *Pyrola grandiflora*

[h] Mostly *Dryas integrifolia* and *Potentilla nivea*

[i] *Oxyria digyna* and *Polygonum viviparum*

[j] Others includes the following families, which represent ≤0.5 % of total biomass in the two habitats: Brassicaceae, Cyperaceae, Equiseraceae, Papaveraceae, Ranunculaceae, Saxifragaceae and Scrophulariaceae

[k] percentage of leaves and buds in parenthesis

Table 2. Percentage of green biomass of the different mosses genus or species found at the peak of growth in the two lemming winter habitats in late summer.

Moss genus or species	Mesic tundra	Stream gullies
Drepanocladus [a]	16.4	27.0
Hylocomium splendens	18.4	19.8
Polytrichum [b]	17.2	14.4
Scapania simmonsii	18.4	12.2
Ditrichum flexicaule	9.3	9.2
Ptilidium ciliare	7.1	0.4
Aulacomnium [c]	5.1	5.8
Tomenthypnum nitens	3.5	5.2
Dicranum [d]	2.1	3.3
Philonotis fontana	0.3	1.3
Gymnommitrion concinnatum	0.8	0.00
Others [e]	1.4	1.4

[a] *Drepanocladus uncinatus* and *D. brevifolius*

[b] *Polytrichum juniperinum*, *P. piliferum*, *P. strictum* and *P. swartzii*

[c] *Aulacomnium turgidum* and *A. palustre*

[d] *Dicranum angustum* and *D. acutifolium*

[e] Others includes the following species, which represent individually ≤0.5 % of total biomass in the two habitats: *Bartramia ithyphylla*, *Blindia acuta*, *Campylium stellatum*, *Ceratodon purpureus*, *Cinclidium stygium*, *Dicranoweisia crispula, Encalypta alpina*, *Hypnum revolutum*, *Meesia triquetra*, *Oncophorus wahlenbergii*, *Orthotrichum speciosum*, *Plagiomnium ellipticum*, *Pohlia cruda* and *Racomitrium anuginosum*

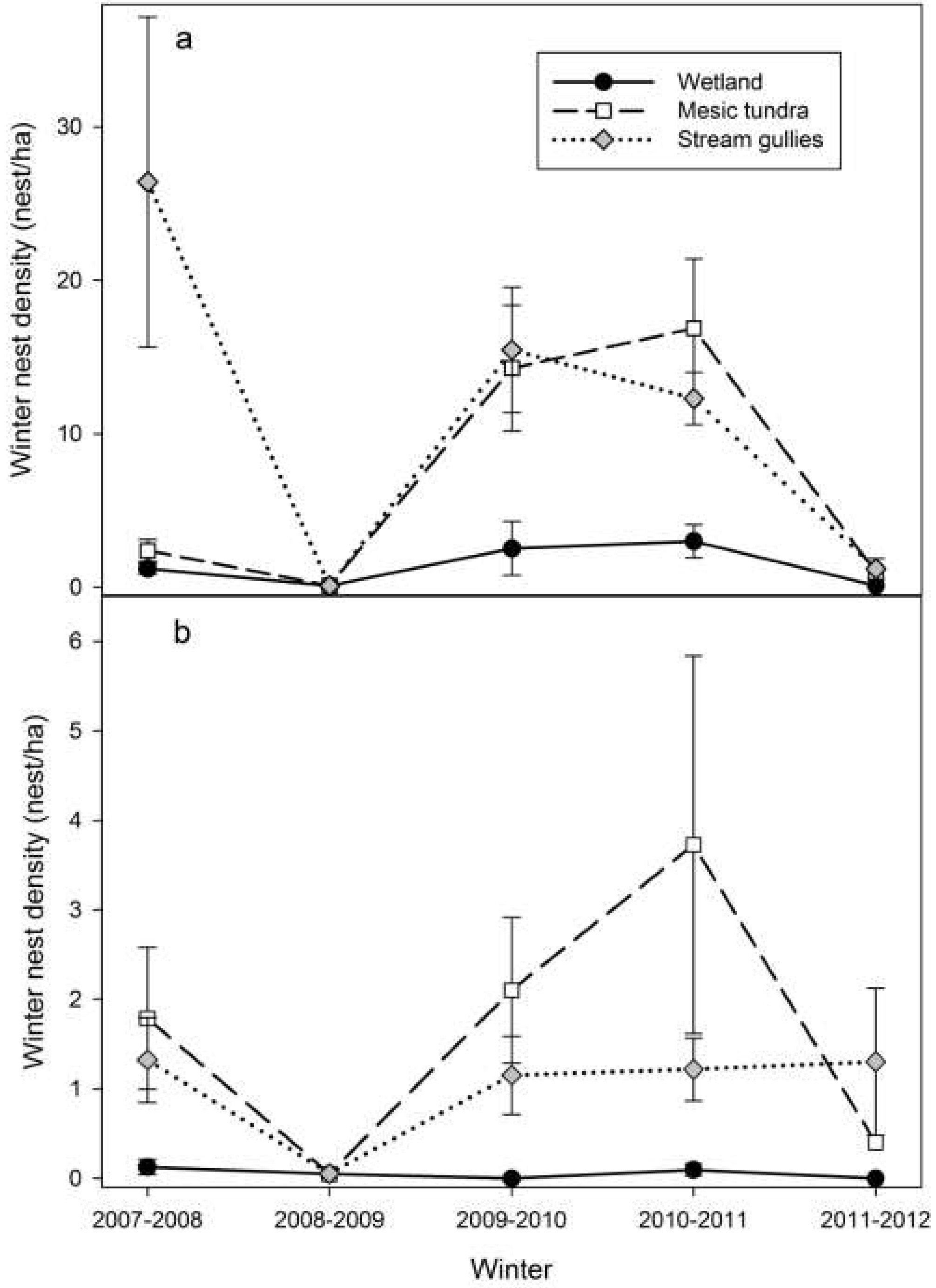

Figure 1. Winter nests densities for brown (a) and collared (b) lemmings from 2008-2012 in wetlands, mesic tundra and in stream gullies.

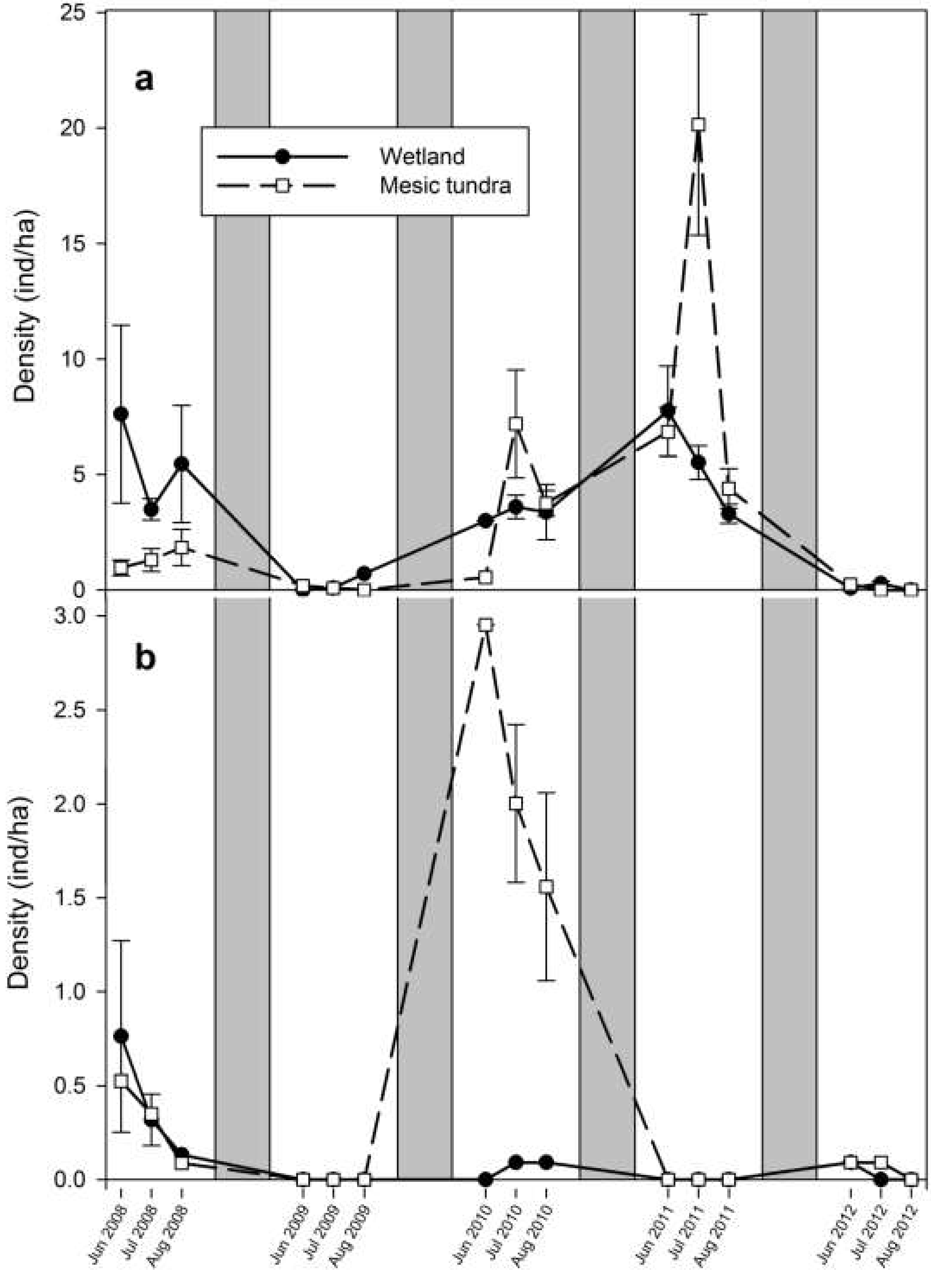

Figure 2. Brown (a) and collared (b) summer densities estimated by capture-mark-recapture using Efford's maximum likelihood method from 2008-2012 in the wetland and mesic tundra grids.

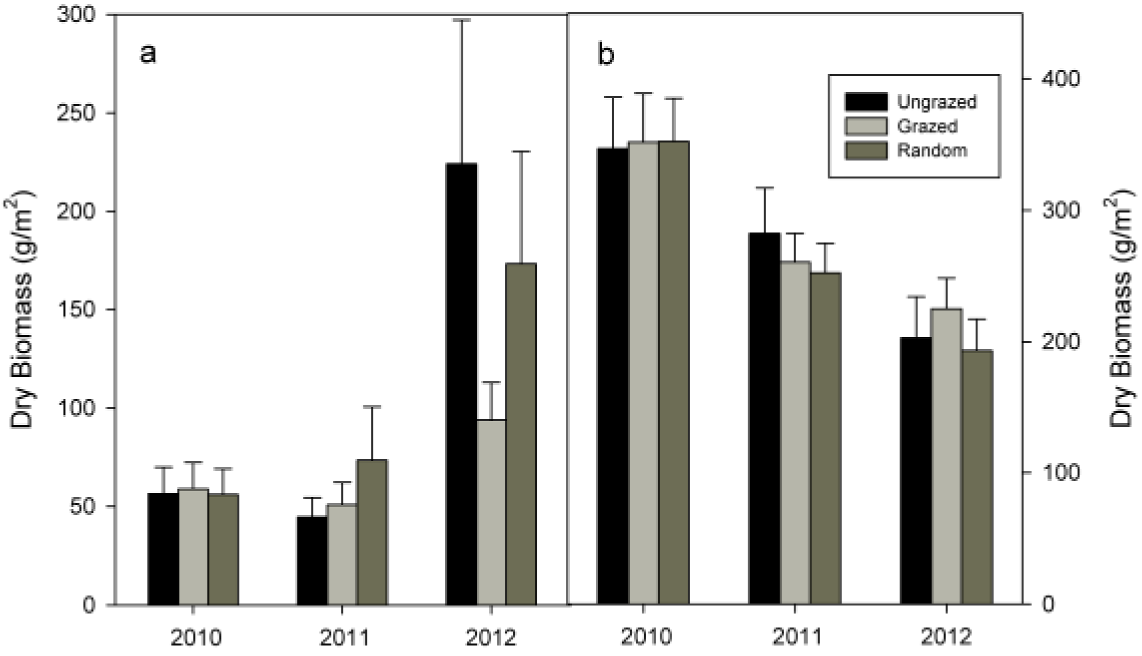

Figure 3. Aboveground live biomass (dried biomass in g/m^2) of vascular plants (a) and mosses (b) shortly after snowmelt in spring 2010-2012 in ungrazed (inside exclosures), grazed and random quadrats (outside exclosures). Error bars represent SE. N = 16 in each treatment and year.

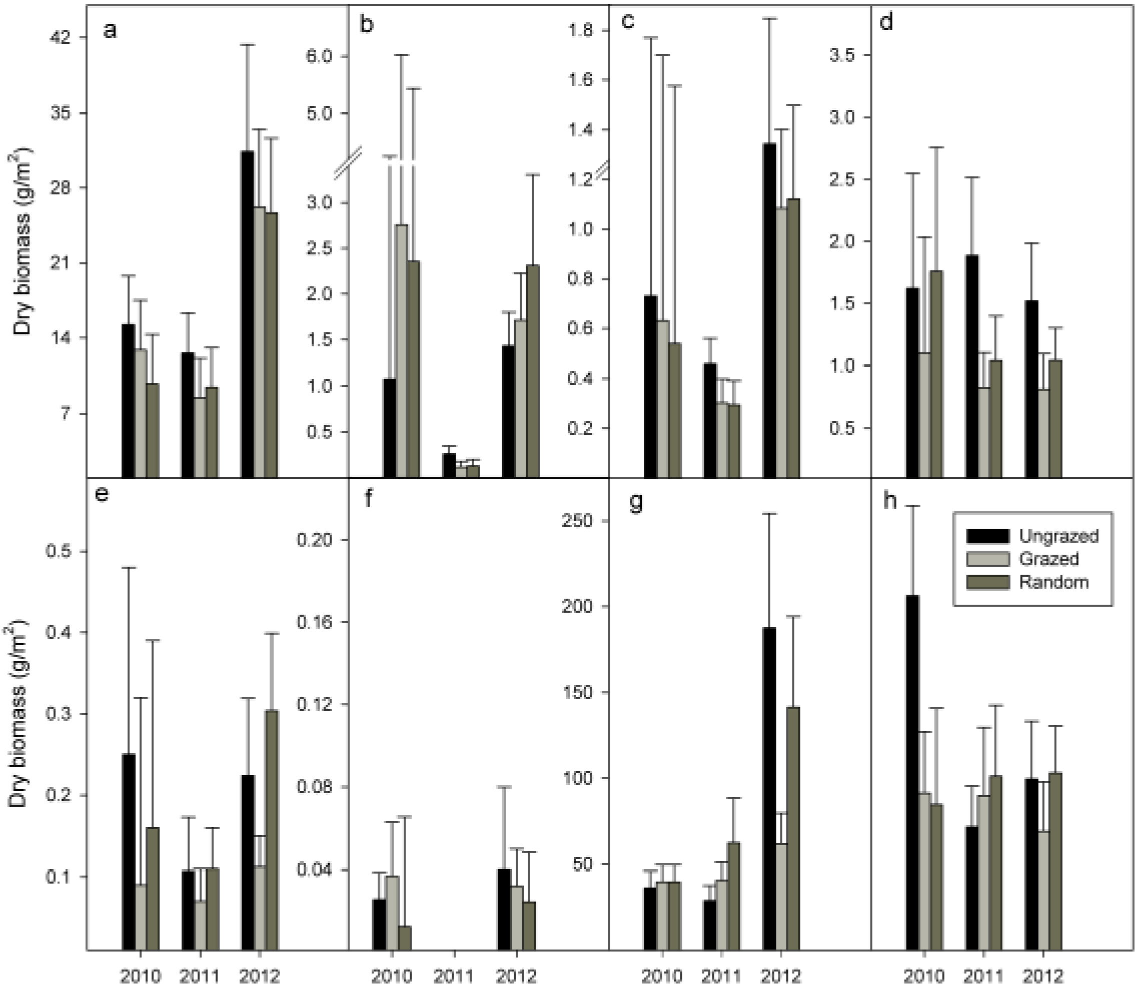

Figure 4. Aboveground live biomass (dried biomass in g/m^2) of Salicaceae wood (a) and leaves (b), Poaceae (c), Juncaceae (d), Caryophyllaceae (e), Polygonaceae (f), Ericaceae (g) and of the moss genus *Polytrichum* (h) shortly after snowmelt in spring 2010-2012 in ungrazed (inside exclosures), grazed and random quadrats (outside exclosures). Error bars represent SE. N = 16 in each treatment and year.

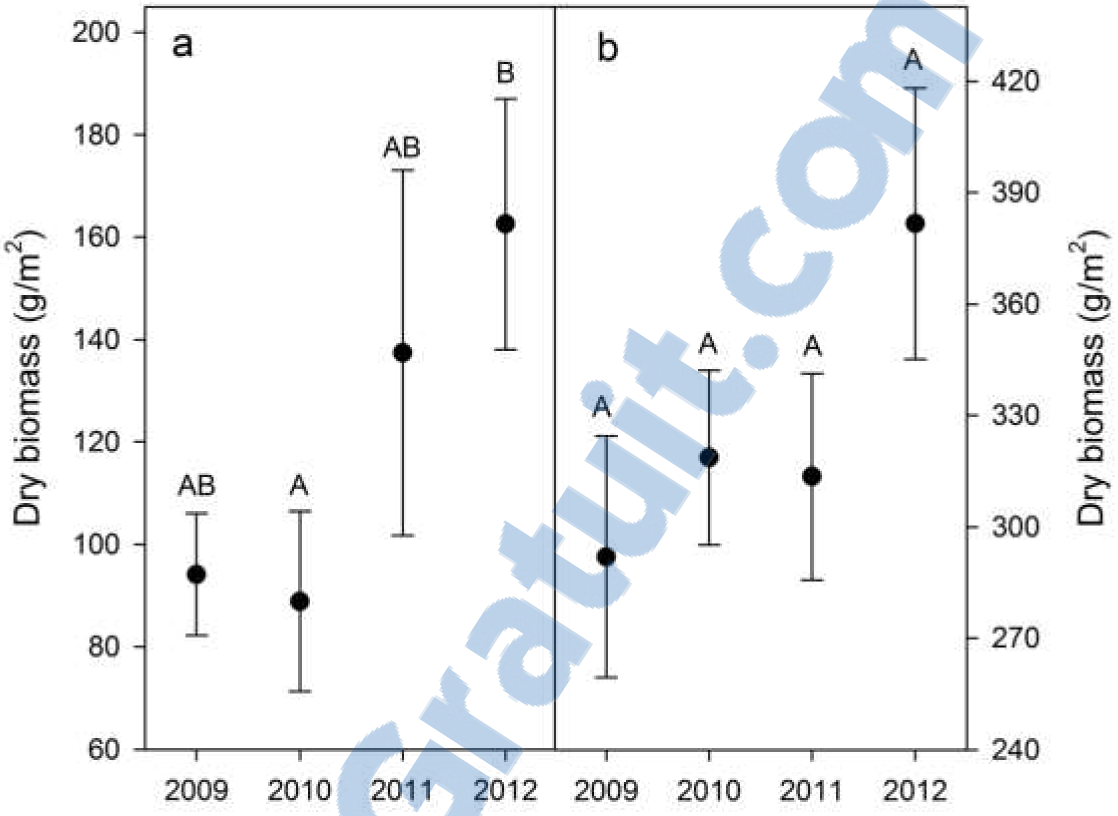

Figure 5. Aboveground live biomass (dried biomass in g/m^2) of vascular plants (a) and mosses (b) at the end of the growing season in August 2009-2012. N = 16 in each treatment and year. Values with the same letter are not significantly different (P < 0.1; Least Square Means or Tukey's test).

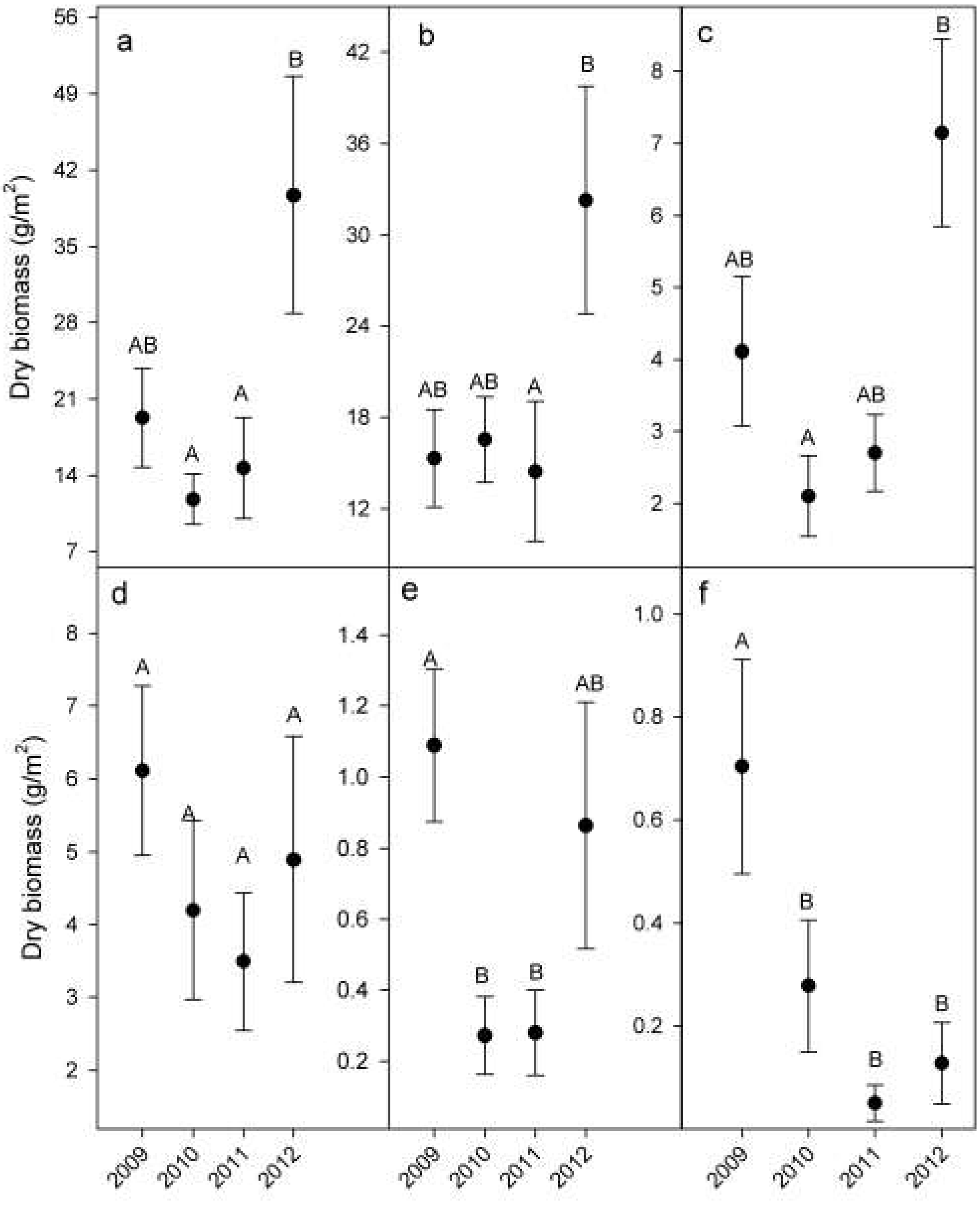

Figure 6. Available live biomass (dried biomass in g/m^2) of Salicaceae wood (a) and leaves (b), Poaceae (c), Juncaceae (d), Caryophyllaceae (e) and Polygonaceae (f) at the end of the growing season in August 2009-2012. N = 16 in each treatment and year. Values with the same letter are not significantly different ($P < 0.1$; Least Square Means or Tukey's test).

Chapitre 5

Effect of snow cover on the vulnerability of lemmings to mammalian predators in the Canadian Arctic

Bilodeau, F., Gauthier, G. & Berteaux, D. Effect of snow cover on the vulnerability of lemmings to mammalian predators in the Canadian. Journal of Mammalogy (in press).

Résumé

Dans la toundra arctique, la neige devrait protéger les lemmings des prédateurs mammaliens pendant l'hiver. Nous avons émis l'hypothèse que (1) la qualité de la neige (épaisseur et dureté) devrait affecter les taux de prédation mammaliens sur les lemmings, mais que cet effet dépendrait de la stratégie de chasse et que (2) la prédation par l'hermine (*Mustela erminea*), qui peut chasser sous la neige, devrait être plus élevée dans les habitats préférés des lemmings. Nous avons mesuré l'épaisseur et la dureté de la neige aux tunnels fait par le renard arctique (*Vulpes lagopus*) lors de tentative de prédation, aux nids d'hiver non-prédatés et prédatés par l'hermine et à des emplacements aléatoires. Nous avons aussi déterminé la densité de nids d'hiver dans trois habitats (humide, mésique et riverain). La neige profonde et dure restreint les tentatives de prédation par le renard faites en sautant à travers la neige, mais pas celles faites en creusant. La prédation par l'hermine n'était pas affectée par l'épaisseur de neige et faiblement par la densité de nids d'hiver, mais était plus élevée dans l'habitat riverain et intermédiaire dans l'habitat mésique, deux habitats qui sont susceptibles à de fortes accumulations de neige, comparativement à l'habitat humide. Ces résultats indiquent que les caractéristiques topographiques reliées à l'habitat sont plus importantes que l'épaisseur de neige ou la densité de nids, à proprement dit, pour affecter la stratégie hivernale de recherche de proie de l'hermine. L'effet relativement faible des caractéristiques du couvert de neige sur la vulnérabilité des lemmings aux prédateurs mammaliens suggère que les taux de prédation hivernal sur les lemmings ne seront pas fortement affectés par les changements à venir dans le couvert nival en relation avec le réchauffement climatique.

Abstract

In the Arctic tundra, snow is believed to protect lemmings from mammalian predators during winter. We hypothesised that 1) snow quality (depth and hardness) should affect mammalian predation rates on lemmings, but that this effect would depend on the predator hunting strategy and that 2) predation by ermines (Mustela erminea), which can hunt lemmings under the snow, should be higher in preferred lemming habitats. We measured snow depth and hardness at tunnels made by arctic foxes (Vulpes lagopus) predation attempts, at winter nests non-predated and predated by ermine, and at random locations. We also determined winter nest density in 3 habitats (wet, mesic, and gully). Deep and hard snow restricted fox predation attempts made by jumping through the snow, but not those made by digging. Ermine predation was unaffected by snow depth and weakly by nest density but was higher in gully and intermediate in mesic habitats, which are conducive to high snow accumulation, compared to the wet habitat. These results indicate that habitat-related topographical features are more important than snow depth or nest density per se in affecting the winter foraging strategy of ermines. Overall, even though we found a relatively weak effect of the snow cover on predation by foxes and ermines, it is hard to predict how upcoming changes to the snow cover will affect lemming vulnerability to mammalian predators as a wide range of snow conditions may result from climate warming.

Introduction

In the Arctic, small mammal populations can support a large diversity of avian and mammalian predators during the short summer (Gauthier et al. 2011; Gilg et al. 2006; Korpimäki et al. 2005). These rodents, particularly lemmings (Dicrostonyx and Lemmus spp.), are well known for their multi-annual, high amplitude population cycles (Gruyer et al. 2008; Krebs et al. 2002; Pitelka and Batzli 2007) and several studies have suggested that predation may play a role in controlling these cycles (Angerbjörn et al. 1999; Gilg et al. 2003; Hanski et al. 2001; Korpimäki and Krebs 1996; Legagneux et al. 2012; Reid et al. 1997). However, when a stable snow cover becomes established, avian predators, which represent a large proportion of the predator guild, leave the area (Gauthier et al. 2011; Gilg et al. 2006) and only mammalian predators, primarily foxes and small mustelids, remain to prey on lemmings. Although many studies have examined the interaction between lemmings and their predators during the summer (e.g., Angerbjörn et al. 1999; Gilg et al. 2006; Wilson et al. 1999), very little is known about these interactions during the long Arctic winter (up to 8 months) when a snow cover is present.

Lemmings remain active under the snow throughout the winter and build winter nests made of vegetation, which they use to insulate themselves from cold temperatures (Casey 1981; Chappell 1980) and to reproduce (Duchesne et al. 2011b; MacLean et al. 1974; Sittler 1995). During winter, the snow cover over much of the wind-swept Canadian tundra is relatively thin (30-50 cm) and hard packed (Atlas of Canada 2010; McKay and Gray 1981; Pomeroy and Brun 2001), except in areas where topographical features such as the leeside of slopes or banks promote the formation of snow drifts. Lemmings show a preference to build their nests in areas of deep snow accumulation, which provide a better insulation from the cold Arctic air (Duchesne et al. 2011b; Reid et al. 2012; Sittler 1995).

A deep snow cover has the potential to hinder predation by foxes (Gilg et al. 2006; Hansson and Henttonen 1985; Lindstrom and Hornfeldt 1994) because, in order to catch lemmings, they must pound through the snow or dig out their winter nests once they have detected them. However, snow depth is less likely to affect predation rate by small mustelids because they can hunt lemmings directly in their tunnels under the snow (Sittler 1995).

Moreover, ermines are known to concentrate their hunting effort in areas of high small mammal densities (Hellstedt and Henttonen 2006; King and Powell 2007; Klemola et al. 1999), and thus deep snow areas could potentially attract those predators if lemmings aggregate there. However, other factors such as snow density or hardness also have the potential to affect vulnerability of lemmings to predation during winter. As temperatures are rising, snow regimes in the Arctic are changing and episodes of winter rain or thaw-frost events are becoming more frequent (SWIPA 2011). Such conditions could contribute to hardening the snow cover and thus make it more difficult for predators to access lemmings under the snow.

With this perspective in mind, we hypothesised that a deep and hard snow cover should affect lemming predation rate by mammalian predators but that this effect should depend on their hunting strategy. We predicted that a deep and hard snow cover should hinder predation by the arctic fox (Vulpes lagopus) because it must forage on top of the snow, but that it should have little effect on predation by the ermine (Mustela erminea), which can forage under the snow. As lemming preferred habitats are conducive to high snow accumulation and densities of winter nests are generally high in such habitats (Duchesne et al. 2011b; Reid et al. 2012), we also tested the hypotheses that predation by ermines should be highest in preferred lemming habitats and in areas of high lemming density.

Materials and methods

Study area

The study was conducted on the south plain of Bylot Island, Sirmilik National Park, Nunavut Territory, Canada (73°08’N, 80°00’W). The main study area (70 km2) consists of tundra polygons, thaw lakes and ponds forming wetlands in parts of the valley bottom and drier mesic habitat in the upland areas and nearby slopes and hills (see Bilodeau et al. 2013b and Duchesne et al. 2011b for details). Small, intermittent streams running through upland areas are often located at the bottom of small gullies where vegetation along the stream edge is similar to that of wetland habitat. We considered this habitat (gully) as a 3rd habitat category because it is conducive to high snow accumulation and can be heavily used by lemmings in winter (Duchesne at al. 2011b). Only 2 species of rodents are present, the brown (Lemmus trimucronatus) and the collared lemming (Dicrostonyx groenlandicus), though the former species is more abundant, especially in peak years (Gruyer et al. 2010). Arctic foxes and ermines are present throughout the winter on Bylot Island. Average fox density is approximately 0.1 individual/km2 on the south plain of Bylot, where up to 25 pairs may breed in a good lemming year (Legagneux et al. 2012).

Average air temperature at our study site from October to June is -23.4 ± 0.4 (*SE*) °C and average temperature under the snow, where lemmings live in winter, is -15.8 ± 0.4 °C (Bilodeau et al. 2013b). A permanent snow cover is usually established in late September and melting occurs in mid-June. Maximum snow depth typically occurs in May and average snow depth at the end of the winter is 33.8 ± 2.5 cm (Bilodeau et al. 2013b), although snow can be as much as 2m deep in areas conductive to high snow accumulation (e.g., gullies). The snow pack is very dry, owing to the very cold temperature prevailing during the winter.

Fox hunting behavior

We sampled fox predation events over a 980 ha area from 19 May to 2 June 2010 and over a 240 ha area from 17 to 26 May 2011. Fresh fox tracks were found opportunistically while travelling on foot or on snowmobile through the study area. When encountered, they were back-tracked to find signs of predation attempts on lemmings. Tunnels in the snow pack that were going straight down to the subnivean space and that were about the size of a fox body were considered to be predation attempts. These tunnels were easy to distinguish from other holes, such as those made by foxes to locate a den, which were associated with characteristic topographical features (Szor et al. 2008). We could recognize 2 hunting techniques used by foxes. The first one involved digging into the snow, as evidenced by digging marks, a small pile of snow near the tunnel entrance, and the rough edges of these entrances. The attempts were primarily directed at lemming nests as nest remains were always found at the bottom of these holes. The 2nd type of tunnel was narrower with no digging marks and often no signs of lemming nests at their bottom. No obvious pile of snow appeared near the tunnel entrance, which had rather smooth edges. Observations of foxes at distance confirmed that these occurred when immobile foxes listened intensely before jumping and pounding through the snow cover, most likely to catch a lemming that they heard moving under the snow. After classifying each type of tunnel encountered (dig or jump), snow depth and hardness were measured at the site (see details below).

Ermine predation

We sampled ermine winter predation annually from 2007 to 2011 by sampling lemming winter nests across the entire study area shortly after snow-melt. We used 500 m transects randomly distributed among our 3 habitats (wet, mesic, and gully habitats; 25, 10, and 20 transects per habitat in 2007, 2008, and 2009-2011, respectively). All winter nests found while walking along the transect line were removed and their position and perpendicular distance to the transect were noted. Nests found opportunistically, away from transects, were also collected and used for the determination of ermine predation rate.

All winter nests were dissected in the laboratory to determine whether they were used by brown or collared lemmings. We based species identification on the length, form, and color of feces found in nests (Duchesne et al. 2011a; MacLean et al. 1974). Collared lemmings have 4-6 mm long, dark reddish feces, while brown lemmings produce 6-10 mm long, green-brown feces. Lemmings reproduce under the snow in their winter nests (Millar 2001; Stenseth and Ims 1993). We determined if reproduction (defined as the production of weaned young) had occurred based on the presence of small juvenile feces in nests (Duchesne et al. 2011a). We also examined nests for signs of ermine predation. When ermines prey on lemmings, they often line the nest with their prey's fur and use the nest themselves, or they leave rodent body parts and partially eaten carcasses in the nest (MacLean et al. 1974; Sittler 1995). Fur lining and lemming body parts were thus used as evidence of predation.

Snow measurements

We measured snow depth with a graduated rod and snow hardness with a custom-made penetrometer (McClung and Schaerer 2006). The penetrometer was a conical-shaped object of dimensions similar to a fox head and about the same mass as an adult fox (3 kg—Audet et al. 2002). The penetrometer was dropped from 60 cm above the snow and we noted how deep it penetrated the snow. Recorded depths of penetration were always <30 cm. For ease of interpretation, we express snow hardness as 30 – penetration depth (highest values represent hardest snow).

Depth and hardness measurements were done at 85 locations where we had found a lemming winter nest in the previous year in 2010 (n = 81 in 2011), as well as at 93 random locations in 2010 and 90 in 2011. These measurements were taken during the same period as those taken at the fox tunnels, before any significant snow-melt had occurred. There was negligible precipitation during the measurement periods and average air temperature during this period was -8.8 ± 1.4 °C. Measurements could not be taken at nest locations of the current year because nests can only be found after snow-melt. To verify if areas of deep accumulation were consistent between years, we selected 30 random locations where snow depth was sampled in 2010 and 2011. Snow depth at these locations was highly correlated between years ($r = 0.76$, $t_{28} = 6.15$, $P < 0.001$).

Snow depth at winter nests where predation by ermine had been detected was estimated in the following spring using the same procedure as described above. The hardness of snow covering nests predated by ermines could not be estimated because it is unlikely to be consistent between years. Indeed, snow hardness can be affected by multiple climatic factors such as snowfall, air temperature, wind erosion, and deposition (Pielmeier and Schneebeli 2002), which vary annually.

Lemming nest density

We estimated nest density on each transect to obtain a local index of lemming density in the area of the transect. Nest density was based on all nests found within 10 m on either side of the transect. This distance corresponds to the effective detection distance for sampling winter nests in this area (Duchesne et al. 2011b). We estimated nest density by dividing the number of nests found by the 1 ha (500 m x 20 m) transect area. Nests found opportunistically, away from transects, were not used to estimate nest densities. Based on the overall abundance of winter nests (Table 1) and live-trapping conducted during the summer (see Bilodeau et al. 2013d), lemming abundance was high in 2008, 2010, and 2011 (3.8 ± 0.8, 4.7 ± 0.5 and 8.0 ± 0.9 lemmings/ha respectively), intermediate to low in 2007 (0.3 ± 0.1 lemmings/ha), and very low in 2009 (0.2 lemmings/ha).

Statistical analyses

To test if snow depth and hardness had an impact on digging and jumping predation attempts by foxes, we compared depth and hardness measurements at tunnels made by foxes, at non-predated winter nest locations, and at random locations using ANOVA (separate analyses for digs and jumps). To test if snow depth had an effect on predation by ermines, we compared snow depth at predated nest sites, non-predated nest sites, and random locations also using an ANOVA. Interaction between year (2010-2011 for fox and 2007-2011 for ermine) and treatment (predated, non-predated, and random) was always tested. When our treatment was significant, we used Tukey's test to compare individual means (or Least Square Means, LSM, when there was a significant interaction).

To test the hypotheses that predation by ermines was greater in habitats preferred by lemmings in winter and in areas of high nest density, we used a logistic regression to determine if the presence or absence of predation on a nest varied according to year (2007-2011), habitat (wet, mesic, gully), average nest density along the transect, and presence or absence of reproduction and species (brown, collared lemming or both). Two-way interactions among habitat, year, density, reproduction, and species were examined. We determined the most important variables using Akaike's Information Criterion adjusted for small sample size (AICc) and AICc weight (Burnham and Anderson 2002). We used model averaging to calculate the slope parameter and associated error of the most influential variables. Because there were 9 times less predated than non-predated nests, we verified if this could bias our results by conducting a 2nd analysis where we reduced (through random sub-sampling) the number of non-predated nests to that of the predated ones. Due to the small resulting sample size, we repeated the sub-sampling and associated analysis 10 times. We then calculated the average cumulative AICc weight of each variable across the 10 analyses. Since the analysis based on sub-sampling did not change our results, we only report those based on the full samples. Analyses were conducted in R 2.13.1 (R Development Core Team 2010).

Results

Effects of snow cover on fox hunting behavior

We found 56 fox tunnels in 2010 (47 digs and 9 jumps) but only 9 in 2011 (all digs). Snow depth varied significantly among treatments for digs ($F_{2,385}$ = 5.73, *P* = 0.004). Lemming winter nests (whether predated or not) had a deeper snow cover than random locations (*P* < 0.001), but snow depth did not differ according to whether nests had been predated or not (*P* = 0.988; Fig. 1) and this was consistent across years ($F_{2,385}$ = 0.74, *P* = 0.480). Snow depth also varied significantly among treatments for jumps in 2010 ($F_{2,184}$ = 14.84, *P* < 0.001) but this time snow was shallower at predated than at non-predated nests (*P* < 0.001; Fig. 1).

Snow was harder in 2011 than in 2010 (random locations, 2010: LSM = 5.17 [3.65-6.69, 95% *CI*]; 2011: LSM = 11.08 [9.55-12.61]) and we detected a significant treatment x year interaction for the effect of snow hardness on digs ($F_{2,385}$ = 5.88, *P* = 0.003; Fig.2). In 2010, snow hardness at predated nests (LSM = 8.58 [6.81-10.35]) did not differ from that at non-predated nests (LSM = 7.73 [6.53-8.93]), but all nests were under harder snow than random locations (LSM = 5.17 [4.03-6.32]; Fig. 2). In 2011, hardness tended to be lower at predated than non-predated nests but the difference was not quite significant (LSM = 4.89 [-1.13-10.91] versus 10.48 [8.46-12.49], respectively; Fig. 2). Snow hardness also varied significantly between jumps, non-predated nests, and random locations ($F_{2,180}$ = 6.15, *P* = 0.003). Lemming winter nests had a harder snow cover than random locations (*P* = 0.004) but snow hardness at jumps did not differ from that at non-predated nest locations (*P* = 0.850; Fig. 2).

Effects of snow cover on predation by ermine

The proportion of transects with winter nests was higher in both mesic and gully habitats than in wet habitat (χ^2_2 = 10.8, *P* = 0.004) and the density of nests was generally highest in gully habitat, intermediate in mesic, and lowest in wet habitat ($F_{2,8} = 6.33$, $P = 0.022$; Table 1). On all transects sampled from 2007 to 2011, 886 winter nests were found and 33 of them (3.7%) were predated by ermine. Snow depth varied significantly among treatments ($F_{2,360} = 5.55$, $P = 0.004$) because lemming winter nests had a deeper snow cover than random locations ($P < 0.001$; Fig. 1) but snow depth at nests predated by ermines did not differ from non-predated ones ($P = 0.330$) and this was consistent across years ($F_{2,360} = 1.70$, $P = 0.185$).

Other determinants of predation by ermine

The probability of predation by ermine was most influenced by lemming species, year, and habitat (cumulative AICc weight = 0.95, 0.93, and 0.91, respectively), and to a lesser extent by nest density (cumulative AICc weight = 0.68; Table 2). Reproduction and two-way interactions among variables had little or no influence (cumulative AICc weight < 0.33). Probability of predation was higher on collared than brown lemming (collared: *beta* = 1.19 ± 0.42 (*SE*); brown was the reference species). Predation also varied among years and was generally highest in 2008 but rather similar in other years. Predation was higher in gully than in wet habitat and intermediate in mesic habitat (gully: *beta* = 1.58 ± 0.92; mesic *beta* = 0.95 ± 0.92; wet was the reference habitat). Finally, probability of predation tended to decrease with increasing nest density (*beta* = -0.19 ± 0.21).

Discussion

Fox hunting behavior

We expected that deep snow should hinder predation attempts by fox on lemmings but we found that this was only partially true and dependent upon the hunting tactic. Only predation attempts made by jumping were limited to sites with a shallow snow cover. Similar results were reported at Wrangel Island, Russia (Ovsyanikov 1993), although maximum snow depths at which foxes could pound through the snow appeared to be limited at 15 cm, perhaps because snow is harder at this site. Obviously, there is a physical limit at which foxes can pound through snow, and in this regard it is surprising that snow hardness did not seem to affect this hunting technique at Bylot Island. However, this was based on only 1 year when the snow pack was relatively soft, and we had a small sample size. Nonetheless, it is possible that foxes are forced to hunt rodents under hard snow due to the preference of lemmings for such sites. Indeed soft, upper snow layers may not provide adequate conditions for a stable sub-nivean space, where lemmings are active in winter, because a soft snowpack is more susceptible to compression (Sanecki et al. 2006).

Despite the preference of lemmings for areas of deep snow cover (Duchesne et al. 2011b; Reid et al. 2012; this study), our results show that this may offer only a limited protection from fox predation. Indeed, predation attempts made by digging, the most frequent hunting technique used in our study, were not affected by snow depth. This was also observed by Ovsyanikov (1993), who reported that foxes dug holes up to 70-80 cm deep to reach lemmings under the snow. However, accessing winter nests through digging may not always guarantee a predation success because lemmings may have enough time to escape from the attack. Nevertheless, some winter nests will hold neonates, which cannot escape, and adults may also come back after the fox has stopped digging and be caught if the fox is patient enough. Interpretation of the effect of snow hardness on predation is difficult because results were inconsistent between years. However, in 2011 when the snow was hardest, foxes showed a tendency to attack nests under a softer snow cover and no attempt to jump through the snow was detected, suggesting that harder snow has the potential to hinder their hunting efficiency. Foxes have the ability to dig through frozen ground to excavate their dens (Prestrud 1991), so digging through hard snow to access a winter nest should be feasible. However, the cost of accessing their prey under such conditions could be above the potential gains and thus not worth it. Therefore, although our results demonstrate that snow can sometimes hinder predation attempts by foxes on lemmings, they can apparently use different hunting techniques to bypass these limitations to some extent.

Predation by ermine

As we expected, snow depth did not affect lemming predation rate by ermine, which suggests that snow has little effect on the activity of this predator. Moreover, the probability of predation was greatest in gully habitat, where both snow accumulation and lemming winter nest densities are generally highest (Duchesne et al. 2011b). However, contrary to what Duchesne et al. (2011b) found, nest density per se did not have an effect on probability of predation. Our results thus suggest that foraging ermines primarily use habitat features to find areas more likely to have high prey densities in winter. Unlike rodents, which may detect areas of deep snow based on local cues such as temperature or light intensity under the snow (Duchesne et al. 2011b; Reid et al. 2012), ermines could use other cues such as topographical features to detect areas where high rodent densities are likely to be found. Areas where snow tends to accumulate, such as the leeward side of slopes or along stream embankment, are visually and rapidly detectable even in winter and could be fairly reliable cues to predict the occurrence of lemmings (Duchesne et al. 2011b). The divergence in cues used by ermines to forage compared to those used by lemmings to settle could explain the absence of an effect of nest density per se on probability of predation. Ermines could successfully predict preferred winter habitats of lemmings, but not necessarily where the highest densities are.

Predation rate was higher on nests used by collared lemming than those used by brown. This could be due to a preference of ermines for one species over the other, as previously suggested by Duchesne et al. (2011b). However, an alternative explanation may be that ermines react differently when they predate one species or the other. Our index of predation is largely based on the presence of lemming fur since ermines often line the nest with their prey's fur and use it for some time. Ermines may show a preference for occupying collared lemming nests because this species has a highly insulative fur (Batzli et al.1983; Ferguson and Folk 1970; Malcolm and Brooks 1993) that could provide better insulation against the cold temperature than brown lemming fur. We found no evidence that ermines selectively prey on nests containing juveniles, contrary to what was previously suggested by Sittler (1995) and Hanski et al. (2001). This is consistent with the hypothesis that selection of winter hunting areas by ermines may primarily be based on topographical features. Finally, the absence of interaction between year and other variables suggests that the ermine hunting strategy during winter may not be affected by the phase of the lemming cycle.

A potential limitation of our study, however, is that we do not know when during the winter predation occurred, and thus actual snow depth at that time is unknown. Moreover, our study took place at the end of the winter, and thus may not be representative of conditions experienced by predators and lemmings throughout the winter. This may be especially true early in the winter, when the snow pack should be thin, and lemmings presumably more vulnerable. Additional studies at this time period would be desirable.

Snow cover, climate change and predation

Several characteristics of snow cover such as its depth, hardness, timing of establishment, and duration are likely to be affected by climate warming (Kausrud et al. 2008; Mellander et al. 2007; Rouse et al. 1997). Hard snow in the polar regions, which could potentially restrict predation by fox, is a consequence of high snow density (Höller and Fromm 2008) and low air temperature (Tusima 1975). Thus, as temperature warms in the Arctic, hardness may decrease, which could increase vulnerability of lemmings to fox predation. However, it is also possible that warming will increase melt/frost and icy rain events, which would have the opposite effect on snow hardness. Therefore, it is difficult to predict how upcoming changes in snow quality due to climate warming will affect mammalian predation on lemmings. Nonetheless, considering the relatively weak effects of snow characteristics on lemming vulnerability to predation that we found, it is possible that aspects of lemming ecology other than mammalian predation will be more affected by changes to the snow cover. For instance, reduced winter habitat quality (due to lower insulative properties of the snow) and food accessibility (due to ground icing or reduced movement in the sub-nivean space) or a prolonged period of vulnerability to avian predators due to a shorter snow season (Gilg et al. 2009) may also affect lemming populations.

Table 1. Proportion of transects with lemming winter nests (*Lemmus trimucronatus* and *Dicrostonyx groenlandicus*) and average density in transect areas where winter nests were found, Bylot Island, Nunavut, Canada. 2007: *n* = 25 transects/habitat; 2008: *n* = 10 transects/habitat; 2009-2011: *n* = 20 transects/habitat.

	Year	**Wet**	**Mesic**	**Gully**
Proportion of transects with winter nests	2007	0.36	0.72	0.84
	2008	0.70	0.90	0.90
	2009	0.15	0.15	0.10
	2010	0.40	0.90	1.00
	2011	0.65	1.00	1.00
Average nest density (nests/ha ± *SE*) in transects with presence of winter nests	2007	2.17 ± 0.35	3.22 ± 0.42	4.20 ± 0.80
	2008	2.86 ± 0.55	6.33 ± 1.08	4.44 ± 0.80
	2009	0.90 ± 0.13	1.00	1.44 ± 0.56
	2010	2.08 ± 0.38	4.34 ± 0.85	5.84 ± 1.13
	2011	2.76 ± 0.50	5.24 ± 0.62	8.40 ± 0.83

Table 2.—Models explaining occurrence of lemming winter nest (*Lemmus trimucronatus* and *Dicrostonyx groenlandicus*) occupancy by ermine (*Mustela erminea*) during winters 2006-2007 to 2010-2011, Bylot Island, Nunavut, Canada. ΔAICc: difference in Akaike's information criterion adjusted for small sample size between the current and the top-ranked model, *k*: number of parameters, w_i: model weight.

Rank	**Variables in the model** [a]	**ΔAICc**	w_i	***k***
1	Dens + Hab + Sp + Yr	0	0.28	7
2	Dens + Hab + Repro + Sp + Yr	0.18	0.25	8
3	Hab+ Sp + Yr	0.63	0.20	6
4	Sp + Yr	3.02	0.06	4
5	Hab + Sp + (Dens × Yr)	3.73	0.04	8
6	Hab + Repro + Sp + (Dens × Yr)	4.06	0.04	9
7	Dens + Hab + Sp	4.81	0.02	6
8	Dens + Hab + Repro + Yr	5.40	0.02	6
9	Hab + Sp	5.53	0.02	5
10	Sp	5.61	0.02	3

[a] Dens: winter nest density (nests/ha), Hab: habitat (gully, mesic, wet), Repro: reproduction (1), Sp: species (both, brown, collared), Yr: year (2006-2007 to 2010-2011).

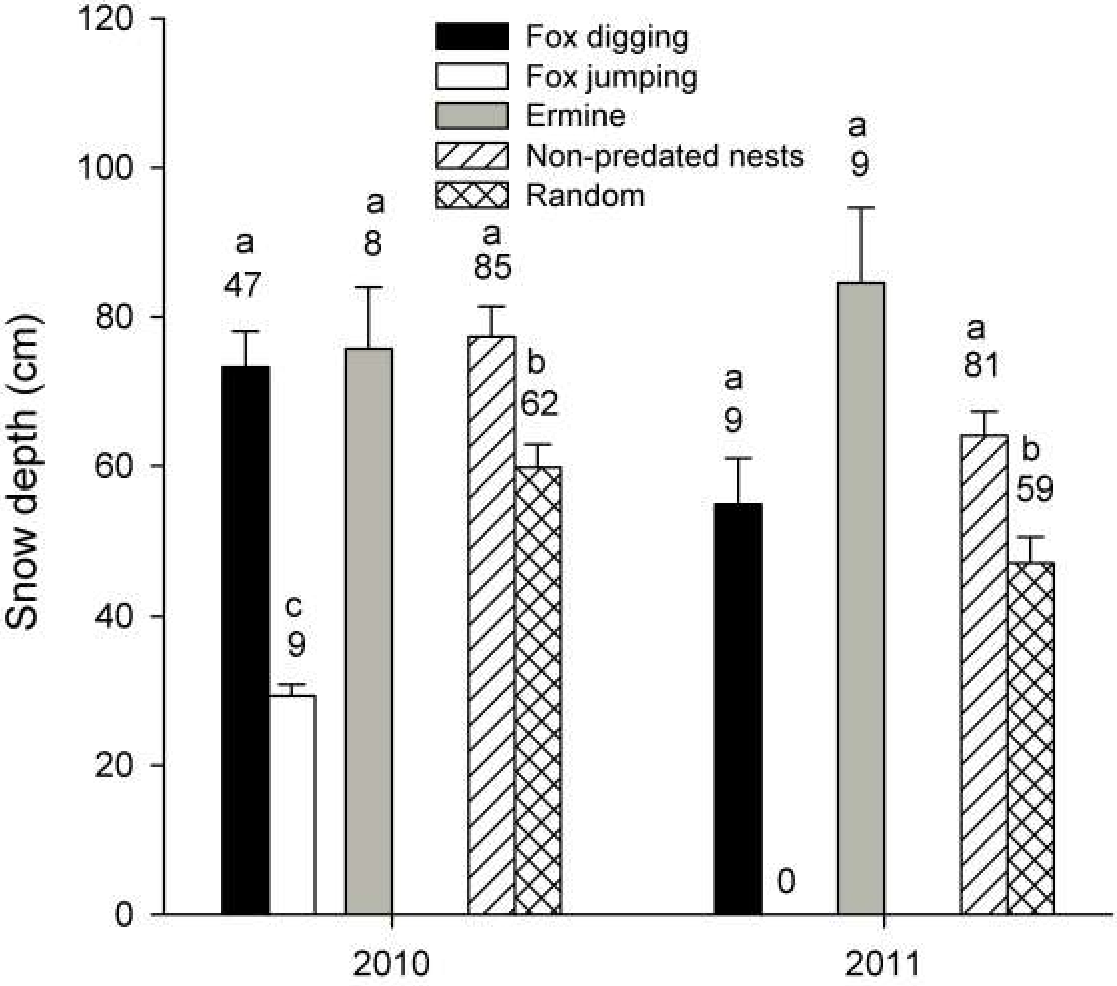

Figure 1. Snow depth measured at tunnels where foxes (*Vulpes lagopus*) made predation attempts on lemmings by digging or jumping, at lemming nests predated by ermine (*Mustela erminea*), at non-predated nests and at random locations, Bylot Island, Nunavut, Canada. Error bars represent SE and N values are shown above bars. Bars with the same letter are not significantly different ($P > 0.05$).

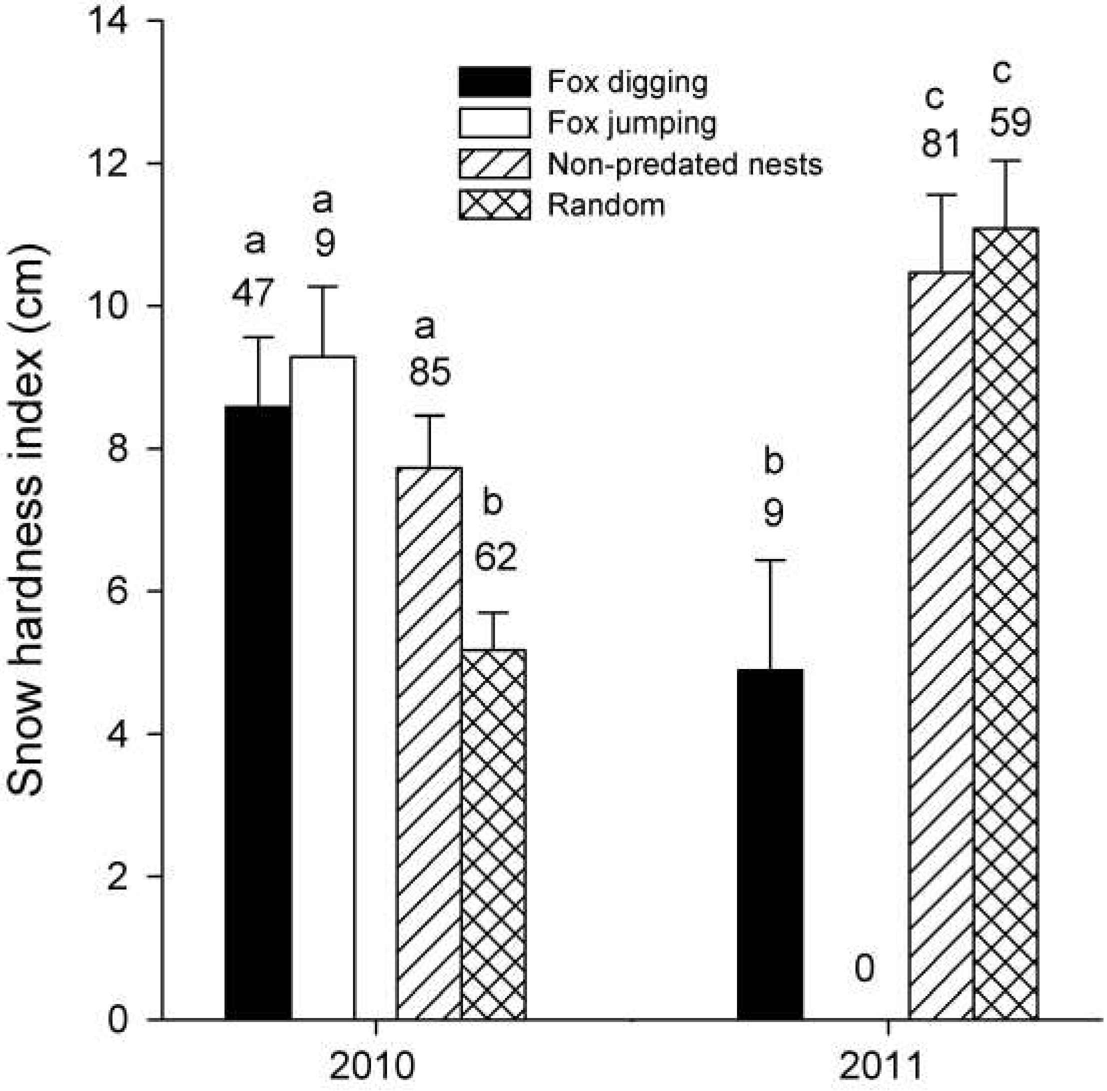

Figure 2. Snow hardness index measured at tunnels where foxes (*Vulpes lagopus*) made predation attempts by digging or jumping, at non-predated lemming nests and at random locations, Bylot Island, Nunavut, Canada. Error bars represent SE and N values are shown above bars.

Chapitre 6

Patterns of predation by ermine on lemmings in the Canadian Arctic

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Résumé

Les prédateurs peuvent parfois réguler leurs proies, spécialement dans les réseaux trophiques simples. Dans les écosystèmes nordiques, il a été suggéré que la prédation par les petits mustélidés pourrait générer les cycles de population de petits mammifères en raison de leur réponse décalée face à l'augmentation de la population de leurs proies. Pourtant, très peu d'information est disponible sur les patrons de prédation des lemmings par les mustélidés dans la toundra. Nous avons travaillé à l'île Bylot dans l'Arctique Canadien où le lemming brun (*Lemmus trimucronatus*) et variable (*Dicrostonyx groenlandicus*) sont présents, ainsi que l'hermine (*Mustela erminea*). Nous avons (1) éxaminé si l'abondance d'hermine montrait une réponse numérique décalée face aux fluctuations des densités de lemming, (2) estimé les taux de consommation de l'hermine à travers des observations sur le terrain et (3) déterminé les taux de prédation globale de l'hermine sur les lemmings. Nous avons estimé l'abondance d'hermine et les taux de prédation pendant l'été et l'hiver en utilisant une combinaison de relevés de nids d'hiver, d'observations directes aux tanières d'hermine, de télémétrie et d'utilisation de boîtes de trappage. Notre indice hivernal de densité d'hermine suggère une réponse numérique instantanée face aux variations annuelles de densité de lemming. Cependant, la proportion de nids d'hiver de lemming prédatés par l'hermine, ainsi que nos indices estivaux d'abondance d'hermine, suggèrent une réponse décalée d'une année. Ceci suggère que le déclin des densités de lemming survient plus rapidement que celui de l'hermine. La reproduction de l'hermine était plus élevée dans les années de fortes abondances de lemming. Le domaine vital d'une femelle suivie au cours de deux étés était de 6.5 km^2 et 1.6 km^2 et son taux de consommation pendant qu'elle nourrissait ses jeunes était en moyenne 3.95 lemmings/jour/hermine. Ce taux de consommation est plus élevé que ceux prédits à partir des calculs énergétiques et indique que l'hermine tue des proies en surplus. Globalement, nous avons estimé le taux de prédation journalier de l'hermine à environ 1.2 % de la population de lemming durant les étés de fortes abondances de proie. Nous concluons que l'hermine pourrait jouer un rôle clé dans la phase du déclin des lemmings en prélevant une grande proportion de la population de lemming durant l'été de pic d'abondance et en maintenant une pression de prédation élevée au cours de l'hiver suivant.

Abstract

Predators may sometimes regulate their prey, especially in simple food webs. In northern ecosystems, it has been suggested that predation by small mustelids may generate population cycles in small mammals due to their delayed response to population increase of their prey. However, little is known about the predation pattern of mustelids on lemmings in the tundra. We worked on Bylot Island in the Canadian Arctic where the brown (*Lemmus trimucronatus*) and collared (*Dicrostonyx groenlandicus*) lemmings are present together with the ermine (*Mustela erminea*). We (1) examined if ermine abundance showed a delayed numerical response to fluctuations of lemming densities, (2) estimated the consumption rate of ermine through field observations and (3) assessed the overall predation rate of ermine on lemmings. We assessed ermine abundance and predation rate in summer and winter using a combination of lemming winter nest observations, direct observations at ermine dens, radio-tracking of ermines and use of trapping boxes. Our winter index of ermine density suggested an instantaneous numerical response to annual variations in lemming density. However, proportion of lemming winter nests predated by ermines, as well as our summer indices of ermine abundance, indicated a delayed response of up to one year. This suggests that the decline of lemmings occurred faster than the decline in ermine density. Breeding activity of ermines was highest in years of high lemming abundance. The home range of one female tracked during two summers was 6.5 km^2 and 1.6 km^2 and her consumption rate while provisioning young averaged 3.95 lemmings/day/ermine. This consumption rate is higher than those predicted from energetic calculations and is indicative of surplus killing. Overall, we estimated the daily predation rate of ermine at about 1.2 % of the lemming population during summers of high prey abundance. We conclude that ermines may play a key role in the lemming decline phase, by removing a large proportion of the lemming population during a summer of peak abundance and by maintaining a high predation pressure during the following winter.

Introduction

Predators may play a key role in simple ecosystems by regulating prey populations (Korpimäki and Krebs 1996, Korpimäki and Norrdahl 1998, Berger et al. 2001). Examples include the control of large ungulate populations by wolves (*Canis lupus*) on Isle Royale and Yellowstone Park, USA (Ripple et al. 2001, Post et al. 1999, Post et al. 2002), and the trophic cascade initiated by the introduction of arctic foxes (*Vulpes lagopus*) in the Aleutian Islands, which preyed on seabirds and induced changes in the vegetation (Croll et al. 2005). In the tundra, which has a simplified food web in comparison to ecosystems located at lower latitudes (Gilg et al. 2003), small mammals are preyed upon by a diverse suite of small to medium-size predators (Krebs et al. 2003, Ims and Fuglei 2005). In such environments, just a few species of rodents typically support a large guild of predators (Legagneux et al. 2012). It has thus been suggested that predation pressure may be a key factor regulating rodent populations, and that predation could control the cyclic dynamic of several species (Korpimäki and Krebs 1996, Reid et al. 1997, Angerbjörn et al. 1999, Hanski et al. 2001, Gilg et al. 2003).

Small mustelids, mainly the ermine (*Mustela erminea*) and least weasel (*M. nivalis*), have been invoked as key predators able to generate a cyclic dynamic in their prey through a delayed response to prey population increase (Korpimäki et al. 1991, Korpimäki and Krebs 1996, Hanski et al. 1993, Heikkilä et al. 1994, Hanski et al. 2001, Gilg et al. 2003, Klemola et al. 2003). Mustelids specialize on rodents and are the only predator that can easily access lemming tunnels under the snow (Bjørnstad et al. 1995, Sittler 1995). The absence of alternative prey combined to the high energetic requirement of mustelids due to their small body size (King and Powell 2007) often lead to high predation rates in winter. Mustelids are also known to have a strong functional response to variations in rodent densities and to show high recruitment rates during years of small mammal abundance (Sundell et al. 2000, King and Powell 2007). These specialist predators are also notorious for surplus killing, presumably an adaptation to survive during periods of low prey abundance (Jędrzejewska and Jędrzejewski 1989). Caching prey could prevent mustelid populations from declining too rapidly during prey population crashes and could contribute to their delayed numerical response.

Mustelids are elusive animals and only anecdotal observations exist on their density and predation rate on arctic small mammals, particularly lemmings (but see Gilg et al. 2006). Direct field observations are rare and most studies trying to assess the impact of mustelid predation on small mammal populations used indirect signs such as predated winter nests (Sittler et al. 1995) or faeces (Gilg et al. 2006). Determining the role of these predators in the population dynamic of lemmings is thus a critical but difficult task as it requires a good understanding of their numerical and functional responses to fluctuations in prey abundance. We examined these questions in a Canadian arctic tundra ecosystem where a single mustelid, the ermine, preys on two lemming species, the brown (*Lemmus trimucronatus*) and collared lemming (*Dicrostonyx groenlandicus*). Our objectives were to (1) determine if ermine abundance showed a delayed numerical response to fluctuations of lemming densities over a 6-year period, (2) estimate the consumption rate of ermines through direct field observations, and (3) assess the potential overall predation rate (i.e. total response) of ermines on lemmings.

Methods

Study area

The study was conducted on Bylot Island, Sirmilik National Park, Nunavut Territory in the Qarlikturvik glacial valley (73° 08’ N, 80°00’ W). The study area (70 km^2) was composed of lowlands bordered by a large river to the north and uplands with rolling hills to the south. Mesic tundra dominated the landscape and was composed mainly of prostrate shrubs (*Salix* spp., *Cassiope tetragona, Dryas integrifolia*), forbs (*Saxifraga* spp*.*, *Potentilla* spp*.*, *Ranunculus* spp*.*, *Pedicularis* spp.), a sparse graminoid cover (*Arctagrostis latifolia, Alopecurus alpinus, Poa* spp*.*, *Luzula* spp.) and mosses and lichens (Duclos 2002). In the lowlands, tundra polygons, thaw lakes and ponds were common and formed wetlands dominated by sedges (*Carex aquatilis*, *Eriophorum sheuchzeri*), grasses (*Dupontia fisheri*, and *Pleuropogon sabinei*) (Massé et al. 2001) and a uniform moss carpet. Small, intermittent streams running through upland areas were often located at the bottom of small gullies and were characterized by a thin band of wetland vegetation surrounded by mesic tundra.

In our study area, only two species of rodents are present, the brown and collared lemming, and they represent the only significant herbivore population during winter. Lemming predators can be numerous in summer and include the snowy owl (*Bubo scandiaca*), long-tailed jaeger (*Stercorarius longicaudus*), rough-legged hawk (*Buteo lagopus*), glaucous gull (*Larus hyperboreus*) and arctic fox, in addition to the ermine. Mammals are the only predators that remain in the area during winter. Nesting passerines (*Calcarius* and *Plectrophenax* spp.) and shorebirds (*Calidris* and *Pluvialis* spp.) are potential alternative prey for the ermine and are abundant in the summer.

Lemming density

Lemming populations are characterized by strong, multi-annual cyclic fluctuations of abundance at our study site (Gruyer et al. 2008) and we monitored their summer abundance by live-trapping from 2004 to 2012. We trapped lemmings on two 10.9 ha grids (one in wet and one in mesic tundra) three times during the summer (mid-June, mid-July and mid-August) to obtain mark-recapture estimation of abundance. The trapping grids were laid out in a Cartesian plane of rows and columns, with numbered stakes spaced every 30 m. At each stake, we set out a Longworth trap baited with apples near signs of lemming use or active burrows. We trapped lemmings during 3 consecutive days (4 days in 2004-2007) at each session and traps were checked twice a day, yielding 6 to 8 capture occasions. We considered the lemming population closed within each trapping session. All density estimates were carried out with DENSITY 4.4 (http://www.otago.ac.nz/density) using Efford's maximum likelihood estimates (Efford et al. 2004, Borchers and Efford 2008; see Krebs et al. (2011) for parameter settings in our analysis). Summer densities used in our analysis were the averaged values between the two grids during the three trapping sessions.

During winter, lemmings build nests for better insulation against cold temperatures (Casey 1981), and nest counts can provide an index of lemming winter abundance (MacLean et al. 1974, Sittler 1995, Duchesne et al. 2011b). Lemming nest density was estimated annually from winter 2006-2007 to 2011-2012 by sampling them soon after snow-melt. Winter nests were systematically counted on our two live-trapping grids by walking parallel lines spaced 5 m from each other. To estimate winter nest density in trapping grids, the total number of nests sampled was divided by the trapping area, assuming all nests were detected. Winter nest density was also estimated on transects (75 in 2007, 30 in 2008 and 60 in 2009-2012) randomly located across the study area. Permanent transects were distributed equally in 3 habitats (wetlands, mesic tundra and along stream gullies) and reused every year. Transects were approximately 500 m long and sampling was done using the line transect method (for details see Buckland et al. 2001). Estimates of winter nest density were obtained with the software for distance sampling analysis Distance 6.0 (http://www.ruwpa.st-and.ac.uk/distance/, Thomas et al. 2009). Winter nest densities used in our analysis were averaged values across all the transects. Nests were also sampled opportunistically in years of low lemming abundance. The locations of all winter nests were taken using a Global Positioning System (GPS). To examine a delayed response of ermines to lemming winter density, we had to estimate nest densities prior to 2007 (our first year when estimates of ermine abundance were available, see below). We did that by transforming spring lemming densities estimated by live-trapping into lemming nest densities using the following equation (a reciprocal of the equation provided by Krebs et al. (2012); $R^2 = 0.64$):

$$\text{Log}_{10}\,(\text{nest density}) = 0.0499 + 0.6842\,\log_{10}\,(\text{spring density})$$

The species of lemming using a given nest was identified through the length, form and color of the faeces left inside (MacLean et al. 1974, Duchesne et al. 2011a). Collared lemmings have dark reddish faeces about 4-6 mm long, whereas brown lemmings produce green faeces about 6-10 mm long (Duchesne et al. 2011a).

Monitoring of ermine activity

When ermines prey on lemmings living in winter nests, they sometimes line the nest with the fur of their prey and use the nest themselves, or leave rodent body parts and partially eaten carcasses in the nest (MacLean et al. 1974, Sittler 1995). It is thus possible to obtain an index of ermine activity by counting nests with fur lining.

We obtained an index of winter ermine density by dividing the number of predated lemming nests (i.e. those lined with fur) found on transects and grids by the surface covered by those transects and grids assuming that each fur-lined nest was predated by a different individual (Gilg et al. 2006). The surface covered by a transect was estimated by multiplying its length (500 m) by the effective detection distance estimated by the program Distance 6.0, which varied across habitats and years. We counted aggregation of predated nests as a single event, because an ermine can use several nests and we wished to reduce inflation of ermine density potentially generated by this behaviour. To do so, we calculated the nearest-neighbor distance for each nest using the "spatstat" package in R (Baddeley and Turner 2005). Multiple predated nests found <500 m from each other where counted as a single predation event. We also estimated the proportion of predated winter nests by dividing the ermine density by the density of winter nests. For calculating this proportion, only nests found along transects and in trapping grids were used and predated nests located close to each other where also counted as a single predation event.

Wooden boxes, originally deployed to trap lemmings under the snow (Bilodeau et al. 2013c), were used to monitor ermine winter and summer activity. In 2009, 40 boxes were deployed in habitats preferred by lemmings during winter (mesic tundra and stream gullies) over a 1.0 km^2 area. Lemmings sometimes used the boxes to make winter nests and some ermines used them to store lemming carcasses and to rest. The boxes (hereafter called shelter boxes) were visited soon after snow-melt in late June or early July, and again in mid-August. At each visit, lemming carcasses, winter nests and faeces were collected, and carcasses were identified to the species and counted. This method provided another index of ermine activity during the period 2010-2012.

During summers 2009 to 2012, we searched opportunistically for signs of ermine activity throughout the study area. From 2009-2011, whenever individuals, tracks or fresh scats were observed, we set 5 to 10 Havahart® live-traps baited with tuna and checked them at 6-hour intervals to capture ermines. Captured animals were sexed, weighed to ± 1 g, anesthetized with isoflurane and marked with 3-g VHF radio-collars (Model Pip-2, Biotrack Ltd., Dorset, UK). Daily locations of radio-marked animals were obtained for periods ranging from 14 to 32 days. Sometimes, a female and her young were captured. The locations obtained then refer to the family group. Family groups were always associated with dens but they frequently changed denning site (they stayed at a den 1.9 ± 0.2 (*SE*) days). Locations of ermines and of their dens were taken using a GPS. We estimated home range of radio-marked individuals (or families) using the 100% minimum convex polygon method (Grigione et al. 2002, Herfindal et al. 2005, Nilsen et al. 2008). We calculated the observation-area curve (Odum and Kuenzler 1955) to determine if sufficient locations had been collected to reach an asymptotic value of home range size. This was the case for the 2 families but not for the only male we radio-tracked. Thus, only home range size of families is presented.

We conducted behavioral observations at the den of radio-marked individuals. The observer stood quietly at a vantage point located 5 to 10 m from the den and observed for periods ranging from 10 to 200 minutes between 6h30 AM and 2h00 AM. Typically, the mother went out hunting lemmings or rested at the den, while young played around the den, even sometimes visiting the observer. We concluded that observation distance did not disturb ermines. We performed 26 observations bouts for a total of 1004 minutes of observation in 2010 and 19 bouts (1607 minutes) in 2011. For each observation period, we noted when the female left and returned to the den, and the number and type of prey brought back to the den (all were lemmings). These observations also allowed us to determine the litter size of each family.

The 17 ermine dens that we found, either through radio-tracking or opportunistically, were revisited several times every summer. If an unmarked family was present, observations were also conducted to determine litter size. The combination of radio-marked animals and incidental ermine observations (mostly near dens) allowed us to determine the minimum number of ermines present in the study area each summer.

Statistical analysis

To fit the numerical responses of ermines, we used a type II response curve following the equation provided by Sundell et al. (2000):

$$Y = a\,N / (b + N)$$

where Y could be either the ermine density (D) or the proportion of predated winter nests (P), a is the asymptotic ermine density (or proportion of predated winter nest), N the density of lemming winter nest (or of lemmings in summer) and b the half-saturation constant. We also fitted a type III response curve following the equation provided by Gilg et al. (2006):

$$Y = a\,N^2 / (c^2 + N^2)$$

where c is the density of winter nests (or of lemmings in summer) at the inflexion point of the curve. We also fitted the same equations with lemming winter nest (or summer) density measured at year t-1 or the mean of years t-1 and t-2, to test if a delayed response fitted the data better based on the R^2. The nls function in program R was used to fit the curves.

We also examined if ermine showed a preference for occupying the nests of a particular lemming species by using a log-linear model, which takes into account the availability of nests each year. All nests, including those found opportunistically were used for this analysis. Analyses were conducted in R 2.13.1 (R Development Core Team 2010).

Results

Lemming densities

Summer densities of brown and collared lemmings ranged from 10 to 800 and from 0 to 112 ind/km^2, respectively, from 2004 to 2012, and their winter nest densities ranged from 10 to 1076 and from 5 to 341 nest/km^2 from 2007 to 2012 (Table 1). Brown lemming density was high in 2004 but had crashed by summer 2005. They peaked again in 2008 but crashed before winter 2008-2009. They started to increase during winter 2009-2010 and peaked again in summer 2011 but crashed before winter 2011-2012. Collared lemmings followed a somewhat different pattern. Summer densities were relatively low in 2004 and 2005 and even lower in 2006. During winter 2006-2007, they reached high densities but apparently crashed before the summer. Densities increased slightly in 2008 but decreased to very low values before winter 2008-2009. Densities increased in winter 2009-2010 and remained high until winter 2010-2011, but crashed before summer 2011 and remained low in 2012. The seasonal dynamic thus appears to differ between the two species, as brown lemming populations crash in late summer whereas those of collared lemmings crash mostly in late winter or early summer.

Ermine response during winter

The index of winter ermine abundance was generally highest in years of high lemming densities (Table 1). Indeed, an instantaneous response between the ermine abundance index in winter and lemming nest densities gave the best fit (both species, type II: $R^2 = 0.60$, $F_{2,4} = 18.3$, $P = 0.010$; estimated parameters, $a = 15.1$, $b = 217$; brown lemming, type II: $R^2 = 0.65$, $F_{2,4} = 20.7$, $P = 0.008$; $a = 14.5$, $b = 110$; collared lemming, type III: $R^2 = 0.45$, $F_{2,4} = 12.5$, $P = 0.019$; $a = 12.0$, $c = 31.5$; Fig. 1). However, the ermine winter activity index from shelter boxes revealed a different picture as it suggested a delayed response to lemming abundance. In 2009-2010, utilisation of boxes by ermines was very low when lemming density were increasing, slightly higher in 2010-2011 when lemmings peaked, and highest in 2011-2012 when lemmings had crashed (Table 1).

The proportion of winter nests predated by ermines also suggested a delayed impact on lemmings. We found that lemming summer densities at time t-1 yielded the best fit with the proportion of winter nests predated for both species combined and for brown lemmings, although the relationships were not significant (both species, type II: $R^2 = 0.33$, $F_{2,4} = 3.89$, $P = 0.116$; estimated parameters $a = 0.05$, $c = 50$; brown lemming, type II: $R^2 = 0.32$, $F_{2,4} = 3.80$, $P = 0.119$; $a = 0.06$, $b = 61$; Fig. 1). For collared lemmings, none of the relations tested showed a good fit ($P > 0.18$).

Ermines showed a preference for collared lemmings in winter as a much higher proportion of collared lemming nests were predated and used by ermines (annual range: 0.05 to 0.29) compared to brown lemming nests (0 to 0.06; $\chi^2 = 26.6$, df = 12, $P < 0.001$; Table 1).

Ermine response during summer

In summer 2009, when lemming densities were very low, only one male ermine was observed. The number of individuals observed increased in 2010 and peaked with lemming density in summer 2011 (Table 1). However, the number of observed individuals remained high in 2012, when lemmings had crashed. Summer use of trapping boxes also revealed evidence of a delayed response. No shelter box was used in 2010 and only one was used in 2011, but in summer 2012 a large proportion of boxes were used as food caches by ermines (Table 1). Ermine families were observed only when summer lemming densities were increasing (N = 1) or when they peaked (N = 2). The family of 8 that was radio-tagged during the year of increasing lemming abundance had a home range of 6.51 km^2 over the period 7 June to 3 August 2010. The same female was again radio-tagged during the peak lemming year; she had 10 young but this time her home range was 4 times smaller (1.64 km^2) although she was monitored during a slightly shorter period of time (12 June to 13 July 2011). However, another female was occupying the western part of her 2010 home range.

The few lemming remains found in shelter boxes in 2010 and 2011 appeared to be all brown lemmings. In 2012, 94 % of lemming carcasses stored in winter (N = 66) and 67 % of those stored in summer (N = 15) were brown lemming. During behavioral observations, all lemmings brought back by the female to the den were brown lemmings in 2010 (N = 30) and 98% in 2011 (N = 45). The female brought back an average of 25.6 ± 7.2 lemmings/day in 2010 and 56.2 ± 12.8 lemmings/day in 2011, the peak lemming year. In 2010, the per capita consumption rate was estimated at 2.8 lemmings/day (25.6 lemmings/day for a family of 9 ermines) and 5.1 lemmings/day (56.2 lemmings/day for a family of 11 ermines) in 2011. These values are higher than the consumption rate estimated by Gilg et al. (2006) in Greenland (1.9 lemmings/day). The body mass of ermines caught on Bylot Island was 175.8 ± 7.9 g for males (n = 10) and 98.5 ± 8.5 g for females (n = 2), which is comparable to those in Greenland (Gilg et al. 2006). If we estimate food requirements to achieve energy balance using the equations provided by Nagy et al. (1999), a 137-g ermine needs to consume only 0.9 lemming/day (assuming a mean lemming mass of 40 g). However, one must consider that the equations are for all mammals in non-breeding state and that mustelids are small predators with a high metabolism (Iversen 1972).

We attempted to determine from our admittedly scant data the predation rate that ermine could impose on lemmings during summers of intermediate (2010) and high lemming abundance (2011). If we assume that (1) all the study area is used by ermines, (2) adult female and male home ranges are contiguous and non-overlapping and (3) adult sex-ratio is 1:1 (King and Powell 2007), we can estimate ermine density in 2010 as 0.8 ind/km^2 ((9 + 1)/(6.51 * 2)) and in 2011 as 2.9 ind/km^2 ((8.5 + 1)/(1.64 * 2)). These estimates are somewhat conservative since densities could be almost twice as high if home ranges overlap between sexes (Johnson et al. 2000). Nonetheless, using our first density estimates combined with our observed consumption rates, the proportion of the lemming population consumed daily by the ermine would be 0.5 % in 2010 ((2.8 lemmings / day x 0.8 ermine / km^2) / 470 lemmings / km^2) and 1.8 % in 2011 ((5.1 lemmings / day x 2.9 ermine / km^2) / 800 lemmings/km^2).

Discussion

Ermine numerical response

Ermines showed a strong numerical response to variations in lemming density on Bylot Island. However, it is unclear to what extent they displayed a delayed response to variations in lemming density, as reported elsewhere (Hanski et al. 1993, Heikkilä et al. 1994, Hanski et al. 2001, Gilg et al. 2003). Our results are conflicting in that respect. Ermine abundance in winter seemed to display a direct response to lemming density (as judged from winter nests) but summer abundance/activity data seemed to indicate a 1-year delayed response, though we have fewer years of data for this season. The low ermine abundance in summer 2009, after the 2008 lemming peak, is apparently not consistent with the idea of a delayed response. However, lemming densities were much lower during the 2008 peak and the following winter than in 2011-2012, suggesting that the lemming decline occurred more rapidly in 2008-2009. A hypothesis is that ermines had more difficulty storing lemmings in 2008 than in 2011, which could have increased their mortality during the winter 2008-2009, hence their low density in summer 2009.

The proportion of winter nests predated by ermines was best explained by lemming density during the previous summer. Therefore, these data also suggest a 6 to 12 month delay in the impact of ermines on lemmings. The proportion of predated nests provides an index of how ermine predation rate changes with lemming abundance. Even though ermine density may start to decline as soon as lemmings crash, a greater proportion of lemming nests can still be predated at that time if the decline in ermine density is more gradual during fall/winter than the lemming decline. Thus, although the absolute number of lemmings killed per day may decline, the proportion of the lemming population consumed by the ermine may actually increase. A reason why we did not find a similar relationship with collared lemming winter nests may be that this species does not exhibit large fluctuations in abundance at our study site. We also found that ermine reproductive activity was directly related to lemming density during the current summer. Thus, ermine abundance should be highest during the winter that follows the peak, provided that young can at least partly survive through the winter. The surplus killing and food caching of mustelids reported in other studies (Jędrzejewska and Jędrzejewski 1989, King and Powell 2007) were also observed on Bylot Island (i.e. lemmings stored in shelter boxes), during fall/early winter, when lemmings were still abundant. This could allow ermines to survive the winter following a peak.

Deriving an index of ermine abundance or predation with lemming winter nests has unfortunately some limitations. A first problem is that ermine density can potentially be overestimated because the same individual may use multiple nests. We strived to reduce this potential bias by counting only one individual when aggregations of predated nests were found, but cannot evaluate the validity of this approach. In future studies, collecting ermine hairs in the nests and identifying individuals through genetic analyses could allow more reliable estimation of the minimum number of individuals present in the study area (Boulanger et al. 2006). A second problem is that a predated winter nest can only provide one data point per winter. Yet, lemming densities can change considerably over the 8-month winter period if the population is in an increasing or decreasing phase. Therefore, similar winter nest densities could be obtained in two years characterized by opposite trends in lemming numbers, although these two years would offer a very different environment for the predator.

Finding an appropriate index of ermine activity or density is challenging. Techniques other than those that we applied exist. For instance, snowtracks have been used (Korpimäki et al. 1991, Klemola et al. 1999) to assess mustelid activity in winter, whereas tracking tunnels were used to assess summer activity (Feige et al. 2012). Yet, these techniques cannot provide robust information on mustelid densities and consumption rates, which are needed to evaluate the role of mustelids in the cyclic dynamic of arctic rodents.

Diet and consumption rate

Data from winter nests indicate that ermines showed a strong selection for collared lemmings in winter. This could reflect their preference for this species or a difference in vulnerability between brown and collared lemmings. However, another possibility is that ermines prefer to occupy collared lemming nests because fur of these lemmings is more insulating (Ferguson and Folk 1970, Batzli et al.1983, Malcolm and Brooks 1993). This point to another limitation of using winter nests to infer ermine predation rate as ermines likely do not occupy all the nests in which they prey on lemmings.

In contrast, observations made during summer and in shelter boxes do not provide evidence that collared lemmings are preferred by ermines. Almost all lemmings caught by the female that we observed in wetlands were brown, although this may not be surprising because collared lemmings usually prefer mesic tundra over wetlands (MacLean et al. 1974, Batzli et al. 1983). However, virtually all carcasses cached by ermines in the trapping boxes in winter 2011-12 were also brown lemmings even though the abundance of the two species was rather similar based on winter nest densities. Similarly, in summer 2012, the percentage of brown lemmings cached in trapping boxes (67%) was virtually identical to the percentage of brown in the population based on live-trapping data (69%; calculated from Table 1). Thus, our results do not offer good evidence for selection by ermine of one lemming species over the other.

Our limited observations suggest that the consumption rate of ermines may have been underestimated in the past. Gilg et al. (2006) and Wilson (1999) based their estimates on the daily energetic requirement of ermines, and reported values of 1.92 and 1.35 lemmings/day/ermine, respectively. We found, based on direct behavioural observations conducted during two summers of high lemming abundance, that breeding ermines can have a consumption rate 2.4 times higher, which can even exceed that of a breeding snowy owl pair with chicks (up to 28.5 lemmings/day vs 56.2 lemmings/day for an ermine female with young; Therrien 2012). These values strongly suggest that ermines engage in surplus killing on lemmings when the latter are abundant, as previously reported in several mustelids, including the ermine (Jędrzejewska and Jędrzejewski 1989, King and Powell 2007). This would explain the large discrepancies between our consumption rates and those based on energetic requirements. Unfortunately, we made observations on only one female caring for large litters in two consecutive years, and we cannot exclude the possibility that this individual had unusually high predation rates.

The role of the ermine in lemming population dynamics

The information presented here can provide us with some insights regarding the potential role of ermines in lemming population dynamics. Therrien (2012) demonstrated that predation rate by avian predators on lemmings was high at our study site and that they had the potential to reduce lemming densities during the summer. However, these predators leave the area for the winter. Moreover, avian predators show a strong and immediate response to lemming fluctuations and thus it is unclear if they could generate a cyclic dynamic without a delayed response (Hanski et al. 1993, Stenseth et al. 1996, Stenseth 1999). The ermine has been shown to exhibit a delayed response to fluctuations in lemming density in Greenland (Gilg et al. 2003, 2006) and we did find some evidence of a delayed response in our data. However, the delay in our system appears shorter (less than 1 year) than what has been reported in Greenland (between 1 and 2 years; Gilg et al. 2006).

According to our estimates, summer daily predation rate of ermine on Bylot Island would be around 1.2% (range: 0.5-1.8%). This is below the maximum potential growth rate of brown lemmings (2.4%; Stenseth and Ims 1993a). However, avian predators and foxes are also present in summer and can also exert heavy predation rates on lemmings (Gilg et al. 2006, Legagneux et al. 2012, Therrien 2012). Combining the total response of all these predators may be sufficient to stop population growth of brown lemmings in peak years and initiate their decline during summer. Although avian predators leave in late summer, ermines and foxes remain and their population should then be at their highest point with the recruitment of young. Their combined effect, along with the cessation of lemming reproduction, could drive further down lemmings before the onset of winter. This would agree with our observation that, for the brown lemming, winter density is always low following a summer peak, suggesting a summer/fall decline. By exhibiting a delay in their population decline (due to food caching during the peak), ermine could depress further lemmings populations during the first winter after the peak and thus deepen and prolong the low phase. Foxes, which are also known to cache lemmings (Careau et al. 2007), could also contribute to the depression of lemming densities because they can still hunt lemmings under the snow, though less efficiently (Bilodeau et al. 2013a) and they can remain on Bylot Island for most of the winter (Berteaux and Lai, unpublished data).

In conclusion, our results suggest that ermines can potentially remove a large proportion of the lemming population during the summer and contribute to their decline in peak lemming years on Bylot Island. Moreover, by maintaining high predation pressure in winter, at least in the winter following the peak, they could play a critical role in lemming population dynamics. However, our results also highlight that ermines alone are unlikely to regulate lemming populations and that the combined effects of other predators, such as birds of prey and possibly also foxes, are probably essential. This suggests that mechanisms controlling the two lemming populations on Bylot Island may be similar to what has been reported in eastern Greenland (Gilg et al. 2003). Nonetheless, more data are needed, in particular about the functional response of ermines to varying lemming density and on the winter ecology of this predator. The use of shelter boxes as described by Bilodeau et al. (2013c) may be an additional tool to assess ermine activity in summer and winter. Use of automated cameras inside such boxes could be a promising tool to provide more information on lemming consumption rates by ermines.

Table 1. Summer lemming density, density of lemming winter nests and various indices of ermine abundance, activity and predation rate on lemming during the summer and winter from 2005 to 2012.

	2004	2005	2006	2007	2008	2009	2010	2011	2012
Total number of individual lemmings captured in summer	172	55	44	35	188	11	222	312	15
Brown lemming summer density (ind/km^2)	470 ± 96	26 ± 4	26 ± 5	21 ± 7	345 ± 79	18 [e]	358 ± 46	800 ± 90	10 ± 3
Collared lemming summer density (ind/km^2)	46 ± 4	46 ± 7	12 ± 3	11 ± 2	36 ± 9	0	112 ± 11	0	5 [e]
Total number of winter nests found [a]	-	-	-	189 (36)	170 (0)	15 (82)	429 (54)	578 (4)	85 (29)
Brown lemming winter nest density (nests/km^2) [b]	491 [f]	65 [f]	24 [f]	20 ± 73	1000 ± 360	10 [e]	1076 ± 202	1072 ± 165	75 ± 22
Collared lemming winter nest density (nests/km^2) [b]	57 [f]	81 [f]	32 [f]	341 ± 100	108 ± 31	5 [e]	109 ± 31	168 ± 71	57 ± 27
Number of nests predated by ermines [a, c]	-	-	-	6 (3)	10 (0)	1 (9)	5 (0)	6 (0)	4 (3)
Density of lemming winter nests predated by ermine (nests/km^2)	-	-	-	8.4	19.6	1.6	10.1	10.2	6.4
Proportion of all lemming winter nests predated	-	-	-	0.02	0.02	0.10	0.01	0.01	0.05
Proportion of brown lemming winter nests predated [d]	-	-	-	0.02 (0.01)	0.06	0.00 (0.00)	0.02 (0.02)	0.01 (0.01)	0.00 (0.02)
Proportion of collared lemming winter nests predated [d]	-	-	-	0.06 (0.08)	0.17	0.20 (0.29)	0.04 (0.03)	0.05 (0.05)	0.13 (0.13)
Proportion of shelter boxes used by ermines in winter (N = 40)	-	-	-	-	-	-	0.03	0.10	0.38
Proportion of boxes used by ermines in summer (N = 40)	-	-	-	-	-	-	0	0.03	0.20

Minimum number of adult ermines sighted in summer	-	-	-	-	-	1	2	5	5
Number of known ermine families in the study area	-	-	-	-	-	0	1	2	0
Individual ermine litter size	-	-	-	-	-	-	8	10, 5	-
Ermine home range (km^2; N = 1 each year)	-	-	-	-	-	-	6.51	1.64	-

[a] Number of opportunistic nests sampled in parentheses.

[b] Because winter nests are sampled at snow-melt, densities refer to the previous winter.

[c] This excludes nests considered to have been used by the same individual (see methods). N excluded: 2007: 3, 2008: 6, 2009: 0, 2010: 1, 2011: 2 and 2012: 0.

[d] Proportion of predated nests including those found opportunistically in parentheses.

[e] Density estimated by using the minimum number know to be alive divided by the effective trapping area.

[f] Winter nest density obtained with the equation provided by Krebs et al. (2012). See text for details.

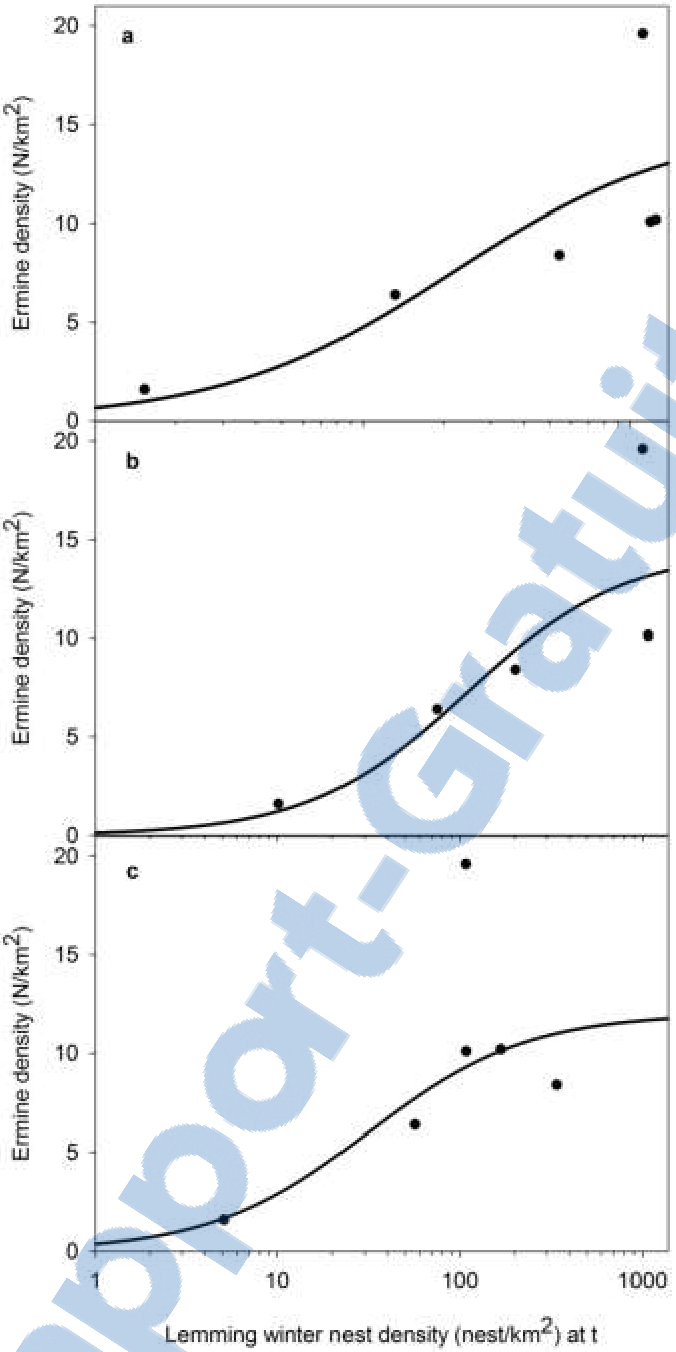

Figure 1. Index of winter ermine abundance (density of lemming winter nests predated and used by ermine) in relation to the density of winter nests of both lemming species (a), brown lemming (b) and collared lemming (c) at time *t*. The lines represent type II asymptotic curves fitted with the data for both species combined and brown lemming and type III sigmoid curve for collared lemming.

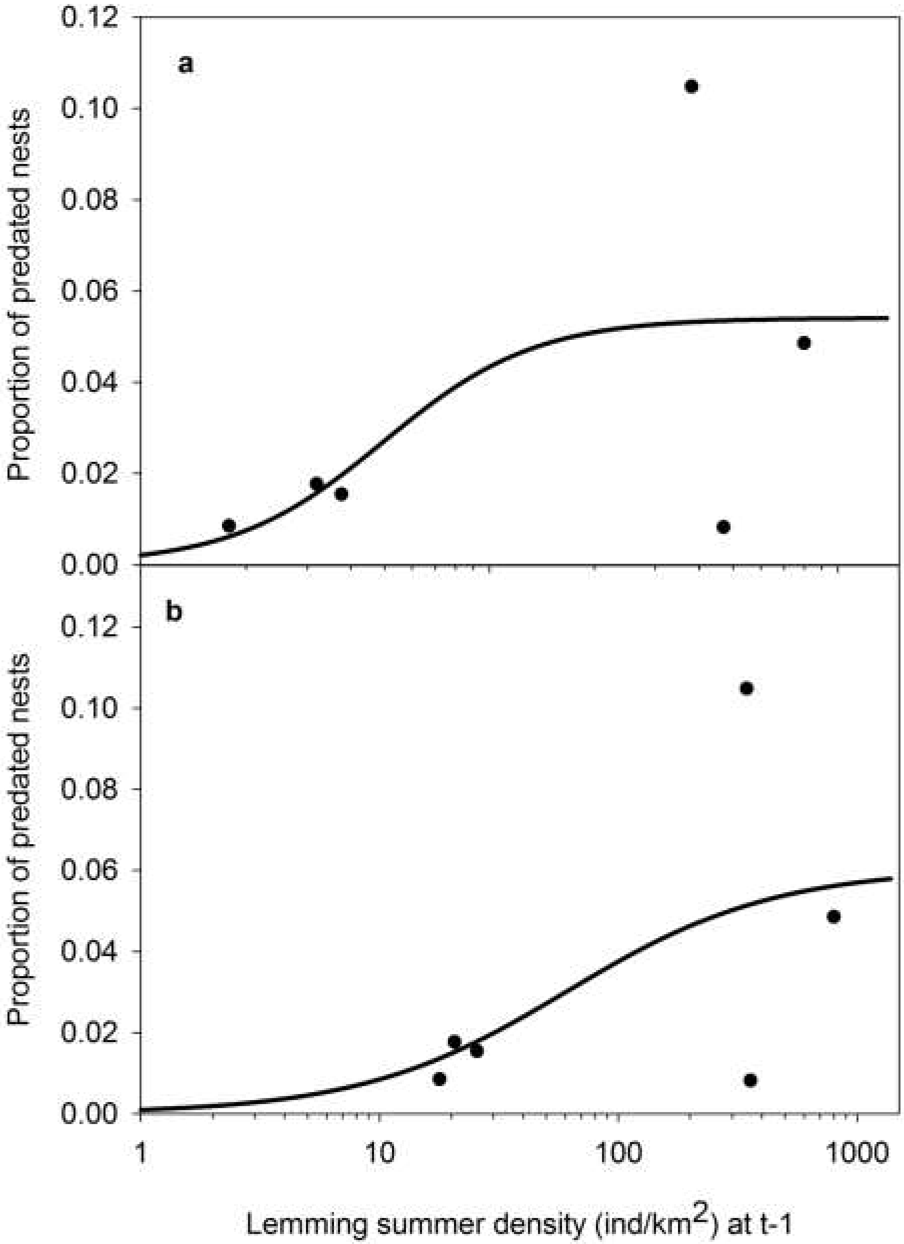

Figure 2. Proportion of predated winter nests by ermine from 2007-2012 in relation with both lemming species (a) and brown lemming (b) summer density at time *t*-1. The lines represent type II asymptotic curves fitted with the data.

Conclusion

Le lemming peut être considéré comme la clé de voute de l'écosystème arctique terrestre (Gauthier et al. 2011, Legagneux et al. 2012). À lui seul, le lemming permet à une vaste guilde de prédateurs de se maintenir (Körpimaki et al. 2005, Gilg et al. 2006, Schmidt et al. 2012) et ce dans un environnement où la production primaire est faible (Gauthier et al. 2004). De plus, ses fluctuations d'abondance vont même influencer la dynamique des autres herbivores et insectivores via les interactions avec les prédateurs (Bêty et al. 2002, McKinnon et al. 2012). Ce n'est donc pas surprenant que les populations de lemming sont étudiées depuis près de cent ans (Elton 1924). Cependant, aucun consensus permettant d'expliquer les causes de la cyclicité de ces populations n'a encore été atteint (Krebs 2011). Jusqu'à très récemment, la majorité des études sur le lemming portaient sur l'écologie estivale en raison des difficultés inhérentes à l'étude des petits mammifères pendant la période hivernale (Aars et Ims 2002), qui représente néanmoins la majorité de l'année dans l'Arctique. Un énorme vide au niveau des connaissances caractérise donc la période hivernale qui apparait critique dans le maintien des cycles de populations de petits mammifères de la toundra. À travers cette thèse, j'ai abordé différents processus liés à la dynamique de ces populations. J'ai examiné des facteurs qui peuvent moduler le cycle des lemmings en m'intéressant principalement à l'écologie hivernale, mais j'ai aussi examiné certains facteurs qui peuvent aussi le contrôler. Dans le souci d'approfondir nos connaissances sur des sujets peu étudiés et où les connaissances sont plutôt anecdotiques, j'ai examiné dans un premier temps, les effets de la qualité de la neige sur les populations de lemmings. Ensuite j'ai examiné à partir du broutage hivernal si les lemmings pourraient être contrôlés par leur nourriture. Finalement, j'ai examiné les patrons de prédation de l'hermine (*Mustela erminea*), considérée par plusieurs comme étant un prédateur essentiel pour générer la dynamique cyclique des lemmings (Korpimäki et al. 1991, Hanski et al. 1993, Heikkilä et al. 1994, Korpimäki and Krebs 1996, Hanski et al. 2001, Gilg et al. 2003).

Effet de la neige sur la démographie des lemmings

L'Arctique est reconnu pour être un des milieux les plus arides de la planète, spécialement en hiver. Plusieurs sites sont pratiquement inaccessibles au courant de la période hivernale et effectuer des relevés fauniques sur le terrain est encore plus ardu. La difficulté d'étudier les micromammifères de l'Arctique s'en trouve décuplée par rapport aux plus gros organismes, puisqu'ils sont actifs sous la neige, présente sur une période d'environ 8 mois, et sont donc pratiquement invisibles et inaccessibles. Puisque les micromammifères se reproduisent sous la neige (MacLean et al. 1974, Sittler 1995, Duchesne et al. 2011a) et que les plus hautes densités peuvent être atteintes pendant l'hiver (Henttonen et Kaikusalo 1993, Ims et Fuglei 2005, Getz et al. 2006a, Kausrud et al. 2008, Ims et al. 2011), un couvert de neige de qualité a été évoqué comme étant un facteur essentiel pour permettre un pic d'abondance de lemming (MacLean et al. 1974, Aars et Ims 2002, Korslund et Steen 2006, Ims et al. 2008, Kausrud et al. 2008), mais jusqu'à ce jour seules des évidences corrélatives supportaient cette hypothèse (Kausrud et al. 2008, Gilg et al. 2009).

Par l'entremise d'une expérience réalisée à l'aide de clôtures à neige déployées sur trois sites différents dans l'Arctique canadien (île Bylot au Nunavut et île Herschel et Komakuk Beach au Yukon; chapitre 1), nous avons été les premiers à vérifier de façon expérimentale l'hypothèse que l'épaisseur de neige influence les paramètres démographiques de trois espèces de petits mammifères de l'Arctique, soit le lemming brun (*Lemmus trimucronatus*), le lemming variable (*Dicrostonyx groenlandicus*) et le campagnol de la toundra (*Microtus Oeconomus*). Les résultats nous ont montré qu'une forte épaisseur de neige entraînait des températures sous-nivales plus clémentes et favorisait une forte réponse numérique agrégative des lemmings vers les sites de haut enneigement. Contrairement à ce qu'on prédisait, toutefois, un enneigement supérieur n'a pas eu d'influence sur la reproduction, peut-être parce que les gains énergétiques associés à la hausse de température sont insuffisants ou parce que l'accumulation de neige ne s'est pas fait suffisamment tôt durant l'hiver.

J'ai également testé l'effet de la neige (par l'entremise de divers paramètres physiques et temporels) sur les amplitudes et la fréquence du cycle du lemming brun (chapitre 2). En utilisant des séries temporelles de 17 et 18 ans dans deux milieux différents, j'ai pu tester les effets qu'a le couvert nival sur le cycle. J'ai pu ainsi démontrer, une fois la cyclicité enlevée de mes séries temporelles, que l'épaisseur et la densité de la neige font varier les amplitudes et peuvent même retarder ou accélérer les pics d'abondance. L'épaisseur de neige va augmenter les températures sous-nivales et donc réduire le stress physiologique que vont subir les lemmings pendant l'hiver. Ceci a probablement un effet positif sur la survie des adultes, mais surtout sur celle des jeunes. Bien qu'expérimentalement nous n'avons pas détecté d'effet de l'augmentation de l'épaisseur de neige sur l'intensité de la reproduction (chapitre 1), nous n'avons pas pu mesurer le nombre et la taille des portées, ainsi que la survie des juvéniles aux nids. Également, plus le couvert de neige est épais et plus les couches près de la surface sont vieilles et compactées, moins les chances de compaction des couches de neige près du sol sont grandes, puisque les cristaux de neige comprimés augmentent la résistance du couvert de neige. Les forces appliquées sur le dessus du couvert nival devront alors être de plus en plus grandes pour affecter les couches près du sol (Pomeroy et Brun 2001). Pour circuler sous la neige sans restriction, les lemmings sont dépendants de la densité des couches de neige près du sol. Se déplacer à travers un couvert de neige très dense demanderait nécessairement une plus grande dépense d'énergie et pourrait restreindre ou rendre plus coûteux l'accès aux ressources alimentaires. De plus, contrairement à ce qui se passe au Groenland (Gilg et al. 2009), les variations temporelles dans la persistance de la neige n'ont pas eu d'effet sur le cycle du lemming brun à l'île Bylot et ce malgré la tendance à atteindre l'épaisseur de neige critique pour les lemmings (i.e. 20-30 cm; Pruitt 1970) plus tôt au courant de l'hiver.

Bien que nous ayant procuré des informations intéressantes, l'expérience de la clôture à neige (chapitre 1) nous a aussi montré certaines limites associées aux méthodes utilisées. En plus de nous donner un indice de densité hivernale, les nids d'hiver nous procurent un indice de reproduction par les lemmings ainsi que de prédation par l'hermine. Toutefois, ils ne nous renseignent pas sur la taille de la portée ou leur nombre. Les nids d'hiver procurent une certaine isolation face aux températures extrêmes de l'hiver (Millar 2001), mais nous ne savons pas à quel point ceci est suffisant pour permettre une bonne survie de nouveaux nés (Casey 1981, Chappell 1990) avant la fin de l'hiver. Cependant, aucune observation ne peut valider ceci pour l'instant. Un autre point critique est relié à la survie des juvéniles et demeure méconnu. Est-ce que les jeunes nés sous un couvert de neige plus épais et donc exposés à des températures sous-nivales plus clémentes ont une meilleure probabilité de survie? En utilisant un enclos similaire à celui de Korslund et Steen (2006) et en installant plusieurs boîtes donnant accès à l'espace sous-nival (Chapitre 3), il serait peut-être possible de déterminer le nombre et les tailles de portées hivernales et surtout à quelle période de l'hiver la reproduction a lieu (début, fin ou tout l'hiver ?). En utilisant deux enclos, un avec fort et l'autre avec faible enneigement il serait également possible de comparer les taux de survie des juvéniles. Évidemment, pour mettre en place un tel dispositif, il faut avoir accès au site tout l'hiver, chose possible en Scandinavie, mais difficile à nos sites d'étude dans l'Arctique Canadien. Réaliser une telle expérience serait essentiel pour répondre à de nombreuses suppositions sur lesquelles reposent nos indices obtenus à partir des nids d'hiver.

Les connaissances sur l'hermine sont très limitées dans la toundra et encore plus lors de la période hivernale. Puisque nos résultats sur la prédation étaient incohérents, l'expérience de la clôture à neige nous a révélé peu de choses sur l'effet de la neige sur la prédation par l'hermine. L'échelle spatiale, bien que suffisante pour des rongeurs, n'a peut-être pas été assez grande pour tester nos prédictions sur des mustélidés (chapitre 1). Malheureusement, aucune information n'est disponible sur la taille des domaines vitaux, ni sur les capacités de mouvements des mustélidés en hiver. Pour répondre à ces questions, il faudra attendre que la technologie des colliers émetteurs satellite ou GPS soit assez développée, afin de débuter des suivis semblables aux renards arctiques (*Vulpes lagopus*) (voir Tarroux 2011 pour plus de détails). Également, l'hermine préfère chasser dans les dépressions bordant les cours d'eau, là où l'accumulation de neige est généralement plus élevée. Toutefois, les résultats de mon chapitre 5 suggèrent que les caractéristiques topographiques de l'habitat seraient probablement plus importantes que l'épaisseur de neige en soit ou la densité de lemming lors de la sélection de sites de chasse pour l'hermine. Il est donc possible qu'en ayant installé nos grilles expérimentales d'enneigement dans l'habitat mésique et non dans des habitats naturellement propices à de fortes accumulations de neige, l'hermine n'ait tout simplement pas visité celles-ci.

Obtenir de l'information directe sur ce qui se passe sous la neige peut être assez difficile. Pour mesurer les patrons de déplacement et l'utilisation de l'habitat des lemmings pendant la période de fonte de la neige, nous avons tenté de capturer des lemmings sous la neige. Bien que l'expérience fût un échec, elle nous a révélé que les lemmings quittaient fort probablement les zones de fort enneigement avant le début de la fonte pour des zones de faibles enneigements ou des zones où le sol est déjà exposé (chapitre 3). Ceci nous a permis de comprendre que pour capturer des lemmings sous la neige avec succès, il faut probablement activer les pièges avant que les températures sous-nivales, normalement plus chaudes aux sites de haut enneigement durant l'hiver, deviennent plus froides que les zones de faible enneigement au printemps et maintenir un régime de capture constant durant l'hiver.

Interaction plantes-herbivores

Le débat sur quelle hypothèse (contrôle par le bas ou par le haut) permet d'expliquer le cycle des lemmings fait toujours rage (Oksanen et al. 2008, 2009, Gauthier et al. 2009) et les résultats favorisant l'une ou l'autre hypothèse divergent selon les régions de l'Arctique. Cependant, chaque site d'études a ses propres particularités, notamment en ce qui concerne les communautés animales. À l'Île Bylot, par exemple, aucun grand herbivore n'est présent et malgré la présence d'une importante colonie de la grande oie des neiges (*Chen caerulescens atlantica*), les lemmings demeurent parmi les herbivores les plus importants puisqu'ils sont les seuls à rester pendant l'hiver (Gauthier et al. 2011). J'ai testé un prérequis important de l'hypothèse du contrôle par le bas, soit qu'un impact significatif du broutement des lemmings soit détectable sur leur nourriture pendant l'hiver, la période durant laquelle les ressources alimentaires sont les moins abondantes, et que cet impact se répercute sur la croissance subséquente des plantes pendant l'été (chapitre 4). Au cours des années où l'expérience a eu lieu, le lemming brun a atteint des densités très élevées sur le site durant deux années consécutives. Le lemming variable a aussi atteint de fortes densités, mais seulement sur une année. Les exclos à lemmings que j'ai déployés ont révélé un impact du broutement hivernal relativement faible et seulement sur quelques familles de plantes et de mousses mangées par les lemmings. De plus, cet impact n'a pas été maintenu et la végétation a récupéré pour atteindre des niveaux semblables aux années précédentes au cours de la saison de croissance. Les résultats issus de cette étude nous révèlent qu'il est peu probable que la dynamique des populations de lemming de l'île Bylot soit contrôlée par leurs ressources alimentaires.

Interaction prédateurs-proies

La neige est un paramètre qui peut potentiellement affecter l'efficacité des prédateurs de lemmings pendant l'hiver comme l'hermine et le renard arctique (chapitre 5). Toutefois, les résultats de mon chapitre 5 ont montré que la neige n'offrait qu'une protection très limitée aux lemmings face à ces deux prédateurs. Le renard, bien que limité par l'épaisseur de neige lorsqu'il tente de prédater des lemmings en sautant, peut changer de technique et aller chercher les lemmings directement dans leur nids d'hiver en creusant, indépendamment de l'épaisseur de celle-ci. De son côté, l'hermine ne semble nullement affectée par l'épaisseur de neige dans son activité de prédation, et pas plus par la densité de proie, ce qui appuie l'idée que l'hermine pourrait se baser davantage sur des caractéristiques topographiques pour sélectionner les endroits où elle chasse en hiver.

Finalement, j'ai tenté d'évaluer au chapitre 6 la réponse numérique de l'hermine face aux fluctuations d'abondance des lemmings, ainsi que les taux de consommation à haute densité de proies. L'index de densité d'hermine pendant l'hiver nous indique une réponse instantanée de l'hermine face aux fluctuations d'abondance des lemmings. Cependant, j'ai soulevé plusieurs problèmes relatifs à l'utilisation des nids d'hiver prédatés comme indice d'abondance ou d'intensité de prédation par l'hermine. En effet, il est difficile d'estimer la densité d'hermine à partir des nids prédatés car on ne sait pas combien de nids peut utiliser une seule hermine, ni la distance des déplacements effectués par une hermine l'hiver. Également, il est pratiquement impossible de déterminer le nombre réel de lemmings tués à partir d'un nid. Une préférence possible pour occuper les nids de variables pose aussi un problème. En effet, est-ce que l'hermine va cibler les nids de lemmings variables pour les occuper ou a-t-elle une véritable préférence pour consommer cette espèce? Bien qu'on ne puisse pas répondre à cette question à partir des nids d'hiver, les observations estivales semblent nous indiquer qu'il n'y ait pas de préférence pour une des deux espèces de lemmings.

Contrairement à l'index basé sur la densité, l'utilisation de la proportion de nids prédatés nous suggère une réponse décalée par l'hermine face aux fluctuations d'abondance de lemmings. De façon générale, une plus grande proportion de nids prédatés témoigne d'une plus grande pression sur la population de lemming. Même si en nombre absolu un plus petit nombre de lemmings est tué lors de la phase du creux, l'hermine va traquer les proies dont sa survie dépend, et il est probable qu'une plus grande proportion de la population de lemming soit consommée de façon journalière à ce moment. Les autres méthodes utilisées, notamment les boîtes de trappage, nous suggèrent aussi une réponse décalée de l'hermine, mais les résultats proviennent d'un nombre trop restreint d'années pour vraiment être concluans. Également, la réponse reproductive instantanée et le nombre d'adultes observés durant l'été nous permettent de croire que le pic de prédation a peut-être lieu à l'automne ou l'hiver suivant le pic d'abondance de lemming.

Les observations faites sur deux familles d'hermine nous révèlent des taux de consommation extrêmement élevés. Aux plus fortes densités de lemmings, une femelle hermine nourrissant ses jeunes tuerait plus de lemming qu'un couple reproducteur d'harfang des neiges. Parce que l'hermine est un animal furtif et difficile à observer, les taux de prédation par l'hermine ont par le passé été calculés à partir des besoins métaboliques (Gilg et al. 2006, Wilson 1999), mais ceux-ci semblent avoir été grandement sous-estimés puisqu'ils ne prennent pas en compte les proies tuées en surplus (King et Powell 2007).

Malgré un faible jeu de données, la réponse totale que nous avons estimée pour l'hermine montre que ce prédateur pourrait jouer un rôle critique dans la dynamique de population des lemmings en prélevant de façon journalière une forte proportion de leur population. Toutefois, mes données montrent seulement des évidences limitées d'une réponse décalée. Tant qu'une réponse décalée claire de la part du prédateur ne sera pas démontrée, on ne peut pas exclure que d'autres mécanismes comme les effets maternels (Boonstra et Hochachka 1997, Inchausti et Ginzburg 2009) ou les parasites (Cattadori et al. 2005, Holmstad et al. 2005) puissent jouer un rôle dans le cycle des lemmings. D'ailleurs, bien que ceci reste anecdotique, plusieurs lemmings trouvés morts dans nos pièges à l'été 2011, lors d'un très gros pic d'abondance, étaient fortement parasités, ce qui permet de croire à la possibilité que d'autres mécanismes pourraient agir en synergie avec la prédation pour contrôler les populations de lemmings. Un suivi pour estimer le taux de parasitisme dans la population en fonction des densités ne serait pas nécessairement difficile à réaliser, surtout que le trappage mortel, permettant d'obtenir un indice d'abondance annuel, est encore utilisé à Bylot.

Message final et apport de la thèse

En conclusion, cette thèse a contribué à approfondir nos connaissances sur l'écologie hivernale du lemming et sur celle de l'hermine, jugée comme étant un élément clé dans le cycle des lemmings (Hanski et al. 2001, Gilg et al. 2006). Ma thèse a aussi permis de montrer à quel point nos connaissances sont limitées. En intégrant différentes approches (expérimentale ou modélisation) j'ai pu démontrer l'importance qu'a la neige dans les fluctuations du cycle d'abondance du lemming. Cependant, beaucoup reste encore à faire et à comprendre sur comment les mécanismes affectant les lemmings sous la neige fonctionnent, notamment en ce qui concerne la reproduction hivernale (phénologie, nombre et taille des portées, survie juvénile). Puisque j'ai évalué le couvert de neige pour le site d'étude à partir d'un seul point, une prochaine étape serait de mesurer les conditions d'enneigement à des échelles plus fines tout au long de l'hiver dans les différents habitats utilisés par les lemmings afin de valider mes résultats.

De plus, j'ai ajouté mon grain de sel dans le débat presque centenaire opposant les hypothèses de contrôle par le bas ou par le haut. En me concentrant principalement sur la période hivernale, j'ai testé les effets des ressources alimentaires et de la prédation sur les populations de lemming. Il apparaît peu probable qu'à l'Île Bylot les processus du contrôle par le bas soient à l'origine du cycle des lemmings. Parallèlement, les résultats nous montrent que la pression combinée des prédateurs mammaliens et aviaires pourrait jouer un rôle majeur dans le cycle des lemmings. Par contre, nous avons seulement trouvé de faibles évidences d'une réponse décalée de l'hermine face aux fluctuations d'abondance des lemmings et plusieurs suppositions sur nos indices de prédation restent à être confirmées avant de pouvoir valider ou invalider que l'hermine joue un rôle clé dans la dynamique de population des lemmings. Augmenter le nombre d'observations comportementales et de suivis télémétriques sur l'hermine, telles que réalisées au chapitre 6, mais pendant toutes les phases du cycle des lemmings apparaît essentiel pour évaluer son rôle. Ceci est réalisable, mais demandera toutefois des efforts considérables sur le terrain.

En étudiant les effets que le couvert de neige a sur les populations de lemming, j'ai constaté à quel point il est difficile de mener des expériences sur l'écologie hivernale. Dans un contexte où les changements climatiques s'accélèrent, et où les événements climatiques extrêmes sont de plus en plus fréquents (Cowie 2007), les difficultés inhérentes à de tels projets croîtront. L'étude de l'écologie hivernale des micromammifères de l'Arctique et de l'hermine recèle de nombreuses avenues prometteuses, mais à la fois risquées. Néanmoins, pour réellement comprendre ce qui se passe sous la neige (et même pendant l'été dans le cas de l'hermine), chaque pièce d'information, aussi minime soit-elle, fait progresser nos connaissances et ouvre de nouvelles avenues. La preuve est que les chapitres 1, 3 et 6 ont contribué à cibler certaines faiblesses de nos approches et nous ont amené à nous questionner sur des suppositions sur lesquelles reposent celles-ci.Par contre nous avons aussi développé de façon inattendue de nouvelles méthodes pour répondre à nos questions, comme l'utilisation de boîte, initialement prévue pour trapper les lemmings sous la neige, pour mesurer les réponses fonctionnelle et numérique de l'hermine.

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Annexe 1

Supplementary material for Chapter 1

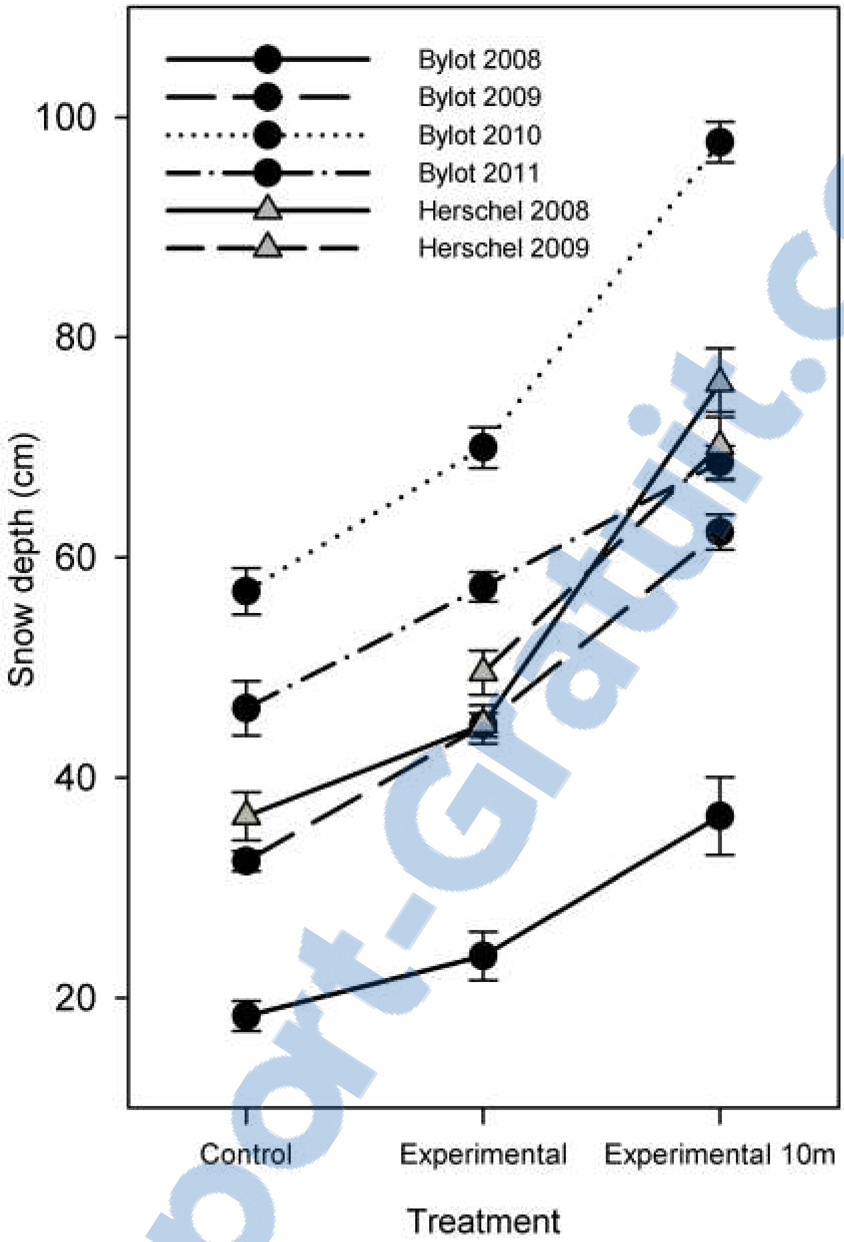

Figure S1. Mean snow depth in control grids, experimental grids (entire treatment) and areas <10-m on either side of snow fences in experimental grids ("Experimental 10 m") according to the field site and years. Error bars represent SE.

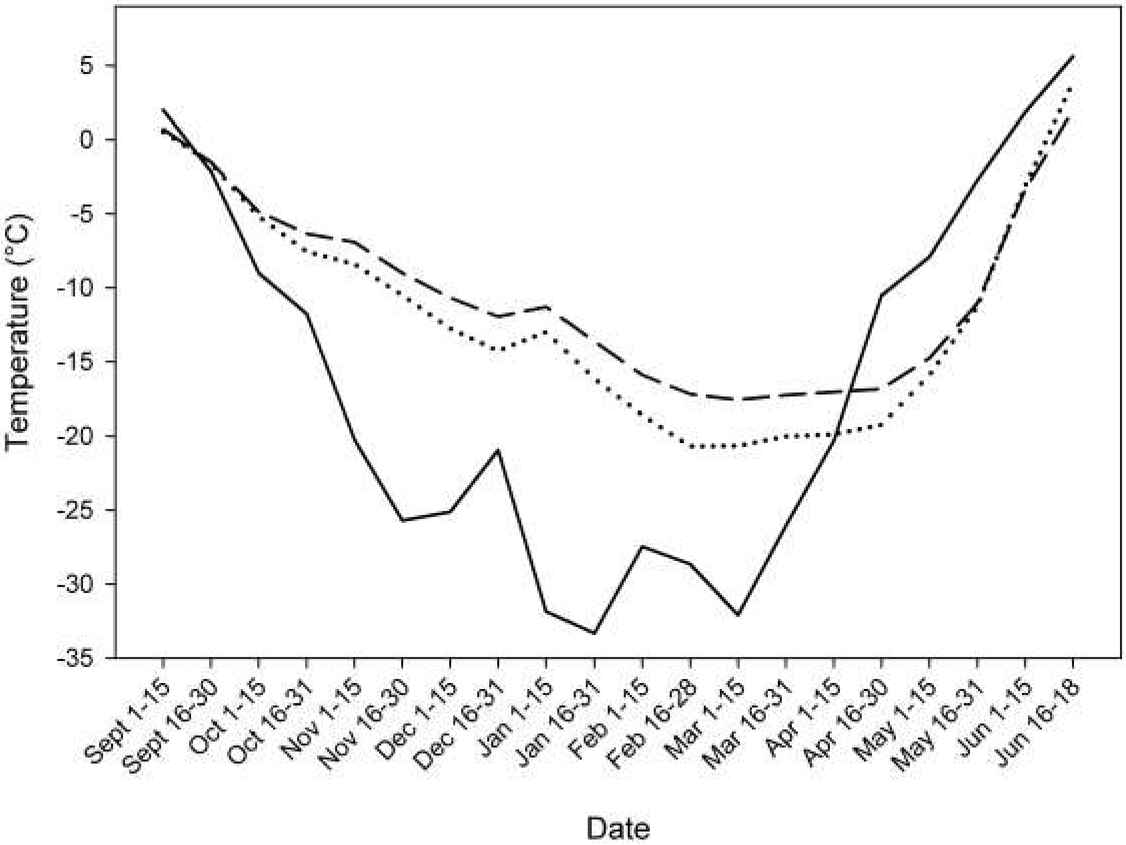

Figure S2. Mean daily temperatures (°C) for Bylot Island over winter 2010-11. Data show temperature of ambient air (solid line; from a weather station at the site), at ground-level on the control grid (dotted lines; *n* = 10 I-Buttons® sensors), and at ground level in the snow-manipulated grid < 10 m from fence (dashed lines; *n* = 10 sensors). See also Reid et al. (2012).

Annexe 2

Modélisation du couvert nival à l’aide du modèle SNOWPACK

Modélisation du couvert nival à l'aide du modèle SNOWPACK

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Introduction

Les stations météorologiques installées sur l'Île Bylot fournissent une panoplie de données climatiques, dont plusieurs sont en lien avec le couvert nival comme l'épaisseur de neige au sol et les températures sous-nivales. Par contre, elles ne peuvent pas nous procurer de l'information sur la densité de la neige, un paramètre susceptible d'influencer les lemmings. En effet, une neige plus dense sera difficile à creuser ou fournira une isolation thermique réduite (Pomeroy et Brun 2001, Sanecki et al. 2006). Cette donnée a pu être mesurée directement sur le terrain à l'Île Bylot à la fin des hivers 2010 et 2011 mais elle n'était pas disponible pour les hivers 1993-2009. Il est cependant possible d'utiliser des outils de modélisation afin d'obtenir cette information. Nous avons utilisé le modèle SNOWPACK (Bartelt and Lehning 2002, Lehning et al. 2002a, 2002b) afin d'estimer ce paramètre important.

Le logiciel SNOWPACK

Le logiciel SNOWPACK permet de modéliser l'évolution temporelle de l'accumulation des couches de neige durant l'hiver et de leurs propriétés physiques à partir de données climatiques standards. Les données requises sont : la température de l'air, l'humidité relative, la vitesse du vent, les radiations solaires (soit incidentes ou réfléchies), la température à la surface de la neige, la température sous-nivale et les précipitations de neige ou l'épaisseur de neige. Les données suivantes sont optionnelles : la direction du vent, les radiations infrarouges incidentes et les températures à différentes hauteurs à l'intérieur du couvert de neige (jusqu'à cinq mesures différentes peuvent être insérées dans le modèle). Pour opérer le modèle, il est préférable d'utiliser le maximum d'information disponible. Afin de caractériser le couvert nival le plus fidèlement possible, il est recommandé d'utiliser les données climatiques disponibles sur une base horaire pour toute la période hivernale et au minimum une donnée par jour. Dans notre cas, les données étaient toutes disponibles sur une base horaire sauf pour l'hiver 1993-1994, pour l'épaisseur de neige avant 2001 et de façon sporadique pour l'épaisseur de neige et l'humidité relative à certaines périodes où elles étaient disponibles sur une base journalière. Dans le cas de l'épaisseur de neige et l'humidité relative, la même valeur a été utilisée 24 fois, soit chaque heure de la même journée.

Provenance des données météos

Au site d'étude de l'Ile Bylot, il existe 3 stations météo automatisées toutes localisées dans un rayon de moins de 1 km. La station BYLOT-S2 est située à ~20 m ASL et enregistre en continue des données depuis le printemps 1994. La station BYLOT-S3 est située à ~400 m ASL et enregistre en continue des données depuis juillet 2001. Finalement, la station BYLOT-SILA est situées à ~30 m ASL et enregistre en continue des données depuis juillet 2004. Pour certaines périodes, les données provenant des stations météorologiques située à l'aéroport de Pond Inlet à 85 km du site d'étude, ~50 m ASL ou de celui de Nanisivik à ~160 km du site d'étude, ~640 m ASL, ont aussi été utilisées.

Température de l'air et température à la surface de la neige

Puisque la température mesurée directement à la surface de la neige n'était pas disponible à partir de nos stations météos, nous avons dû utiliser les données de température de l'air pour les deux variables. Ces données proviennent de la station BYLOT-S2, sauf pour certaines périodes où il n'y a pas eu d'enregistrement.

- Hiver 1993-1994. Pour la période du 28 septembre 1993 au 17 mars 1994, les données ont été estimées à partir de celles de la station météo de Pond Inlet à l'aide de la relation établie entre les températures journalières disponible à Bylot et Pond Inlet pour la période du 18 mars 1994 au 31 mai 1997 (Tableau 1).
- Hiver 1997-1998. Pour la période du 27 février 1998 au 31 mai 1998 les données ont été estimées à partir de celles à 2 cm dans le sol à l'aide de la relation entre les températures horaires de l'air et à 2 cm dans le sol à la station BYLOT-S2 pour les années 1994 à 2009 (Tableau 1).
- Hiver 2009-2010. Pour la période du 26 septembre 2009 au 16 juin 2010 les données ont été estimées à partir de celles de la station BYLOT-SILA à l'aide de la relation entre les températures horaires de l'air des stations BYLOT-S2 et BYLOT-SILA pour les années 2004 à 2009 (Tableau 1).

Tableau 1 : Résultats des modèles linéaires reliant la température de l'air à 2 m de la station météo BYLOT-S2 ($T_{air\ S2}$) aux températures enregistrées à d'autres stations ou par d'autres senseurs. La pente (β), l'ordonnée à l'origine, le R^2 ajusté et le test F associé sont présentés pour chaque relation.

Relation	Ordonnée (±SE)	β (±SE)	R^2	Test
$\log(T_{air\ S2}+50)$ vs $\log(T_{air\ Pond}+50)$	0.11 (0.08)	0.96 (0.02)	0.69	$F_{1,787} = 1730; P<0.001$
$\log(T_{air\ S2}+55)$ vs $\log(T_{sol\ 2cm\ S2}+45)$	-0.08 (0.01)	1.06 (0.00)	0.69	$F_{1,128957} = 2.93e+5; P<0.001$
$T_{air\ S2}$ vs $T_{air\ SILA}$	-0.15 (0.01)	1.08 (0.00)	0.99	$F_{1,32493} = 3.10e+6; P<0.001$

Humidité relative

Les données d'humidité relative proviennent de la station BYLOT-S2, sauf pour certaines périodes où il n'y a pas eu d'enregistrement.

- Hivers 1993 à 1998 et 2007-2008. Pour les périodes du 28 septembre 1993 au 17 mars 1994, 3 janvier au 1er juin 1995, 18 septembre 1995 au 22 juin 1996, 10 septembre 1996 au 31 mai 1997, 1er janvier au 31 mai 1998, et 29 août 2007 au 6 juin 2008, les données ont été estimées à partir de la station météo de Pond Inlet à l'aide de la relation établie entre l'humidité relative journalière à Bylot et Pond Inlet pour les années 1998 à 2009 (Tableau 2).
- Hiver 2009-2010. Pour la période du 26 septembre 2009 au 16 juin 2010, les données ont été estimées à partir de la station BYLOT-SILA à l'aide de la relation entre l'humidité relative horaire de la BYLOT-S2 et la température de l'air et la pression barométrique de la station BYLOT-SILA pour la période du 27 juillet 2008 au 15 juin 2009 (Perry and Green 2007; Tableau 2).

Tableau 2 : Résultats des modèles linéaires reliant l'humidité relative de l'air à 2 m de la station météo BYLOT-S2 ($H_{rel\ S2}$) à l'humidité relative de l'air à Pond Inlet ou à la température de l'air et la pression barométrique de la station BYLOT-SILA ($P_{bar\ SILA}$). La pente (β), l'ordonnée à l'origine, le R^2 ajusté et le test F associé sont présentés.

Relation	Ordonnée (±SE)	β (±SE)	R^2	Test
$\log(H_{rel\ S2}+1)$ vs $\log(H_{rel\ Pond}+1)$	2.08 (0.01)	0.52 (0.00)	0.31	$F_{1,83355} = 3.759e+4$; $P<0.001$
$\log(H_{rel\ S2})$ vs $\log(T_{air\ SILA}+50) + \log(P_{bar\ SILA})$	-14.45 (2.30)	$\beta_{Tair} = 0.11$ (0.01) $\beta_{Pbar} = 3.36$ (0.57)	0.31	$F_{2,6304} = 1421$; $P<0.001$

Vitesse du vent

Les données de vitesse du vent proviennent de la station BYLOT-S2, sauf pour certaines périodes où il n'y a pas eu d'enregistrement.

- Hivers 1993-1994, 1994-1995, 1997-1998 et 2001-2002. La relation établie entre la vitesse de vent journalière disponible à Bylot et Pond Inlet était trop faible pour être utilisée ($R^2 = 0.03$). Pour les périodes où ces données sont manquantes, nous avons donc utilisé les valeurs moyennes de vitesse de vent mesurées aux dates correspondantes durant les autres années. Ces données ont été utilisées pour les périodes du 28 septembre 1993 au 14 mars 1994, du 29 octobre au 1er novembre 1994, du 24 novembre au 27 décembre 1994, du 19 février au 13 mars 1995, du 18 au 21 mars 1995, du 10 au 12 novembre 1997, du 24 décembre 1997 au 7 janvier 1998, du 18 au 20 et 23 au 29 octobre 2001 et du 5 au 17 décembre 2001.

- Hiver 2001-2002. Pour tout cet hiver, les données ont été estimées à partir de celles de la station météo BYLOT-S3 à l'aide de la relation entre la vitesse de vent horaire des stations BYLOT-S2 et BYLOT-S3 pour les hivers 2002-2003, 2003-2004 et 2005-2006 (Tableau 3).
- Hiver 2009-2010. Pour tout cet hiver, les données ont été estimées à partir de celles de la station météo BYLOT-SILA à l'aide de la relation entre la vitesse de vent horaire des stations BYLOT-S2 et BYLOT-SILA pour les hivers 2004 à 2009 (Tableau 3).

Tableau 3 : Résultats des modèles linéaires reliant la vitesse de vent à 3m de la station météo BYLOT-S2 (Vvent S2) aux vitesses de vent enregistrées à d'autres stations. La pente (β), l'ordonnée à l'origine, le R^2 ajusté et le test F associé sont présentés.

Relation	Ordonnée (±SE)	β (±SE)	R^2	Test
$V_{vent\ S2}$ vs $V_{vent\ S3}$	0.41 (0.01)	0.55 (0.00)	0.63	$F_{1,26327}$ = 4.51e+4; P<0.001
$V_{vent\ S2}$ vs $V_{vent\ SILA}$	-0.30 (0.01)	0.85 (0.00)	0.85	$F_{1,32493}$ = 1.78e+5; P<0.001

Direction du vent

Les données de direction du vent proviennent de la station BYLOT-S2, sauf pour les cas suivants. Les modèles pour corriger les données manquantes de cette variable à partir d'autres stations étant très mauvais (R^2 = 0.01), cette valeur n'a pas été utilisée pour la période du 28 septembre 1993 au 14 mars 1994 et l'hiver 2009-2010.

Radiation solaire incidente (short wave)

Les données de radiation solaire incidente proviennent de la station BYLOT-S2, sauf pour certaines périodes où il n'y a pas eu d'enregistrement.

- Hiver 1993-1994. Pour la période du 28 septembre 1993 au 17 mars 1994, les données ont été estimées à partir des moyennes journalières calculées à la station BYLOT-S2 pour la période 1995-2004. Il est à noter que les variations saisonnières de radiations sont très similaires d'une année à l'autre. Par exemple, entre les années 1994-1995 et 1995-1996, il y a une relation très forte entre les valeurs de radiations horaires enregistrées aux mêmes dates les deux années (R^2 = 0.95; $F_{1,8583}$ = 1.75e+5; P<0.001)
- Hiver 2005-2006 à 2010-2011. Pour tous ces hivers, les données proviennent de la station BYLOT-SILA. Il est à noter que le senseur utilisé est le même que celui de BYLOT_S2, il a été déplacé au courant de l'été 2005.

Radiation solaire réfléchie et radiation infrarouge incidente (long wave)

Ces variables ne sont pas essentielles pour faire fonctionner le modèle. Elles n'étaient disponibles que pour les hivers 2005-2006 à 2007-2008 à partir station BYLOT-SILA et elles ont donc été utilisées que pour ces années. Les données de radiation infrarouge incidente (RI) ont également dû être corrigées pour la température du boîtier (TB) qui contenait le senseur par la formule suivante : 5.6704^{-8} x $(TB (K))^4$ + RI (Isabelle Laurion, comm. pers.).

Température sous-nivale à 2cm dans le sol

Les données de température sous-nivale proviennent de la station BYLOT-S2, sauf pour certaines périodes où il n'y a pas eu d'enregistrement.

- Hiver 1993-1994 et 2000-2001. Les données pour la période du 28 septembre 1993 au 17 mars 1994 et celles du 4 janvier 2001 au 25 mai 2001 ont été estimées à partir de celles de la température de l'air corrigée (voir plus haut) à l'aide de la relation entre la température horaire de l'air et celle à 2 cm de la station BYLOT-S2 (Tableau 4).
- Hivers 2001-2002 à 2003-2004. Pour les hivers 2000-2001, 2002-2003, 2003-2004 du 27 février au 1er mai 2002, les données ont été estimées à partir des températures de sol à 2 cm de la station BYLOT-S3 à l'aide de la relation entre les données horaires des stations BYLOT-S2 et BYLOT-S3 pour les hivers 2001-2002, 2004-2005 et 2005-2006 (Tableau 4).
- Hiver 2009-2010. Pour tout cet hiver, les données ont été estimées à partir des températures de sol à 5 cm de la station BYLOT-SILA à l'aide de la relation entre les données horaires à 2 cm de la station BYLOT-S2 et à 5 cm de la station BYLOT-SILA pour les hivers 2004 à 2009 (Tableau 4).

Tableau 4 : Résultats des modèles linéaires reliant la température du sol à 2cm de la station Bylot-S2 ($T_{air\ S2}$) aux températures de sol enregistrées à d'autres stations. La pente (β), l'ordonnée à l'origine, le R^2 ajusté et le test F associé sont présentés pour chaque relation.

Relation	Ordonnée (±SE)	β (±SE)	R^2	Test
$\log(T_{sol\ 2cm\ S2}+45)$ vs $\log(T_{air\ S2}+55)$	1.14 (0.00)	0.66 (0.00)	0.69	$F_{1,128957} = 2.93e+5$; $P<0.001$
$\log(T_{sol\ 2cm\ S2}+45)$ vs $\log(T_{sol\ 2cm\ S3}+45)$	1.03 (0.01)	0.73 (0.00)	0.90	$F_{1,21528} = 1.89e+5$; $P<0.001$
$\log(T_{sol\ 2cm\ S2}+35)$ vs $\log(T_{sol\ 5cm\ SILA}+35)$	-0.84 (0.01)	1.26 (0.00)	0.92	$F_{1,32493} = 3.95e+5$; $P<0.001$

Épaisseur de neige

À partir de 2001, les données d'épaisseur de neige proviennent de la station BYLOT-S2, sauf pour certaines périodes où il n'y a pas eu d'enregistrement. Les données provenant des années antérieures à 2001 proviennent de données corrigées issues de la station de Pond Inlet.

- Hiver 1993-1994 à 2000-2001. Pour cette période, seulement des données de précipitation de neige journalière à Pond Inlet sont disponibles. L'épaisseur au neige au sol à Bylot durant cette période a été estimé à l'aide d'une relation établie entre l'épaisseur de neige journalière mesurée à la station BYLOT-S2 et le cumul des précipitations enregistrées à Pond Inlet durant tout l'hiver pour la période 2001-2007 (Tableau 5).
- Avril et mai 1994. Pour ces deux mois, seulement les données de précipitation de Nanisivik sont disponibles. L'épaisseur au neige au sol à Bylot durant cette période a été estimée à l'aide d'une relation établie entre l'épaisseur de neige journalière mesurée à la station BYLOT-S2 et le cumul des précipitations enregistrées à Nanisivik durant tout l'hiver pour la période 2001-2007 (Tableau 5).
- Hiver 2009-2010. Pour tout cet hiver, SNOWPACK n'a pas pu être utilisé pour modéliser la densité de la neige car aucune données d'épaisseur de neige n'était disponible. En effet, la relation entre les données d'épaisseur de neige horaire provenant des stations BYLOT-S2 et BYLOT-SILA (la seule station météo où cette variable était disponible en 2009-2010) était trop mauvaise durant la période 2004 à 2009 (R2 = 0.03).
- 2011. Pour la période du 27 janvier au 18 juin 2011, les données d'épaisseur de neige ont été estimées à partir de la station de Pond Inlet à l'aide de la relation entre les données d'épaisseur de neige journalière provenant des stations BYLOT-S2 et de Pond Inlet pour l'hiver 2010-2011.

Tableau 5 : Résultats des modèles linéaires reliant l'épaisseur de neige au sol à la station Bylot-S2 ($D_{snow\ S2}$) au cumul des précipitations (R_{cum}) aux stations de Pond Inlet ou de Nanisivik ou de l'épaisseur de neige à la station de Pond Inlet. La pente (β), l'ordonnée à l'origine, le R^2 ajusté et le test F associé sont présentés.

Relation	Ordonnée (±SE)	β (±SE)	R^2	Test
$\log(D_{snow\ S2}+1)$ vs $\log(R_{cum\ Pond}+1)$	-0.19 (0.06)	0.59 (0.02)	0.67	$F_{1,464} = 959.2$; $P<0.001$
$\log(D_{snow\ S2}+1)$ vs $\log(R_{cum\ Nanisivik}+1)$	0.07 (0.01)	0.42 (0.04)	0.14	$F_{1,719} = 116.1$; $P<0.001$
$\log(D_{snow\ S2}+1)$ vs $\log(D_{snow\ Pond}+1)$	1.99 (0.07)	0.36 (0.03)	0.53	$F_{1,94} = 107$; $P<0.001$

Précipitations

Cette variable est optionnelle pour faire fonctionner le modèle et n'était jamais disponible aux stations de l'Île Bylot, elle n'a donc pas été utilisée.

Préparation des données

Une fois les données climatiques rassemblées, il faut les ordonner à l'intérieure d'un fichier qui prend la forme présentée au Tableau 7. Dans ce fichier, chaque colonne correspond à une variable climatique et chaque ligne représente une heure de la journée. Les variables sont :

1. La lettre M en première colonne
2. La date
3. L'heure
4. La date en jour Julien
5. Une colonne vide
6. La température de l'air (°C)
7. L'humidité relative (%)
8. Une colonne vide
9. La vitesse du vent (m/s)
10. La direction du vent (°; optionnelle)
11. Une colonne vide
12. Les radiations solaires incidentes (W/m^2)
13. Les radiations solaires réfléchies (W/m^2; optionnel)
14. Les radiations infrarouges réfléchies (W/m^2; optionnel)
15. Une colonne vide
16. La température à la surface de la neige (°C)
17. La température sous-nivale (°C)
18. Les précipitations (kg/m^2; optionnel)
19. L'épaisseur de neige (m)
20. Une colonne vide
21. Les températures des différentes épaisseurs de neige (°C; on peut ajouter quatre autres colonnes si l'on détient d'autres données, comme par exemple la température à 10 cm d'épaisseur).

Il est très important de respecter cet ordre et le format présenté en exemple au Tableau 6 (les décimales aussi), sinon le modèle ne fonctionnera pas. Lorsqu'on n'a pas de données pour une variable optionnelle, comme par exemple pour les précipitations de neige, il faut indiquer 0.0. Les séries pour les valeurs obligatoires doivent être complètes.

Profils de neige

Afin d'améliorer les estimations du modèle, il est possible d'intégrer des données mesurées directement à partir de profils de neige. Le tableau 7 montre un exemple de fichier utilisé pour les profils de neige. Pour chaque profil, on a une série de lignes, chacune contenant l'information suivante (chaque valeur sur une même ligne doit être séparée par une virgule).

- La première ligne commence par le code 0900, suivie du numéro de profil, la date à laquelle le profil a été fait, l'épaisseur de neige (m) et l'équivalent en eau de la neige (kg/m^2). Cette dernière donnée n'a pas été mesurée à l'Île Bylot en 2010 et 2011, mais elle peut être facilement obtenue en multipliant la densité de chaque couche de neige (kg/m^3) avec son épaisseur et en additionnant ensuite l'équivalent en eau de chaque couche.
- La deuxième ligne commence par le code 0901, suivie du nombre de couche de neige dénombré et puis l'épaisseur de neige de chaque couche à partir du sol en m.
- Chaque ligne suivante commence par un code différent numéroté de façon séquentielle (i.e. 0902, 0903, etc. voir tableau 7) et est toujours suivi du nombre de couche de neige. Les lignes 0902 et 0903 représentent le niveau d'humidité de la neige de chaque couche. Il est possible que le niveau d'humidité varie sur une même couche de neige. Il faut alors indiquer sur la ligne 0902, le niveau d'humidité le plus représentatif de la majorité de la couche de neige et sur la ligne 0903, le niveau représentant les zones qui diffèrent de la majorité. Si ces données ne sont pas disponibles, on doit remplacer la valeur manquante par « -1 ».
- La ligne 0904 représente le type de grains majoritaires selon le « Swiss Snow Type Classification » (SSTC; voir Colbeck et al. 1990 et Spreitzhofer et al. 2006) et les lignes 0905 et 0906 le type de grains minoritaires.
- La ligne 0907 représente la dimension des grains de neige dominants, la 0908 celle des grains minoritaires.
- La ligne 0909 représente la dureté de la neige mesurée avec les mains selon la classification internationale (IC; Colbeck et al. 1990) et la ligne 0910 la dureté secondaire, c'est-à-dire la dureté des zones qui diffèrent de la dureté représentative de la majorité de la couche de neige.
- À partir de la ligne 0921, on ne considère que les couches de neige pour lesquelles on a pris des mesures (lorsque l'information n'est pas disponible on indique simplement « 0 »). Les lignes dont le code se termine par un chiffre impair (e.g. 0921, 0951, etc) représentent les couches de neige considérées et leurs épaisseurs respectives, et les lignes se terminant par un chiffre pair (e.g. 0922, 0952, etc) correspondent aux données associées à chaque couche de la ligne précédente.
- Les lignes 0921 et 0922 concernent l'équivalent en eau de chaque couche (kg/m^2).

- Les lignes 0951 et 0952 concernent la densité de la neige de chaque couche (kg/m^3).
- Les lignes 0955 et 0956 concernent la teneur en eau de la neige de chaque couche (% par volume).
- Les lignes 0961 et 0962 les températures (K) des différentes couches.

Opération de SNOWPACK

Nous devons d'abord créer un fichier « input » où on indique la date à laquelle nos données climatiques commencent. Préférablement, on commence lorsque le couvert de neige est à 0. Ensuite, il faut indiquer la latitude (73°) et la longitude (79°). Les autres données peuvent garder les valeurs initiales par défaut, soit une altitude d'environ 0 m sur une pente de 0°. L'albedo du sol par défaut est mis à 0.2 et celle de z_0, qui correspond à la longueur de rugosité (la hauteur du plan où la vitesse du vent est nulle), à 0.02, ce qui semble représentatif pour un sol de toundra recouvert de neige (Panofsky et Dutton 1984). Pour l'onglet concernant l'effet de la canopée, dans la toundra aucune canopée n'influence la neige, donc la valeur à entrer sous l'onglet correspondant est 0. Dans le fichier « input », on peut ignorer l'étape 2 si l'on commence la série temporelle avec une épaisseur de neige à 0 cm, sinon l'on doit décrire les caractéristiques initiales de celles-ci.

L'étape suivante consiste à ouvrir l'onglet « model setting » afin de noter le pas de temps entre nos différentes données (par exemple 60 ou 1440 minutes) et définir quelles sont les données dont on dispose (concerne surtout les données optionnelles ou celles où un choix entre 2 variables est disponible). Il suffit donc de suivre les étapes en fonction des données dont nous disposons. Notez que dans la partie « Model », sous l'onglet « Boundary conditions », le manuel de SNOWPACK recommande de sélectionner « Dirichlet if Ts < 0 » et « Neumann else » lorsqu'on a des températures sous zéro. De même, sous l'onglet « Atmospheric Stability », on recommande une stratification neutre lorsqu'on utilise l'option « Dirichlet Boundary conditions ». Une fois toutes ces étapes complétées, il suffit de démarrer le modèle et de visualiser les résultats.

Exemple de résultats possibles

SNOWPACK peut estimer un grand nombre de paramètres relatifs à la neige, dont celui qui nous intéresse, sa densité. Le modèle va nous donner les valeurs pour chaque couche de neige et à chaque pas de temps (précisé dans les options de l' « output »). La Figure 1 donne un exemple graphique de données de densités estimées par SNOWPACK. À partir des fichiers d' « output » estimés par le modèle, il est possible d'obtenir directement ces données.

Tableau 6 : Exemple de lignes de fichier à utiliser pour faire fonctionner SNOWPACK. Dans cet exemple de fichier, toutes les lignes sont obligatoires.

```
MTO <STN_BYLOT20022003> 6940

M    31.08.2002    23:00    37497.9583        1.2     0.970        1.9    174.0        0.9    1.1        1.2     3.5    0.0    0.0000

M    01.09.2002    00:00    37498.0000        0.2     0.975        1.8    182.7        1.3    0.8        0.2     2.9    0.0    0.0075

M    01.09.2002    01:00    37498.0417        0.3     0.983        1.2    153.5        0.3    0.5        0.3     2.4    0.0    0.0070

M    01.09.2002    02:00    37498.0833        0.1     0.988        1.1    119.7        0.4    0.3        0.1     2.2    0.0    0.0056

M    01.09.2002    03:00    37498.1250        -0.8    0.993        0.8    129.5        1.4    0.1        -0.8    2      0.0    0.0153

….

END
```

Tableau 7 : Exemple de fichier de profils de neige pour utilisation dans SNOWPACK.

```
;
[ DATA Pit Profiles log1_60 ]
0900,1,21.05.2010 16:30,0.095,15.9
0901,6,0.005,0.010,0.030,0.035,0.075,0.095
0902,6,-1,-1,-1,-1,-1,-1
0903,6,-1,-1,-1,-1,-1,-1
0904,6,5,8,4,8,4,6
0905,6,5,8,4,8,4,6
0906,6,-1,-1,-1,-1,-1,-1
0907,6,2.00,-1,1.00,-1,0.50,1.00
0908,6,-1,-1,-1,-1,-1,-1
0909,6,-1,6,-1,6,1,4
0910,6,-1,-1,-1,-1,-1,-1
0921,0
0922,0
0951,3,0.030,0.075,0.095
0952,3,88.0,72.0,80.0
0961,2,0.000,0.095
0962,2,269.15,272.45
```

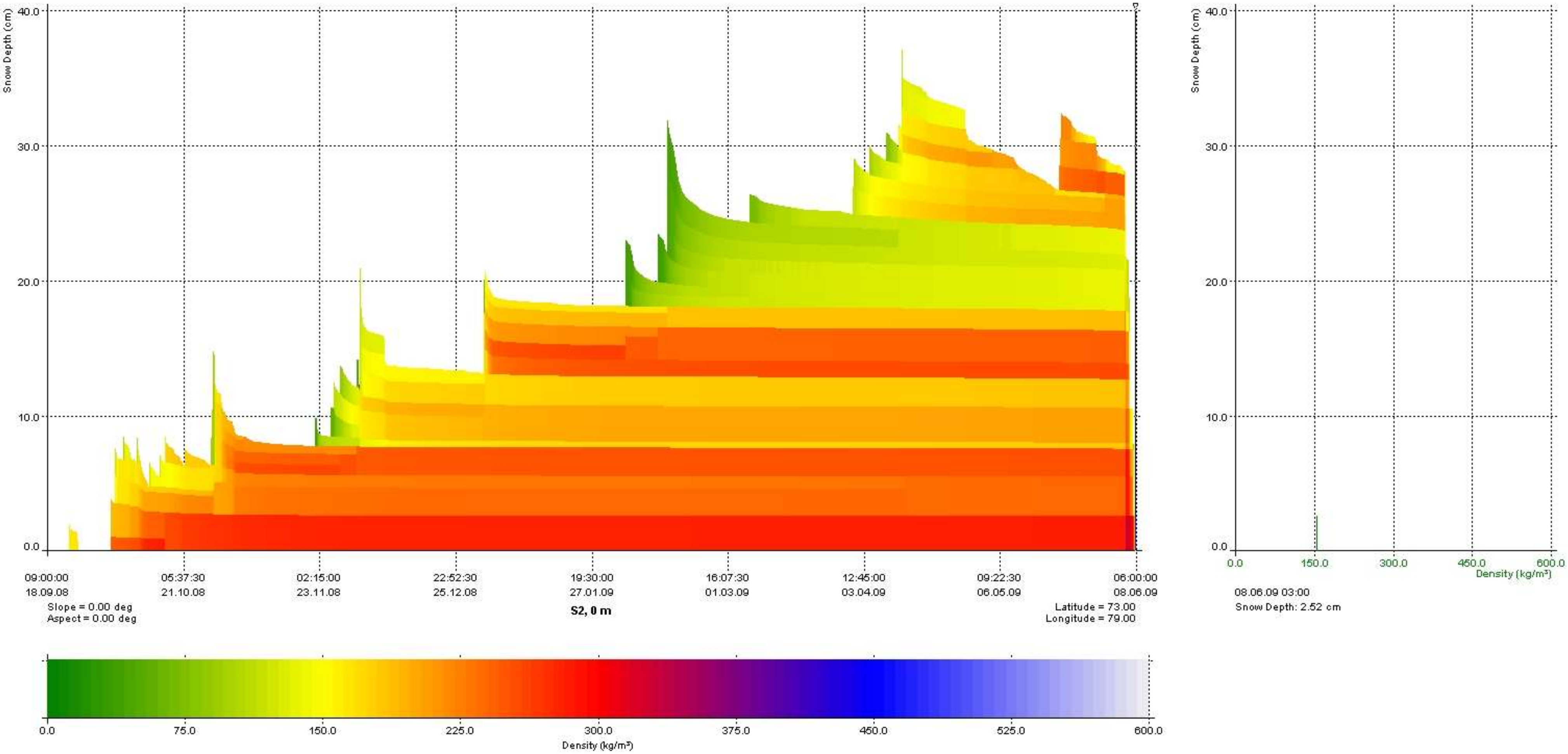

Figure 1 : Exemple graphique de la densité des différentes couches de neige estimées par SNOWPACK en fonction du temps au cours d’un hiver.

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Annexe 3

Supplementary material for Chapter 4

Table 1: Effect of treatment, habitat, year and 2-way interactions with treatments for all vascular plant families and moss genus sampled shortly after snowmelt in spring 2010-2012. For each taxon, two analyses were run, one where the treatment included ungrazed (inside exclosures) and random plots (outside exclosures) and one where treatments included ungrazed plots and plots showing sings of grazing (outside exclosures). See text for details. P values and degree of freedom are shown for each test. Significant values (P < 0.05) are in bold.

		Treatment		Habitat		Year		Treatment x Habitat		Treatment x Year	
Family/genus	Outside	df	*P* value	df	*P* value	df	*P* value	df	*P* value	df	*P* value
Total Plant Biomass	Random	1	0.561	1	0.189	2	**0.017**	1	0.847	2	0.539
	Grazed	1	0.339	1	0.340	2	**0.001**	1	0.277	2	0.521
Salicaceae (wood)	Random	1	0.629	1	0.655	2	**0.003**	1	0.060	2	0.779
	Grazed	1	0.515	1	0.105	2	**0.037**	1	0.798	2	0.688
Salicaceae (leaves and buds)	Random	1	0.364	1	0.230	2	**<0.001**	1	0.265	2	0.389
	Grazed	1	0.749	1	0.113	2	**0.023**	1	0.459	2	0.619
Juncaceae	Random	1	0.799	1	0.884	2	0.984	1	0.668	2	0.757
	Grazed	1	0.476	1	0.160	2	0.608	1	0.707	2	0.867
Poaceae	Random	1	0.390	1	0.744	2	0.150	1	0.405	2	0.874
	Grazed	1	0.375	1	0.196	2	0.064	1	0.268	2	0.956
Caryophyllaceae	Random	1	0.395	1	0.212	2	0.114	1	0.921	2	0.511
	Grazed	1	**0.017**	1	0.207	2	0.292	1	0.145	2	0.521
Ranunculacaea	Random	1	0.896	1	0.167	2	0.098	1	0.864	2	0.486
	Grazed	1	0.763	1	0.258	2	0.235	1	0.386	2	0.354
Polygonaceae	Random	1	0.256	1	0.396	2	0.716	1	**0.050**	2	0.993
	Grazed	1	0.802	1	0.802	2	0.157	1	0.233	2	0.939
Saxifragaceae	Random	1	0.587	1	0.511	2	0.593	1	0.993	2	0.843
	Grazed	1	0.477	1	0.808	2	0.808	1	0.159	2	0.750

Ericaceae	Random	1	0.924	1	0.070	2	0.842	1	0.457	2	0.290
	Grazed	1	0.780	1	0.449	2	0.069	1	0.219	2	0.103
Cyperaceae	Random	1	0.600	1	0.600	2	0.711	1	0.333	2	0.363
	Grazed	1	0.320	1	0.049	2	0.717	1	0.320	2	0.372
Pyrolaceae	Random	1	0.579	1	**0.010**	2	**0.018**	1	0.663	2	0.867
	Grazed	1	0.904	1	**0.035**	2	**0.074**	1	0.940	2	0.995
Brassicaceae	Random	1	0.857	1	0.227	2	**0.003**	1	0.356	2	0.213
	Grazed	1	0.858	1	0.068	2	0.831	1	0.595	2	0.590
Scrophulariaceae	Random	1	0.776	1	0.776	2	0.475	1	0.569	2	0.741
	Grazed	1	0.914	1	0.914	2	0.313	1	0.830	2	0.313
Equisetaceae	Random	1	0.320	1	0.320	2	0.718	1	0.320	2	0.372
	Grazed	1	0.320	1	**0.049**	2	0.717	1	0.320	2	0.372
Papaveraceae	Random	1	**0.049**	1	**0.049**	2	0.055	1	0.320	2	0.372
	Grazed	1	**0.049**	1	0.320	2	0.717	1	0.320	2	0.372
Fabaceae	Random	1	0.707	1	0.707	2	**0.044**	1	0.452	2	0.653
	Grazed	1	0.356	1	0.356	2	0.505	1	0.300	2	0.273
Rosaceae	Random	1	0.454	1	0.454	2	0.474	1	0.136	2	0.111
	Grazed	1	0.868	1	0.868	2	0.074	1	0.740	2	0.895
Total Moss Biomass	Random	1	0.984	1	0.724	2	**0.016**	1	0.928	2	0.876
	Grazed	1	0.989	1	0.531	2	**0.025**	1	0.897	2	0.795
Polytrichum	Random	1	0.086	1	0.174	2	0.844	1	0.522	2	0.089
	Grazed	1	0.082	1	0.271	2	**0.032**	1	0.775	2	0.197
Drepanocladus	Random	1	0.358	1	**0.016**	2	0.620	1	0.073	2	0.877
	Grazed	1	0.528	1	0.373	2	0.851	1	**0.037**	2	0.985
Ptilidium	Random	1	0.052	1	**0.004**	2	0.932	1	**0.014**	2	0.898
	Grazed	1	0.059	1	0.662	2	0.794	1	**0.013**	2	0.701

Ditrichum	Random	1	0.430	1	0.310	2	0.640	1	0.742	2	0.806
	Grazed	1	0.200	1	0.314	2	0.365	1	0.937	2	0.566
Hylocomium	Random	1	0.904	1	0.420	2	0.554	1	0.953	2	0.439
	Grazed	1	0.685	1	0.252	2	0.471	1	0.761	2	0.337
Philonotis	Random	1	0.374	1	**<0.001**	2	0.791	1	0.145	2	0.487
	Grazed	1	0.621	1	**0.045**	2	0.936	1	0.192	2	0.803
Gymnommitrion	Random	1	**0.049**	1	0.320	2	0.717	1	0.320	2	0.372
	Grazed	1	**0.049**	1	**0.049**	2	0.055	1	0.320	2	0.372
Blindia	Random	1	0.618	1	0.618	2	0.718	1	0.320	2	0.372
	Grazed	1	0.816	1	0.816	2	**0.040**	1	0.642	2	0.805
Plagiomnium	Random	1	0.158	1	0.564	2	**0.019**	1	0.843	2	0.304
	Grazed	1	0.777	1	0.102	2	0.175	1	0.813	2	0.620
Aulacomnium	Random	1	**0.003**	1	0.142	2	**0.001**	1	0.494	2	**0.023**
	Grazed	1	**0.007**	1	0.243	2	0.680	1	0.136	2	0.138
Dicranum	Random	1	0.489	1	0.663	2	0.906	1	0.426	2	0.876
	Grazed	1	0.284	1	0.771	2	0.733	1	0.667	2	0.739
Scapania	Random	1	0.801	1	0.074	2	0.497	1	0.319	2	0.789
	Grazed	1	0.974	1	0.281	2	0.143	1	0.725	2	0.745
Encalypta	Random	1	0.320	1	0.320	2	0.718	1	0.320	2	0.320
	Grazed	1	0.320	1	**0.049**	2	0.717	1	0.320	2	0.372
Campylium	Random	1	NA	1	NA	2	NA	1	NA	2	NA
	Grazed	1	0.229	1	0.282	2	0.613	1	0.898	2	0.607
Oncophorus	Random	1	0.289	1	0.337	2	0.733	1	0.337	2	0.348
	Grazed	1	0.289	1	0.057	2	0.669	1	0.337	2	0.348
Tomenthypnum	Random	1	0.268	1	0.866	2	0.591	1	0.362	2	0.437
	Grazed	1	0.270	1	0.289	2	0.652	1	0.414	2	0.500

Racomitrium	Random	1	0.754	1	0.754	2	0.325	1	0.531	2	0.835
	Grazed	1	0.643	1	0.643	2	0.939	1	0.355	2	0.526

Table 2: Effect of habitat, year and interaction for all vascular plant families and moss genus sampled at the end of the growing season. P values and degree of freedom are shown for each test. Significant values (P < 0.05) are in bold.

Fall	Habitat		Year		Habitat x Year	
Family/genus	df	P value	df	P value	df	P value
Total Plant Biomass	1	0.220	3	0.114	3	0.201
Salicaceae (wood)	1	0.497	3	0.509	3	0.340
Salicaceae (leaves and buds)	1	0.724	3	0.523	3	0.751
Juncaceae	1	0.841	3	0.888	3	0.444
Poaceae	1	0.537	3	0.054	3	0.327
Caryophyllaceae	1	0.248	3	**0.012**	3	0.846
Polygonaceae	1	0.151	3	**0.010**	3	0.981
Ranunculacaea	1	**0.002**	3	**<0.001**	3	**0.010**
Saxifragaceae	1	0.063	3	0.121	3	0.181
Ericaceagreen	1	0.153	3	0.495	3	0.261
Cyperaceae	1	0.149	3	0.370	3	0.186
Pyrolaceae	1	0.829	3	0.450	3	0.527
Brassicaceae	1	0.102	3	0.652	3	0.098
Scrophulariaceae	1	0.515	3	0.439	3	0.387
Equisetaceae	1	**0.022**	3	1.000	3	0.222
Papaveraceae	1	**<0.001**	3	**<0.001**	3	**<0.001**
Fabaceae	1	1.000	3	0.612	3	0.600
Rosaceae	1	1.000	3	0.394	3	0.493
Total Moss Biomass	1	**0.004**	3	0.415	3	0.257
Aulacomnium	1	0.675	3	0.163	3	0.948
Cinclidium	1	0.170	3	**0.021**	3	0.696
Scapania	1	0.689	3	**<0.001**	3	**0.013**
Ditrichum	1	**0.011**	3	**0.012**	3	**0.027**

Hylocomnium	1	0.112	3	0.213	3	0.057
Polytrichum	1	**0.004**	3	0.858	3	0.318
Philonotis	1	0.427	3	0.522	3	0.326
Bartramia	1	0.050	3	0.124	3	0.400
Gymnommitrion	1	0.050	3	0.124	3	0.400
Blindia	1	0.050	3	0.124	3	0.400
Plagiomnium	1	0.636	3	0.252	3	0.449
Drepanocladus	1	0.919	3	0.498	3	0.504
Dicranoweisia	1	0.050	3	0.124	3	0.400
Meesia	1	0.050	3	0.124	3	0.400
Dicranum	1	0.587	3	0.284	3	0.717
Ptilidium	1	0.088	3	0.898	3	0.788
Encalypta	1	0.874	3	0.126	3	0.376
Pohlia	1	0.050	3	1.000	3	0.400
Campylium	1	**<0.001**	3	**<0.001**	3	**<0.001**
Oncophorus	1	0.491	3	0.208	3	0.508
Tomenthypnum	1	1.000	3	0.230	3	0.611
Hypnum	1	1.000	3	0.878	3	0.314
Ceratodon	1	1.000	3	0.124	3	0.400
Orthotrichum	1	1.000	3	0.124	3	0.400
Racomitrium	1	1.000	3	0.739	3	0.912