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ÉTUDE COMPARATIVE DE LA DÉMOGRAPHIE DE DEUX ESPÈCES DE LEMMINGS *(LEMMUS SIBERICUS* ET *DICROSTONYX GROENLANDICUS)*, À L'ÎLE BYLOT, NUNAVUT, CANADA

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Résumé

L’objectif principal de ce mémoire était d’approfondir nos connaissances sur la dynamique des populations de deux espèces sympatriques de lemming, le lemming brun (*Lemmus sibericus*) et le lemming variable (*Dicrostonyx groenlandicus*) à l’Île Bylot, Nunavut, Canada. Une première analyse a permis de caractériser les fluctuations interannuelles d’abondance des deux espèces sur une période de 13 ans. Cette analyse a montré que la cyclicité des deux espèces diffère, malgré une période équivalente de 3-4 ans. Les variations d’amplitude chez le lemming brun, l’espèce la plus abondante, étaient plus importantes que chez le lemming variable, mais synchrones entre les deux espèces. Nous avons aussi analysé la démographie des deux espèces au cours de deux années consécutives, une de pic d’abondance et une de déclin. Nos résultats suggèrent une plus grande variation interannuelle de la démographie et de la densité pour le lemming brun par rapport au lemming variable. On n’a noté aucune différence dans les variations saisonnières entre les deux espèces. De façon générale, la taille de la population adulte diminuait durant l’été alors que le taux de reproduction et l’abondance des jeunes augmentaient.

Abstract

The main objective of this thesis was to improve our knowledge on the population dynamic of two sympatric lemming species, the brown lemming (*Lemmus sibericus*) and the collared lemming (*Dicrostonyx groenlandicus*) on Bylot Island, Nunavut, Canada. In a first analysis, we characterised inter-annual fluctuations in abundance of both species over a 13-year period. The cyclicity differed between the two species but periodicity was the same (3-4 years). Fluctuations were of greater amplitude in the brown lemming, the most abundant species, than in the collared lemming but nonetheless synchronous between species. We also analysed the demography in both species during two consecutive years, a peak and a declining year of abundance. Our results suggest that the demography and density of brown lemmings was more variable than those of collared lemmings. We found no differences between the two species in seasonal variations. Generally, adult population size decreased during the summer and the reproductive rate and abundance of juveniles increased.

Avant-Propos

Ce mémoire est constitué de quatre parties. Tout d'abord, une introduction présente le contexte général de l'étude et les objectifs atteints au cours de cette maîtrise. La seconde partie est constituée par un chapitre rédigé sous forme d'article scientifique en anglais. Ce chapitre correspond à l'analyse de données à long terme (de 1993 à 2005), obtenues par piégeage mortel. La troisième partie est également rédigée sous forme d'article scientifique. Elle regroupe toutes les analyses réalisées grâce au piégeage vivant mis en place en 2004 et 2005. Tout cela nous a permis d'étudier de manière approfondie différents paramètres démographiques des deux espèces de lemmings et leurs variations saisonnières et annuelles. Enfin, la dernière partie est constituée de la conclusion générale de ce mémoire. Les points les plus importants y sont rappelés ainsi que des suggestions pour des recherches futures.

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INTRODUCTION GÉNÉRALE

Contexte général

L'effectif d'une population n'est pas constant au cours du temps. Cependant, les variations peuvent être d'intensité très différente selon l'espèce, le milieu et l'échelle de temps considérés. Il apparaît aujourd'hui que ces fluctuations sont la règle et non l'exception dans les populations naturelles. En effet, quels que soient les facteurs responsables de la dynamique d'une population, les situations d'équilibre sont probablement rares dans les systèmes naturels.

Certaines espèces animales sont connues pour leurs fluctuations violentes d'abondance, en particulier les petits mammifères comme les rongeurs. Les écarts entre les pics (limite supérieure) et les creux (limite inférieure) de populations peuvent être considérables (parfois plus de 100 x). Il est aussi connu depuis longtemps que les fluctuations d'abondance peuvent parfois présenter un patron cyclique d'une régularité déconcertante. Par exemple, le lièvre d'Amérique (*Lepus americanus*) a un cycle d'abondance d'une durée d'environ 10 ans, et beaucoup d'espèces de campagnols et de lemmings de l'Arctique présentent des cycles de 3 à 5 ans (Elton 1924, Akcakaya 1992, Krebs et al. 1995, Turchin et al. 2000, Predavec et al. 2001). Toutefois, des études récentes ont démontré que les fluctuations d'abondance de certaines espèces peuvent présenter des patrons variables dans le temps et l'espace: ainsi, certaines populations d'une même espèce peuvent être cycliques à un site et pas à d'autres, alors que d'autres populations peuvent être cycliques durant une période et pas durant d'autres périodes (Stenseth 1999, Angerbjorn et al. 2001), ce qui complique l'étude de ces phénomènes.

Les auteurs qui ont étudié les cycles de population de petits rongeurs comme ceux des lemmings distinguent généralement quatre phases au cours du cycle (Krebs 1964, Stenseth et al. 1993, Gilg 2002a). D'abord, il y a la phase de croissance qui a tendance à être très variable selon les endroits considérés. Habituellement cette phase est moins longue que celle de déclin. À l'Île Bylot, notre site d'étude, cette phase dure généralement un an seulement (Bêty et al. 2002). Elle est suivie de la phase de pic qui se caractérise par de fortes abondances de lemmings sur une courte période, souvent quelques mois seulement. Vient ensuite la phase de déclin au cours de laquelle les paramètres démographiques de la phase de croissance sont inversés. Finalement, on a une phase de très faible abondance dont la durée peut également être très variable. Elle se caractérise par des densités de populations de 10 à 100 fois inférieures aux densités maximales observées lors de la phase de pic (Krebs 1964, Stenseth et al. 1993, Gilg 2002a).

Les causes de ces cycles sont encore mal connues et de nombreuses hypothèses ont été formulées depuis près d'un siècle afin de les comprendre et de tenter d'aboutir à un consensus sur le « mystère » des cycles de population. Cela a aussi beaucoup fasciné l'imaginaire depuis longtemps et a donné lieu à de nombreux mythes et légendes (Stenseth et al. 1993, Chitty 1996). Les causes des fluctuations cycliques de certaines populations animales ont été l'objet de nombreuses études, et plusieurs ont cherché à connaître les facteurs de régulation impliqués dans l'accroissement ou la diminution de l'abondance de ces espèces. Pendant plusieurs décennies, l'importance relative des facteurs de contrôle biotiques et abiotiques a notamment été débattue vigoureusement (Murdoch 1994, Berryman 2004, White 2004).

De nombreuses hypothèses ont été émises pour tenter d'expliquer les cycles de populations des rongeurs en général, et en particulier ceux des lemmings (Boonstra 1994, Krebs et al. 1995, Reid et al. 1995, Chitty 1996, Boonstra et al. 1998, Turchin et Hanski 2001, Gilg 2002, Norrdahl et Korpimaki 2002, Banks et Powell 2004). Selon l'école des facteurs dits intrinsèques, des changements dans la qualité des individus selon les phases du cycle en seraient la cause. Effectivement, des changements de masse et même de comportement sont souvent visibles. Toutefois, ces changements sont de plus en plus considérés comme des conséquences des fluctuations de population durant le cycle et non comme la cause (Klemola et al. 2000). Néanmoins l'hypothèse de « Senescence effect » (changement de la qualité individuelle, notamment au niveau de la reproduction, selon les phases; Boonstra et al. 1994) demeure un facteur intrinsèque plausible pour expliquer les fluctuations cycliques.

Par opposition, il semble de plus en plus acquis que les facteurs dits extrinsèques seraient à l'origine des cycles de populations. Au sein de cette école de pensée, deux grandes hypothèses tendent à se démarquer. La première considère que la régulation de ces populations ainsi que les cycles seraient causés par la prédation (Hansson 1979, Reid et al.

1995, Korpinaki et Krebs 1996, Klemola et al. 2000, Norrdahl et Korpimaki 2000, Norrdahl et Korpimaki 2002, Korpimaki et al. 2003, Norrdahl et al. 2004). La prédation est considérée ici comme un facteur nécessaire pour limiter la phase d'accroissement de population des petits mammifères comme les lemmings, particulièrement celle par les prédateurs spécialistes comme l'Hermine (*Mustela erminea*) et le Harfang des neiges (*Nyctea scandiaca*). Un délai dans les réponses numériques et fonctionnelles de ces prédateurs aux fluctuations d'abondance de leur proie jouerait un rôle important dans la création de ces cycles (Gilg et al. 2006). Selon cette hypothèse, le contrôle des petits mammifères s'opèrerait donc par le haut de la chaîne trophique. La seconde hypothèse considère que la régulation des populations se fait via la nourriture, soit les plantes. Le broutage excessif lors des pics d'abondance réduirait la quantité ou la qualité de nourriture disponible, provoquant alors une chute de la population (Hansson 1979, Seldal 1994, Agrell et al. 1995, Turchin et al. 2000). Les cycles seraient donc générés par un mécanisme de contrôle opérant par le bas de la chaîne trophique.

Également, de nombreux modèles mathématiques de variation d'abondance de populations ont été formulés afin de voir sous quelles conditions on peut arriver à générer des cycles de population. Par exemple, on peut citer des modèles simples comme le modèle logistique en temps discret avec délai (May 1975) ou encore des modèles plus complexes d'interactions à deux niveaux trophiques (plantes-herbivores ou prédateurs-proies) de nature spécialiste (Kendall et al. 1999, Ekerholm et al. 2001, Turchin et Hanski 2001, Gilg et al. 2006). Ces modèles arrivent tous à générer des dynamiques de population cycliques sous certaines conditions ou certaines valeurs de paramètres.

Le cas des milieux arctiques

La dynamique des interactions trophiques joue un rôle primordial dans l'organisation des écosystèmes. Le contrôle des chaînes trophiques est un sujet controversé car deux processus fondamentaux opposés peuvent opérer. D'une part, le contrôle peut se faire par les ressources disponibles à la base du réseau, soit une régulation par le bas ou « bottom-up » ; à l'opposé, le contrôle peut venir des prédateurs, on parle alors de régulation par le haut ou « top-down ». Dans les écosystèmes, d'après le modèle d'Exploitation des

Écosystèmes d'Oksanen (EEH), la production primaire détermine ultimement la longueur des chaînes alimentaires (Oksanen et al. 1981, Oksanen et Oksanen. 2000). Si la chaîne alimentaire est courte (i.e. deux niveaux trophiques), ce sont les interactions plantes-herbivores qui domineront mais si la chaîne comporte trois niveaux, alors les interactions prédateurs-proies domineront le système. Selon Oksanen et ses collaborateurs, la faible production primaire de la toundra serait sous le seuil requis pour supporter des populations d'herbivores suffisamment grandes pour maintenir des populations viables de prédateurs. Le modèle EEH prédit alors que la chaîne alimentaire en Arctique devrait être dominée par l'interaction plantes-herbivores, et que l'impact des herbivores sur les plantes est fort à cause de l'absence de prédateurs fonctionnels.

Dans la toundra arctique, les lemmings sont souvent les herbivores les plus importants. En accord avec l'EEH, l'impact des lemmings sur la végétation durant les pics semble fort en Fennoscandinavie (Moen et al. 1993, Virtanen et al. 1997, Moen et Oksanen 1998), ce qui a amené certains chercheurs à proposer que le cycle de lemmings serait causé par l'interaction plantes-herbivores (Turchin et al. 2000). Cependant, on trouve peu d'évidences similaires en Amérique du Nord. Par exemple, contrairement au modèle d'Oksanen, les lemmings ne semblent pas avoir d'impact significatif sur les plantes à l'Île Bylot dans l'Arctique canadien (Gauthier et al. 2004).

Par ailleurs, il y a de plus en plus d'évidences que les interactions prédateurs-proies pourraient être importantes en milieu arctique, en contradiction avec l'EEH. L'abondance et le succès reproducteur de nombreux prédateurs tels le Harfang des neiges (*Nyctea scandiaca*), le Renard arctique (*Alopex lagopus*), l'Hermine (*Mustela erminea)*, et les labbes (*Stercorarius pomarinus* et *Stercorarius parasiticus*) semblent dépendre directement de l'abondance de lemmings (Gilg 2002, Gilg et al. 2003, Gauthier et al. 2004). De plus, d'autres espèces d'herbivores comme les oies sont influencées indirectement par les cycles de population de lemmings parce qu'elles partagent les mêmes prédateurs et qu'elles deviennent des proies alternatives quand l'abondance des lemmings est faible (Bêty et al. 2002, Gauthier et al. 2004). Les lemmings semblent donc avoir un rôle central dans le fonctionnement de tout l'écosystème arctique, et leur effet sur de nombreuses espèces pourrait se faire sentir surtout par l'interaction prédateur-proies.

Analyse démographique des populations

Les variations des paramètres démographiques d'une population sont responsables des changements d'abondance et de densité. Ainsi, l'estimation des différents paramètres démographiques et leur analyse sont primordiales afin de comprendre la dynamique d'une population. L'estimation de ces paramètres se fait le plus souvent à partir d'individus marqués individuellement et qu'on recapture subséquemment. L'analyse de tels jeux de données par modèles de capture-marquage-recapture (CMR) a connu un essor fulgurant en écologie au cours des récentes décennies. Les modèles de CMR utilisent des séances multiples (plus de 2) de capture et de marquage des individus, le plus souvent à intervalles de temps régulier. On distingue deux grandes classes de modèles de CMR, soit ceux pour les populations fermées (i.e. la population ne change pas durant la période de l'étude) et ceux pour les populations ouvertes (i.e. avec changement de nombre via la natalité, la mortalité, l'immigration et l'émigration).

Les modèles développés pour populations fermées sont généralement utilisés pour estimer l'abondance. La précision de l'estimation d'abondance est augmentée en ajoutant des séances de capture (>2), en autant qu'elles soient rapprochées dans le temps et que la prémisse de population fermée puisse s'appliquer (aucune naissance, mortalité, immigration ou émigration). Otis et al. (1978) ont développé une série de modèles pour estimer l'abondance avec des populations fermées basés sur >2 séances de capture (logiciel CAPTURE ; Otis et al. 1978, Williams et al. 2002). Une prémisse essentielle à ce modèle de base est l'homogénéité des probabilités de capture entre les individus, une prémisse souvent violée. Cependant, différents modèles alternatifs permettant de prendre en compte l'effet du temps, du comportement ou de l'hétérogénéité individuelle sur les probabilités de capture ont été développés, ce qui réduit les biais sur les estimations. La sélection du meilleur modèle s'ajustant aux données se fait alors selon le Critère d'Information d'Akaike (AIC ; Burnham and Anderson 1998)

Par opposition, les modèles de CMR pour populations ouvertes (modèle de Cormak-Jolly-Seber et ses dérivés; Lebreton et al. 1992) sont utilisés principalement pour estimer la survie des individus dans le temps en contrôlant pour la probabilité de capture. Cependant, il existe des modèles combinant ces 2 approches (i.e. pour populations fermées et ouvertes) permettant alors d'estimer à la fois une abondance et une survie. Ce sont les modèles basés sur le design robuste (Kendall et al. 1995, 1997). Dans ce design, on a *K* occasions de captures primaires séparées par des intervalles plus on moins longues où les populations sont considérées ouvertes (naissances, mortalité, et immigration/émigration possibles). On estime donc la survie entre ces occasions primaires à l'aide des modèles de population ouverte (Cormak-Jolly-Seber). Toutefois, chaque occasion primaire est constituée d'un certain nombre d'occasions secondaires (jours consécutifs) où les intervalles entre chaque occasion sont très courts. La population est alors considérée comme fermée durant cette période et les modèles de population fermée (ceux d'Otis et al. 1978) sont alors appliqués afin d'obtenir des estimés d'abondance. La combinaison des deux approches dans le design robuste permet une utilisation plus efficace des données. La sélection du modèle s'ajustant le mieux aux données se fait également selon le critère d'AIC (Burnham and Anderson 1998).

Les méthodes de capture-recapture précédentes fournissent des estimés de l'abondance absolue, i.e. la taille de la population. Par contre, une mesure plus utile est la densité, soit la taille de la population divisée par la superficie de piégeage (i.e. taille effective de la zone de piégeage). Or, la détermination de la taille effective de piégeage est souvent difficile et sujette à des biais (Parmenter et al. 2003). Récemment, Murray Efford (Efford 2004, 2005) a proposé une méthode alternative pour estimer la densité d'une population fermée par capture-recapture. Cette méthode estime directement la densité. La probabilité qu'un animal soit capturé dépend de la distance *r* entre le centre de son domaine vital et la trappe. Cette distance *r* est décrite par la fonction g(*r*) à l'aide de 2 paramètres: g(0) (probabilité de capture quand la trappe se situe exactement au centre du domaine vital) et σ (taille du domaine vital). Le problème est d'estimer la densité D, g(0) et σ avec les données obtenues par capture-marquage-recapture. Or, la distance moyenne (*d*) entre les différentes captures d'un individu contient de l'information sur la distance des déplacements (σ). De plus, des informations relatives à la densité (D) et g(0) sont également contenues dans les estimations de la taille de la population (N) et dans la probabilité de capture (*p*) (Voir Efford 2004 pour les détails).

Dans notre étude, nous avons fait appel aux développements les plus récents dans les modèles de CMR, notamment le design robuste et la méthode d'Efford, pour estimer et analyser les paramètres démographiques des populations étudiées.

Sujets d'étude

Les lemmings ont une distribution circumpolaire et comptent 20 espèces. Ces espèces se divisent en deux genres, le genre *Lemmus* et le genre *Discrostonyx*. Dans l'arctique canadien, ces deux genres sont surtout représentés par le Lemming variable (*Dicrostonyx groenlandicus*) et le Lemming brun (*Lemmus sibiricus*). Les deux genres de lemmings ont typiquement une écologie différente. Par exemple, on retrouve généralement le lemming brun dans les milieux humides où il s'alimente de plantes comme les cypéracées et les graminées, ainsi que de mousses en hiver. À l'opposé, le lemming variable préfère les habitats plus secs (milieux mésiques et xériques) où il s'alimente principalement de plantes herbacées et d'arbustes (Batzli et Jung 1980, Stenseth et al. 1993). Les refuges utilisés par les lemmings diffèrent également selon les saisons. En été, ils vivent dans des terriers dans le sol alors qu'en hiver ils construisent des nids fait de végétation sous la neige (Wilson et Ruff 1999).

Les mâles comme les femelles peuvent s'accoupler quelques semaines après leur naissance et donc plus d'une génération par année est possible. Les femelles sont plus sédentaires (i.e. déplacement moindre) du fait de leurs portée, alors que les mâles se déplacent plus pour pouvoir s'accoupler (Banks et al. 1975, Predavec and Krebs 2000). Malgré les températures hivernales extrêmes de l'Arctique, le lemming n'hiberne pas et il trouve suffisamment d'énergie pour survivre et même se reproduire. C'est souvent en hiver que la population enregistre son taux de croissance le plus élevé parce que les lemmings sont alors mieux protégés des prédateurs et des rigueurs climatiques sous la neige que pendant l'été, et la mortalité est donc souvent réduite à cette saison (Stenseth et al. 1993).

Site d'étude

Notre projet s'est déroule à l'Île Bylot qui est située à la pointe Nord de l'Île de Baffin, Nunavut, dans l'archipel arctique canadien. Des études sur les interactions trophiques et sur les lemmings sont déjà en cours à ce site depuis plusieurs années (Bêty et al. 2001, Bêty et al. 2002, Gauthier et al. 2004). Le projet s'est principalement effectué dans une grande vallée glaciaire (Vallée Qarlikturvik, 70 km²) à l'extrémité sud-ouest de l'île (73°08'N, 80°00'W). Les deux espèces de lemmings se retrouvent à ce site, quoique l'Île Bylot constitue la limite nord de distribution du lemming brun dans l'est de l'Arctique canadien (Banfield 1974).

Le site d'étude est constitué d'un assemblage de polygones, de lacs de dégel et d'étangs (Gauthier et al. 1996). La capacité de rétention d'eau de ces composantes topographiques, combinée à la faible capacité de drainage du pergélisol contribue à la formation de milieux humides. La végétation caractéristique de ces milieux humides se compose principalement de cypéracées, de graminées et de plusieurs espèces de mousses brunes. On retrouve également des habitats plus secs, les milieux mésiques, où la diversité floristique est plus grande et où les plantes les plus communes sont les plantes herbacées, quelques graminées et des arbustes.

La température annuelle moyenne à l'Île Bylot est –14.8°C. Pendant la saison estivale (juin, juillet, août), cette moyenne augmente à 4.5°C alors qu'au cours de l'hiver (décembre, janvier, février), elle peut descendre aussi bas que –32.6°C (Gagnon et al. 2004).

Problématique, objectifs et hypothèses de l'étude

Cette étude porte sur la dynamique de population d'espèces reconnues pour être cycliques, les lemmings. Une analyse approfondie de leur démographie est primordiale afin de mieux comprendre la dynamique cyclique de leurs populations et leur rôle clef dans l'écosystème arctique.

Plusieurs approches sont possibles. L'analyse détaillée de séries temporelles de taille de population en termes de périodicité ou d'amplitudes des fluctuations à l'aide de modèles mathématiques est une approche couramment utilisée. Toutefois, cette approche, dite paradigme de densité, est limitée pour une analyse approfondie de la démographie car elle permet uniquement de mettre en relation la croissance de la population avec sa taille. Cette approche est donc appliquée *a posteriori* et ne permet pas de comprendre les causes des changements de taille d'une population. Par opposition, une approche dite approche mécanistique (sensu Krebs 2002) peut aussi être adoptée. Cette approche est plutôt basée sur une étude détaillée des principaux paramètres démographiques, telles que les variations annuelles et saisonnières de densité, de survie et de recrutement. Cette approche a comme avantage de mettre en relation les processus écologiques affectant la taille de la population. Elle permet donc d'examiner les différents facteurs responsables des changements de taille de la population, comme par exemple les différents paramètres démographiques.

Notre étude combinera ces deux approches afin de mieux comprendre certains aspects de la dynamique des populations de lemmings. Plus précisément, nos objectifs sont de:

1) Estimer et comparer les fluctuations d'abondance de deux espèces de lemmings à l'Île Bylot (périodicité, amplitude) à partir d'une série temporelle d'indice d'abondance de 13 ans.

2) Comparer la performance de trois méthodes d'estimation de la densité de lemmings à partir de données de capture-marquage-recapture.

3) Comparer les paramètres démographiques des deux espèces de lemmings au même site sur une base saisonnière (i.e. au cours de la période estivale) et annuelle. Les paramètres examinés seront :

    - ➢ L'abondance et la densité
    - ➢ La survie
    - ➢ Le recrutement

4) Déterminer la taille des domaines vitaux des lemmings par la radiotélémétrie.

À travers cette étude, j'ai également formulé un certain nombre d'hypothèses que j'ai tenté de vérifier. Ces hypothèses sont:

H_1 : Les fluctuations d'abondance des deux espèces de lemmings présentes à l'Île Bylot sont cycliques. Si cette hypothèse est juste, je prédis que :

- Les séries temporelles des deux espèces auront une amplitude et une périodicité typique des populations cycliques (succession de forte et de faible amplitude, période de 3-4 ans).

- Les paramètres statistiques issus de l'analyse des fluctuations d'abondance des deux espèces vont satisfaire aux critères quantitatifs habituellement utilisés (période et amplitude) pour définir les cycles de population.

H_2 : Les fluctuations d'abondance des deux espèces de lemmings seront synchrones et en phase. Si cette hypothèse est juste, je prédis que:

- Les fluctuations d'abondance des deux espèces seront corrélées positivement.

H_3 : En dépit de la reproduction, la taille des populations de lemmings devrait diminuer au cours de la période estivale à cause du nombre plus élevé de prédateurs, et donc d'une mortalité plus forte, qu'en hiver. Si cette hypothèse est juste, alors je prédis:

- Une diminution de l'abondance et de la densité pour les deux espèces de lemming sera visible au cours de la période estivale.

H_4 : La reproduction des lemmings, qui commencerait durant hiver, s'interromprait à la fonte de la neige quand les individus sont forcés de changer de site, pour reprendre ensuite durant l'été. Si cette hypothèse est juste, alors je prédis:

- La proportion de femelles lactantes augmente durant la période estivale.

- La proportion de juvéniles augmente durant la période estivale.

H_5 : Les paramètres démographiques (survie, reproduction, recrutement) changent durant les phases du cycle de population. Si cette hypothèse est juste, alors je prédis:

- La survie des individus sera plus élevée durant les phases de croissance et du pic que durant les phases de déclin et du creux.

- Le recrutement des individus dans la population sera plus élevé durant les phases de croissance et du pic que durant les phases de déclin et du creux.

H_6 : Les femelles se déplacent moins que les mâles, d'une part à cause de leurs portées, et d'autre part parce que les mâles recherchent des femelles pour l'accouplement (Schmidt et al. 2002). Si cette hypothèse est juste, alors je prédis:

- Les domaines vitaux des mâles seront plus grands que ceux des femelles.

Les résultats obtenus pour l'objectif 1 et les hypothèses 1 et 2 sont présentés dans le chapitre 1, alors que ceux correspondant aux objectifs 2 à 4 et aux hypothèses 3 à 6 sont présentés dans le chapitre 2.

CHAPITRE 1

LONG-TERM DYNAMICS OF LEMMING (*LEMMUS SIBERICUS* AND *DICROSTONYX GROENLANDICUS*) POPULATIONS ON BYLOT ISLAND, NUNAVUT, CANADA

N. Gruyer, G. Gauthier, and D. Berteaux

RÉSUMÉ

L’occurrence de cycles de populations chez les petits rongeurs nordiques a été pendant longtemps et demeure une énigme en écologie. Nous avons étudié les caractéristiques (amplitude, périodicité) des cycles de deux espèces sympatriques, le lemming brun (*Lemmus sibericus*) et le lemming variable (*Discrostonyx groenlandicus*) à l’Île Bylot (Nunavut, Canada). Un indice annuel d'abondance a été obtenu par trappage mortel à deux sites distants de 30 km durant 13 et 9 ans respectivement. Les séries temporelles ont été analysées par analyses spectrales et modèles autorégressifs. Au site avec la série temporelle la plus longue, le lemming brun présentait des fluctuations cycliques typiques avec des variations d’abondance de grande amplitude (>40x), alors que les fluctuations du lemming variable étaient plus faibles et de moindre amplitude (4x). De plus, le lemming brun était plus abondant que le lemming variable, sauf durant les années de faible abondance du cycle. À l’autre site, la population de lemmings variables était plus importante qu’au site principal, mais le lemming brun était plus abondant lors de l’année de pic. Les périodes du cycle ont été estimées à 3.69 ± 0.04 ans pour le lemming brun et 3.92 ± 0.24 ans pour le variable. Les modèles prédictifs de 2ème ordre obtenus par l’analyse spectrale des données étaient fortement corrélés aux données observées (brun: r = 0.96; variable r = 0.86; les deux, df = 12, P < 0.01). Les fluctuations d’abondance à un même site étaient relativement bien synchrones entre les deux espèces (r_s = 0.67, df = 11, P = 0.02), mais apparemment pas entre les deux sites (les deux espèces combinées; r_s = 0.40, df = 8, P = 0.28).

ABSTRACT

Cyclic population fluctuations in northern species of small rodents have been reported for a long time, and are still an enigma in ecology. We characterized the fluctuations (amplitude, periodicity) of two sympatric species, the brown lemming (*Lemmus sibiricus*) and the collared lemming (*Dicrostonyx groenlandicus*) on Bylot Island (Nunavut, Canada), a High Arctic site. An annual index of lemming abundance was obtained using snap-traps at two sites separated by 30 km over 13 and 9 years, respectively. The time series were analysed by spectral analyses and autoregressive modelling. At the site with the longest record, brown lemming showed typical cyclic population fluctuations of large amplitude (>40 fold), whereas collared lemming fluctuations were weak and of much smaller amplitude (4 fold). Furthermore, brown lemmings were more abundant than collared lemmings, except in the low years of the cycle. At the other site, the collared lemming population was higher than at the main site, but brown lemmings were still most abundant in the peak year. The periods of the cycles were estimated at 3.69 ± 0.04 years for brown lemmings and 3.92 ± 0.24 years for collared lemmings. The model with a 2^{nd} order function obtained from a spectral analysis of the data fitted well the observed abundance data (brown: $r = 0.96$; collared: $r = 0.86$; both, df = 12, $P < 0.01$). Fluctuations in abundance at the same site were relatively well synchronized between species ($r_s = 0.67$, df = 11, $P = 0.02$), but apparently not between sites (both species combined; $r_s = 0.40$, df = 8, $P = 0.28$).

INTRODUCTION

Lemmings are recognized for their multiannual fluctuations in density known as cycles. These cycles typically have a fairly regular periodicity between 3 and 5 years, although the amplitude of these fluctuations can vary considerably (Elton 1924, Stenseth et al. 1993). Moreover, the regularity of these oscillations may vary spatially as well as temporally (Krebs et al. 1995, Stenseth 1999, Angerbjorn et al. 2001). “Cyclic” species are not necessarily cyclic throughout their distribution range: typically, southern populations are less cyclic than more northern ones (Stenseth et al. 1996, Stenseth et al. 2003). Additionally, populations that have been cyclic for several decades may not continue to do so indefinitely whereas the reverse can also be true (Stenseth et al. 1993, Angerbjorn et al. 2001, Predavec et al. 2001).

Krebs et al. (2002) suggested that rodent cyclic fluctuations in the Canadian Arctic were synchronized at both the local scale and over large geographic areas, and that sympatric species were locally synchronized. Two aspects of synchrony must be distinguished: spatial synchrony refers to populations of the same species fluctuating in phase over small or large geographic regions whereas interspecific synchrony refers to all rodent species present at a given site fluctuating in phase (Krebs et al. 2002). Climate is one factor that may contribute to impose synchrony in rodent cyclic fluctuations. Interactions with specialist predators, which is currently one of the most popular hypotheses to explain rodent population cycles, may also contribute to impose both interspecific and spatial synchrony (Stenseth et al. 1993, Viljugrein et al. 2001). However, the scale of spatial synchrony in lemming cycles remains poorly known, although it apparently does not extend to whole continents (Erlinge et al. 1999, Krebs et al. 2002).

Long time-series of lemming population fluctuations are essential to characterize their fluctuations and to examine questions related to interspecific and spatial synchrony. However, such data sets are scarce in the nearctic (Krebs et al. 2002) compared to the palearctic (e.g. Angerbjorn et al. 2001). In this study, we used a long-term data set to examine features of population fluctuations for two sympatric species of lemmings, the brown (*Lemmus sibiricus*) and the collared lemmings (*Dicrostonyx groenlandicus*), in the

Canadian Arctic. Trapping was conducted at two sites distant by 30 km over a 13 and 9-year period, respectively. Our objectives were to characterize the amplitude and periodicity of the oscillations, and the degree of interspecific synchrony in fluctuations. We also examined the order of density dependence (i.e. direct or delayed density-dependence) present in the data for each species at our study site. Delayed density-dependence (i.e. second order) has been found in many cyclic populations, and is often an indication that specialised trophic interactions is a cause of the observed cyclicity (Stenseth 1999, Turchin and Hanski 2001, Jiang and Shao 2003).

METHODS

Study area and species

Field work was carried out at Bylot Island, Sirmilik National Park, Nunavut, Canada (73°N, 80°W). The landscape in the area is a mixture of wetlands dominated by graminoids and mosses in lowland areas, mesic tundra dominated by shrubs, forbs and some graminoids in both lowlands and rolling hills areas, and, at higher elevation, xeric tundra (Gauthier et al. 1996). Data were collected at two sites separated by 30 km, Site-1 (Qarlikturvik Valley) and Site-2. The Site-2 was located in the center of a large greater snow goose (*Chen caerulescens atlantica*) nesting colony.

Two species of rodents are found on Bylot Island, the collared and the brown lemmings. Brown lemmings are typically found in wetlands where they feed primarily on sedges and grasses, as well as mosses in winter. In contrast, collared lemmings prefer drier habitats where they mainly feed on forbs and shrubs (Rodgers and Lewis 1986a, Batzli 1980). The two species present different levels of adaptation to the arctic environment, which is reflected in their distribution range. The range of collared lemmings extends to the northernmost land mass in the Arctic (Golley et al. 1975). On the other hand, brown lemmings reach the northern limit of their geographical range precisely on Bylot Island in eastern North America (Banfield 1974).

Trapping protocol

Lemming abundance was estimated annually with snap-traps from 1994 to 2005 at Site-1 and 1997 to 2005 at Site-2. Trapping was conducted between 5 and 15 July at Site-2 and 21 and 31 July at Site-1. At Site-1, trapping was simultaneously conducted in two plots, one located in wet meadow habitat and one located in drier mesic habitat. At Site-2, trapping took place in only one plot located in a mixed wet-mesic habitat. In each plot, 50 Museum special traps baited with peanut butter and rolled oat were set every 10 m on two parallel transects lines (100 m apart) and checked daily during 10 days following the protocol of Shank (1993). Traps were set within 1-2 m of each station, preferably near a lemming burrow if one was found within this radius. One trapping day was added when the number of misfired traps was greater than 25. The total number of trap nights was thus around 1000 at Site-1 and 500 at Site-2 each year. The following data were noted for each capture: date, trap station, and species.

Although no trapping was conducted in 1993, a quantitative estimate of lemming abundance is nonetheless available based on winter nest surveys, which were conducted at our study site in 1993 and 1996 (Olivier Gilg, pers. com.). The ratio winter nest /lemming abundance obtained in 1996 was applied to the nest survey data in 1993 to estimate lemming abundance that year. Both 1993 and 1996 were peak lemming years at our study site and thus data should be comparable. To obtain the species composition of the estimated abundance in 1993, we applied the average ratio of brown/collared lemmings observed in other peak years at our study site.

Statistical analyses

We calculated the number of individuals caught per 100 trap-nights (lemmings' index: N) by dividing the total number of lemmings trapped by the standardized total number of trap-nights (STN) over the whole period multiplied by 100, where STN = total number of trap-nights - [(number of lemmings caught + misfires) x 0.5]. We subtracted 0.5 night for each sprung trap to improve estimates of sampling effort (Beauvais and Buskirk 1999). Trapping data from the two plots were pooled at Site-1. Annual time-series data are presented in the form of N_1, N_2… N_T, where each N is the number of individuals caught per trapping effort in a particular year, and T is the total number of years for which we have such data. The level of synchrony for both species at each site was quantified with Spearman rank correlations (r_s) over the period 1994-2005 at Site-1 and 1997-2005 at Site-2.

We used spectral analyses to determine to which extent fluctuations in abundance were regular and to estimate their period. The spectral density function is a natural tool to examine the properties of periodic processes (Priestley 1981). This analysis was carried out with Proc SPECTRA (SAS Institute Inc. 1999). The Fisher's Kappa statistic (Fuller 1976) tests the null hypothesis of no cycle and the periodogram provides a graphic representation of the period in the times series. The spectral function uses Fourier transformations to describe the time series by transforming it into a sum of sine and cosine functions of different period lengths. It is then possible to use this sum to determine a frequency or range of frequencies in the periodogram that best describe the cyclic process present in the time series (Henttonen et al. 1985, Bjornstad et al. 1996, Ranta et al. 2006). The significance of the period detected was tested by adjusting the spectral density function to the datas taking into account the serial correlation between observations. This was done with the Proc MODEL (SAS Insititute Inc. 1999). We use Godfrey's statistic to test the assumption of independence of the data. In presence of non-independence of the data we added an autoregressive process of order one AR (1). The order of the process corresponds to the number of lags included in the model. The AR (1) allowed revising the model for the non-independence.

We also analysed each population for direct and delayed density dependence (Stenseth 1999). We used autoregressive modelling (Proc REG, maximum likelihood option; SAS Institute Inc. 1999) to explore the dynamic properties of our time series data. All series were logarithmically transformed with $X_t = \ln(N_t+C)$, where C is constant because of zero in some years. We used half of the smallest abundance estimate that could be obtained at each site; Site-1: 0.05 (1 lemming for 1000 night-traps), Site-2: 0.1 (1 lemming for 500 night-traps). A second-order log-linear autoregressive model was chosen on the basis of previous work (Turchin 1993, Bjornstad 1995, Stenseth 1999) and of the shortness of the time series (Erb et al. 2000). When defining the growth rate as $R_t = X_{t+1} - X_t$, the second-order autoregressive model takes the following form:

[1] $R_t = \beta_0 + \beta_1 X_t + \beta_2 X_{t-1}$

Or equivalently

[2] $X_t = \beta_0 + (1 + \beta_1) X_{t-1} + \beta_2 X_{t-2}$

where β_1 and β_2 are the first and second order autoregressive coefficients, respectively, and β_0 the intercept with no dynamic effects. β_1 is referred to as the direct annual density-dependence effect and β_2 the delayed annual density-dependence (Stenseth 1999). Hence, absence of direct annual density-dependence corresponds to $\beta_1 = 0$ whereas increasing level of it corresponds to β_1 being progressively more negative (i.e. $1 + \beta_1$ being progressively less than one; Bjornstad 1995).

RESULTS

Temporal variation in brown lemming abundance at Site-1 was indicative of cyclic variations with peak populations occurring in 1993, 1996, 2000 and 2004, i.e. at approximately 3 or 4-year intervals (Fig.1). Annual abundance ranged from 0 to 3.99 lemmings/100 trap-nights. Considering the resolution of our trapping index (i.e. 1 lemming for 1000 trap-nights), this indicates that annual abundance could vary by more than 40 times. Interestingly, the year of peak abundance always followed the year of lowest abundance since the previous peak. Thus, abundance appears to build up abruptly (i.e. within one year) whereas the decline, though rapid in the year following the peak, was not complete until at least two years after the peak, and was thus more gradual. At Site-2, where the time series was shorter (9 years) than at Site-1 (13 years), only one peak of abundance of brown lemmings was recorded. Though its amplitude was similar to Site-1, surprisingly, it occurred one year later (2001) than the corresponding peak in Site-1 (2000) (Fig. 1). The weak peak of 2004 at Site-1 was not detected at Site-2.

The population of collared lemmings at Site-1 tended to show a pattern different than brown lemmings (Fig. 1). Annual abundance ranged from 0 to 0.41 collared lemmings/100 trap-nights, indicating only a 4-fold variation in annual abundance. Overall, brown lemmings were about 5.8 times more abundant than collared at Site-1, though both species were generally equally scarce in years of low abundance. Collared lemmings were more abundant at Site-2 (abundance ranging from 0 to 1.08 lemmings/100 trap-nights), and, if we exclude the 2001 peak in brown lemmings abundance, they were 5.3 times more abundant than brown lemmings. Considering the resolution of our trapping index, annual abundance of collared lemmings showed an at least a 5-fold variation at Site-2 compared to a 19-fold variation for browns.

Both lemming species at Site-1 seemed to be synchronized in their fluctuations ($r_s = 0.67$, df = 11, $P = 0.02$). However, fluctuations were apparently less synchronized at Site-2 ($r_s = 0.40$, df = 8, $P = 0.28$), though the time series there was relatively short.

The periodogram of both species showed some peaks (Fig. 2) although the Fischer's Kappa tests were not significant, ($K= 2.42$ for brown lemmings and $K = 2.17$ for collared, both $P > 0.05$), possibly due to the shortness of the time series. We nonetheless examined how well the predictions derived from the Fourier functions fitted the observed data, correcting for the lack of independence detected (Godfrey's test LM = 8.26, $P = 0.02$ and LM = 5.30, $P = 0.07$ for brown and collared lemmings, respectively). For the brown lemmings, a first order Fourier function estimated a period of 1.87 ± 0.07 (SE) years, which corresponded to the first peak of the periodogram (Fig. 2), whereas a second order function estimated a period of 3.69 ± 0.04 years, which corresponded to the second peak. Observed data showed a much higher correlation with values predicted by the second order Fourier function ($r = 0.96$, df = 12, $p < 0.001$) than with those predicted by the first order function ($r = 0.63$, df = 12, $P = 0.02$; Fig. 2). For the collared lemmings, the first order Fourier function estimated a period of 3.87 ± 0.26 years whereas the second order function estimated a period of 3.92 ± 0.24 years, both of which apparently corresponding to the second peak of the periodogram (Fig. 2). It thus appears that the first peak in the periodogram of collared lemmings corresponded to noise in the data. Again, the observed data showed a higher correlation with values predicted by the second order Fourier function ($r = 0.86$, df = 12, $P = 0.002$) than with those predicted by the first order function ($r = 0.62$, df = 12, $P = 0.02$; Fig.3).

The estimates of coefficients for direct (β_1) and delayed annual density dependence (β_2) were negative for both species, as expected (Table 1). However, none of these were significant, possibly due to the shortness of our time series. When the values of these coefficients were positioned in the parameter space graph of Stenseth (1999), they fell in the portion of the graph characterising populations with proper multi-annual population cycle of periodicities between 3 and 4 years for both species, a result consistent with the previous analysis.

DISCUSSION

Our analysis supports the hypothesis that brown lemming populations showed typical fluctuations of large amplitude with a periodicity of 3 to 4 years as found in many other *Lemmus* populations (Krebs 1964, Pitelka 1973, Erlinge et al. 1999, Angerbjorn et al. 2001). The cycle was not symmetrical on either side of the peak as populations generally tended to have a rapid explosion of abundance lasting at most one year followed by a period of decline over one to three years. In contrast, evidence for population cycles was weaker in collared lemmings as their fluctuations were of much smaller amplitude than in the brown. Collared lemmings fluctuations appeared to be confined to relatively low densities unlike the dramatic fluctuations observed in the brown.

The differential pattern between the two species is intriguing, especially the absence of irruptions of large amplitude in the collared lemmings. Indeed, cyclic fluctuations of large amplitude have been reported in collared lemmings at many sites (e.g. Greenland, Gilg et al. 2003; Kent Peninsula, Canada, Wilson et al. 1999; Devon Island, Canada, Fuller et al. 1975), although at other sites their populations appear to be limited at low density with little cyclicity (Pearce Point, Canada, Reid et al. 1995). When both species occur in sympatry, others have also reported that population fluctuations tend to be of greater amplitude in the brown than the collared lemmings (Baker lake, Canada, Krebs 1964).

Interestingly, the predictions of the model proposed by Hanski and Henttonen (1996) to explain the dynamics of two competing vole species seem to fit with our observations on brown and collared lemmings. This model explains the dynamics of multispecies rodent assemblage in presence of predators. In their model, both species share the same predators but one (*Microtus*) is competitively superior and more vulnerable to predation than the other (*Clethrionomys*). Under these conditions, the model predicts multi-annual oscillations with a shift from dominance of the competitively superior species near the peak of the cycle to dominance of the competitively inferior species during the low phase of the cycle due to the higher vulnerability to predation of the former. In lemmings, patterns of habitat use have been found to be density-dependent, with brown lemmings excluding collared lemmings from some habitats at high density, presumably because they are superior competitors (Morris et al. 2000, Predavec and Krebs 2000). However, little information is available on relative vulnerability of the two species to predation.

Another factor that may promote greater fluctuations in brown lemmings is its higher potential for population growth (i.e. greater fecundity) than collared lemmings (Negus and Berger 1998). Although the mean litter size is generally the same in both species, there is a difference in the age at first reproduction, brown lemmings reaching maturity at a younger age than collared lemmings (Negus and Berger 1998). Collectively, these observations allow us to formulate a hypothesis to explain the difference in population dynamics of the two species at our study site. When populations start to increase due to low predator abundance, the brown lemming population may quickly outnumber the collared one due to a higher rate of population growth. Being a superior competitor, it could further limit the expansion of collared at high density and thus reach a much higher abundance. As predators build up due to the high prey abundance (Gilg et al. 2003), populations of both species may start to decline due to increased predation mortality in combination with density-dependent effects. During the low phase of the cycle, both species may be equally low or the competitively inferior species (collared lemmings) may even become relatively more abundant than its competitor if it is less vulnerable to predation (Hanski and Henttonen 1996). According to this scenario, the interaction between brown lemmings and predators would have a dominant impact on the dynamic, forcing synchronous oscillations in the collared lemmings due to shared predation.

Our observation that populations of brown and collared lemmings fluctuated in temporal synchrony at one site is consistent with this hypothesis. The apparent lack of synchrony at our second study site may be explained by the short time series available at Site-2. In northern Fennoscandia, synchrony between microtine species occupying the same habitat is well documented (Heikkila et al. 1994, Norrdahl and Korpimaki 1996, Angerbjorn et al. 2001, Huitu et al. 2004). Interactions with shared specialist predators have often been invoked as the causal factor behind interspecific synchrony in population fluctuations of small mammals (Erlinge et al. 1999, Norrdahl et al. 1996, Stenseth et al. 1993).

Many studies have suggested that population cycles of northern rodents are generated by combined effects of delayed and direct density dependence (Hanski et al. 2001, Klemola et al. 2003, Turchin 2003). If lemming abundance is controlled by a specialised trophic interaction of the type predator-prey, then delayed density dependence effects (i.e. second order process) should be detected (Stenseth 1999). Our auto-regressive model yielded negative second-order coefficients as expected, though they were not significant. Although specialised plant-herbivore interactions could also yield the same second-order effects, such interaction is unlikely in our system. Indeed, given that brown and collared lemmings eat different types of plants (Batzli and Jung 1980, Rodgers and Lewis 1986a), it seems doubtful that food depletion could impose synchrony in density fluctuations of both species.

Our data suggest some level of asynchrony in the pattern of population fluctuations between our two study sites separated by 30 km. Most notably, the 2000 peak in brown lemming abundance at Site-1 apparently occurred 1 year later at the Site-2. However, one should be cautious in concluding to a lack of spatial synchrony at the level of our two study sites. This conclusion is based on a single annual data point at each site and we cannot exclude the possibility that the actual peak in lemming density occurred before or after our annual mid-summer sampling. Hence, it is still possible that peaks in lemming abundance at our two study sites could have overlapped somewhat during winter 2000-2001 (i.e. the peak density at Site-2 may have been reached before the peak density at Site-1 started to decline). Spatial synchrony in lemming population fluctuations has previously been reported at a relatively large scale (i.e. several hundred kilometres; Erlinge et al. 1999, Krebs et al. 2002).

We conclude that brown lemming fluctuations observed at our study site were cyclical in nature and typical of cyclic small mammal populations, but evidence for the collared lemmings were equivocal. Both species nonetheless fluctuated in synchrony.

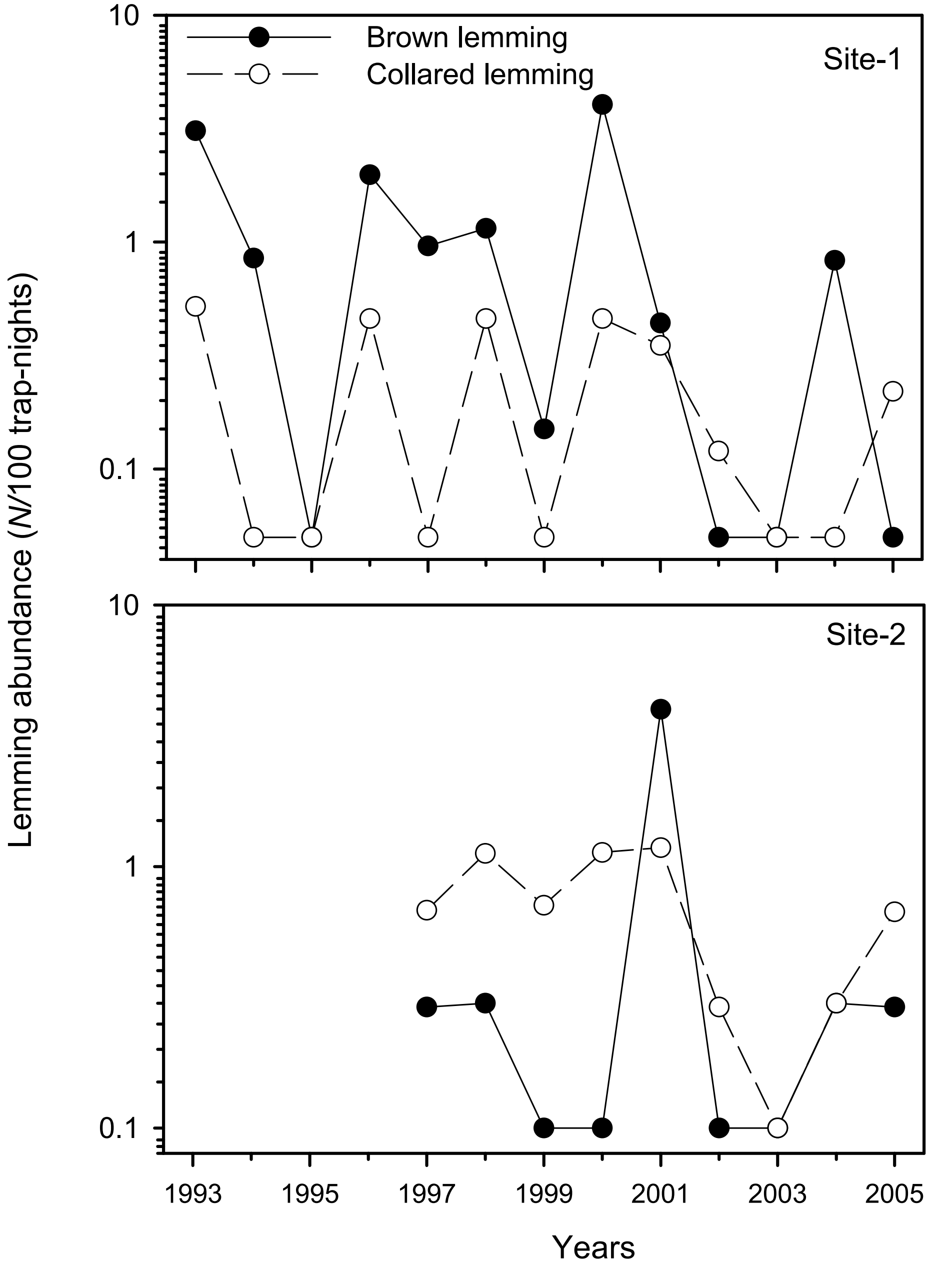

Figure 1. Fluctuation in abundance (*N*, in number of lemmings/100 trap-nights) of brown and collared lemmings at two sites on Bylot Island, Nunavut, Canada, over 13-year (Site-1) and 9-year (Site-2) periods. Because we used a log scale, when abundance was estimated at 0, we added a constant (*C* = 0.05 at Site-1 and 0.1 at Site-2) calculated as half the smallest number of lemmings that could be trapped (see methods).

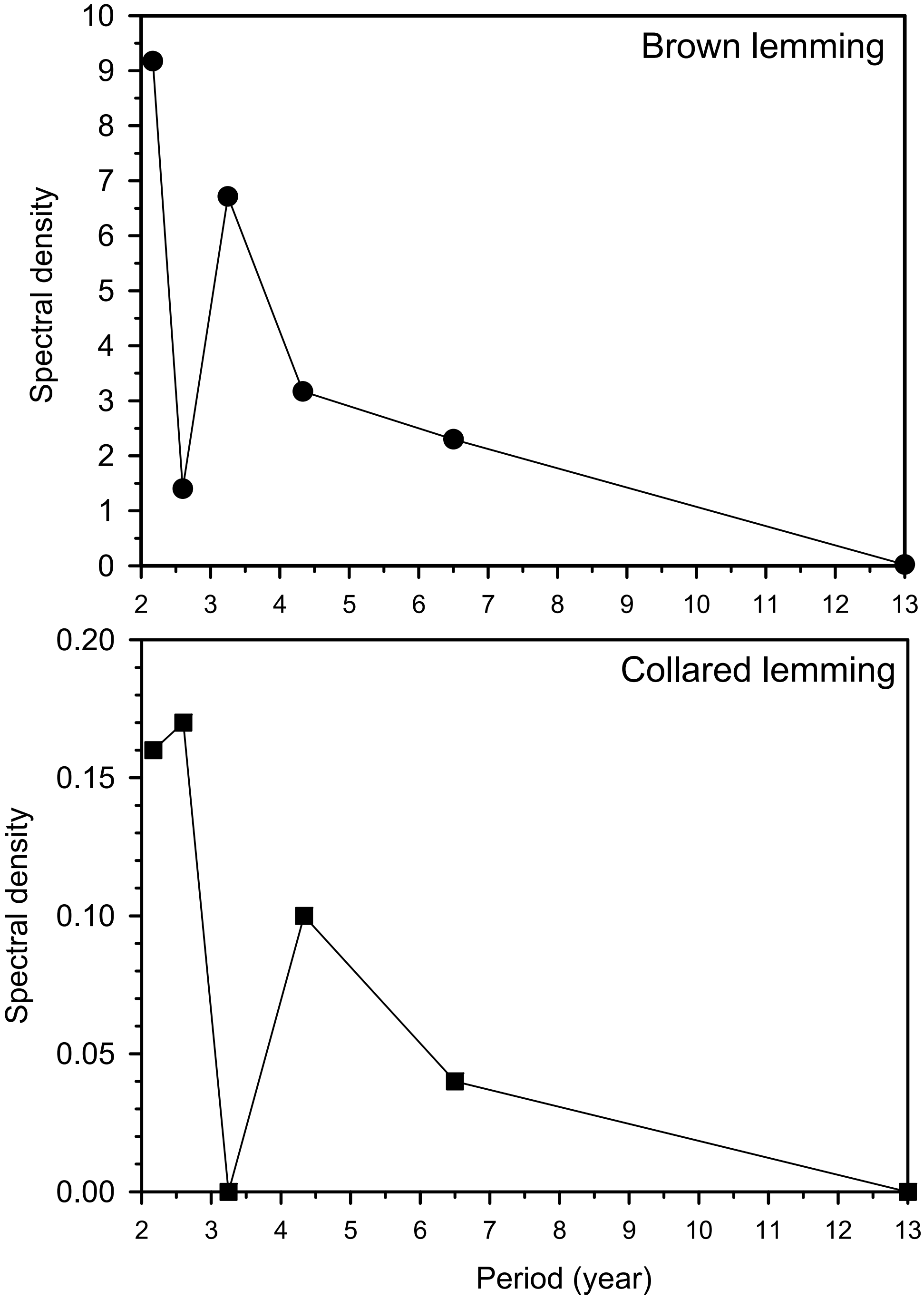

Figure 2. Spectral density of the time series obtained by Fourier transformations for brown and collared lemmings over a 13-year period at Site-1, Bylot Island, Nunavut, Canada.

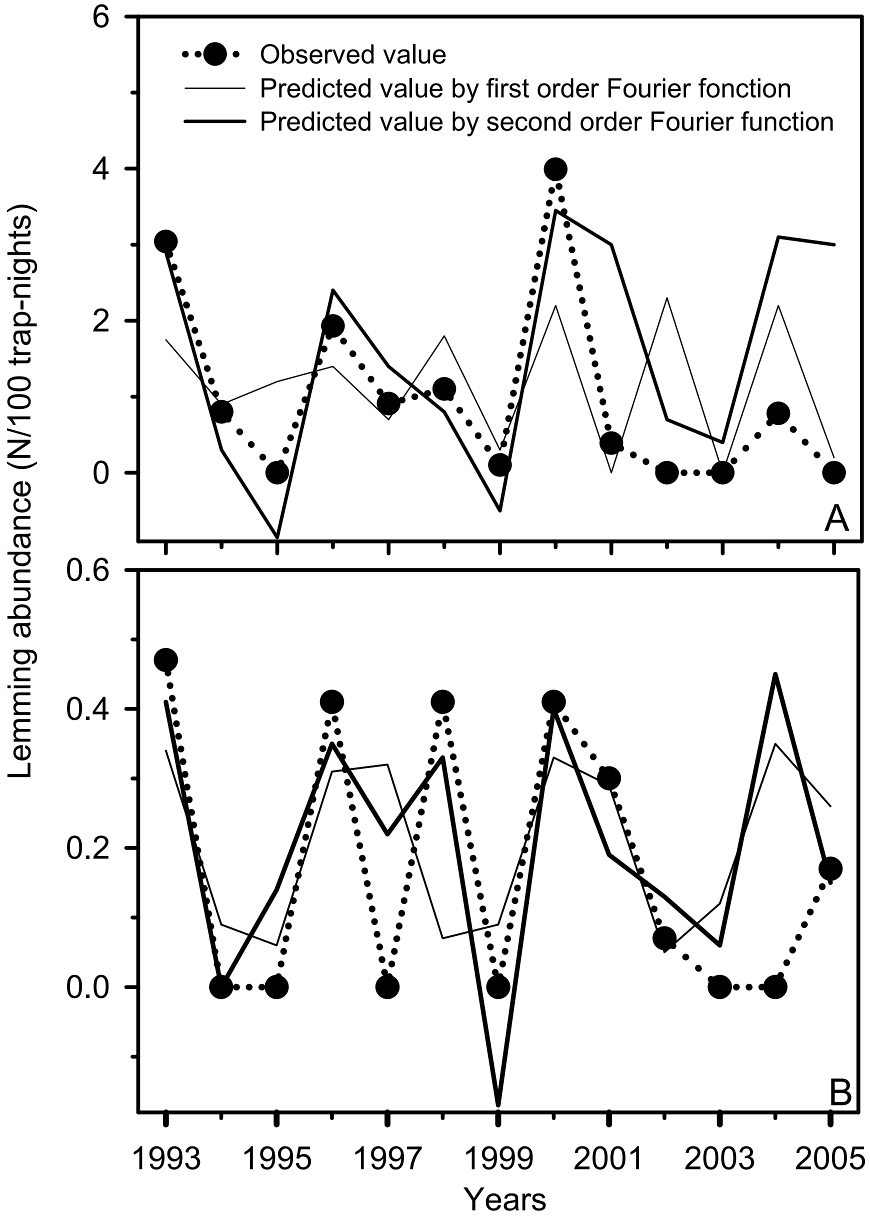

Figure 3. Time series of lemming abundance observed and predicted by first and second order Fourier functions for brown and collared lemmings at Site-1, Bylot Island, Nunavut, Canada, over 13 years.

Table 1 Estimates of autoregressive coefficients (± SE) and their level of significance for brown and collared lemmings over a 13-year period at Site-1, Bylot Island, Nunavut, Canada. Coefficient β_1 is the direct density dependence effect, β_2 the delayed-density dependent effect, and β_0 the intercept (see methods).

	β_{1-1}	β_2	β_0
Brown lemming $R^2 = 0.06$	- 0.22 ± 0.36	- 0.13 ± 0.34	- 1.06 ± 0.55
P	0.56	0.71	0.09
Collared lemming $R^2 = 0.11$	- 0.35 ±0.35	- 0.10 ±0.33	- 2.34 ± 0.93
P	0.35	0.76	0.04
Both species pooled $R^2 = 0.09$	- 0.26 ± 0.34	- 0.19 ± 0.32	- 0.82 ±0.48
P	0.48	0.57	0.12

CHAPITRE 2

<u>DEMOGRAPHY OF TWO LEMMING SPECIES (*LEMMUS SIBERICUS* AND *DICROSTONYX GROENLANDICUS*) ON BYLOT ISLAND, NUNAVUT, CANADA</u>

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RÉSUMÉ

Les lemmings occupent une place primordiale dans le réseau trophique arctique et leurs fluctuations d'abondance ont un effet sur d'autres composantes de l'écosystème. Nous avons comparé la démographie de deux espèces sympatriques, le lemming brun (*Lemmus sibericus*) et le lemming variable (*Dicrostonyx groenlandicus*), au cours de deux étés à l'Île Bylot, Nunavut, Canada. Nous avons réalisé du trappage vivant sur deux grilles afin d'estimer les variations saisonnières et annuelles de l'abondance, de l'activité reproductrice et de la survie, et nous avons mesuré la taille des domaines vitaux par radiotélémétrie. Notre échantillonnage était basé sur le design robuste et nous avons aussi utilisé des modèles de population fermée afin d'estimer l'abondance (avec les logiciels CAPTURE, MARK et DENSITY). Des modèles de population ouverte ont été appliqués pour estimer la survie. Nous avons trouvé que les densités estimées par CAPTURE et MARK étaient similaires mais légèrement plus faible que celles obtenues par DENSITY. La densité du lemming brun a décliné entre les deux années (de 2.43 ind/ha en 2004 à 0.45 ind/ha en 2005) alors que celle du lemming variable est restée constante (de 0.43 ind/ha en 2004 vs 0.47 ind/ha en 2005). Pour le lemming brun, 2004 peut être considérée comme une année de pic et 2005 comme une phase de déclin d'abondance. L'abondance des lemmings bruns adultes a décru au cours de l'été, alors que celle des juvéniles a généralement augmenté. Le recrutement des lemmings bruns juvéniles dans la population a été moins important lors de la phase de déclin par rapport à celle de pic mais n'a pas différé entre les deux années pour le lemming variable. La proportion des juvéniles dans la population a augmenté au cours de l'été pour les deux espèces. Le taux de survie a été plus faible durant l'année de pic que lors de l'année de déclin suivante et la survie des mâles adultes a été moindre que celle des femelles adultes et des juvéniles. La masse corporelle des lemmings bruns a été plus importante lors du pic par rapport à l'année de déclin, mais cette différence interannuelle n'a pas été retrouvée chez le lemming variable. La taille du domaine vital des mâles a été plus grande que celle des femelles mais aucune différence entre les deux espèces n'a été détectée. Nos résultats laissent penser en une plus grande variabilité de la démographie et de la densité chez le lemming brun que chez le lemming variable.

ABSTRACT

Lemmings play a key role in the tundra food web and their cyclic oscillations in abundance may have a strong effect on other components of this ecosystem. We compared the demography of two sympatric species, the brown lemming (*Lemmus sibiricus*) and the collared lemming (*Dicrostonyx groenlandicus*), over two summers on Bylot Island, Nunavut, Canada, a high Arctic site. We live-trapped lemmings on two grids to estimate seasonal and annual variations in abundance, reproductive activity, and survival, and we radio-tracked some individuals to estimate their home range size. Our sampling was based on the robust design and we used different capture-recapture models for closed populations to estimate abundance (with software CAPTURE, MARK and DENSITY). We used open-population models to estimate survival. We found that density estimates derived from CAPTURE, MARK and DENSITY were generally similar. The density of brown lemmings declined markedly between the two years (from 2.43 ind/ha in 2004 to 0.45 ind/ha in 2005) while that of collared lemmings was relatively constant (0.43 ind/ha in 2004 vs 0.47 ind/ha in 2005). For brown lemmings, 2004 appeared to be a peak year in their cycle and 2005 a decline phase. Abundance of adult brown lemmings declined throughout the summer whereas that of juveniles generally increased. The recruitment of juvenile brown lemmings in the population was lower in the decline than in the peak phase, but did not differ between years in the collared. The proportion of juveniles in the population increased seasonally in both species. Survival rates were lower during the peak year than in the following year, and were also lower in adult males than in adult females or juveniles in one year. Body mass of brown lemmings was higher in the peak year than in the declining year but not in collared lemmings. Home ranges were larger for males than for females, but did not differ between species. Globally, our results suggest that the demography and density of brown lemmings are more variable than those of collared lemmings at our study site.

INTRODUCTION

Cyclic fluctuations of large amplitude have been reported for a long time in small mammal populations (Elton 1924, Krebs et al. 1973, 1995). These fluctuations are usually characterized by a regular periodicity between successive density peaks but can be of highly variable amplitude, and are most prevalent in northern species (Stenseth et al. 1993, Stenseth 1999, Angerbjorn et al. 2001). However, cyclic fluctuations can vary in space or time within a given species (Stenseth 1999, Angerbjorn et al. 2001). Lemmings (genus *Lemmus* and *Dicrostonyx*) inhabit the tundra and are widespread throughout the Arctic. Lemming populations typically reach peak densities every 3 to 4 years (Elton 1924, Krebs et al. 1995, Turchin and Berryman 2000) and, because they are at the base of the tundra food-chain, their population fluctuations have considerable impact on the whole food web (Krebs et al. 2003, Gauthier et al. 2004, Ims and Fuglei 2005). The cause of cyclic fluctuations in lemmings and other small mammals is a lasting enigma and a source of controversy (Chitty 1996). Although there is a growing consensus that cycles may result from specialised trophic interactions, some argue that they are driven by lack of food (i.e. bottom-up forces, Turchin et al. 2000, Turchin and Batzli 2001, Turchin and Hanski 2001) whereas others advocate that predation by specialised predators drives the cycles (top-down forces, Reid et al. 1995, Hanski et al. 2001, Gilg et al. 2003, 2006, Krebs et al. 2003).

Some believe that progress in our understanding of the cause of population cycles in small mammals has been hindered by the fact that many studies have focused only on the dynamic patterns (e.g. occurrence or not of multiannual cycles and their shape; the density paradigm) rather than on the underlying demographic mechanisms (Krebs 2002). Population fluctuations are the results of basic demographic processes, such as survival, birth, emigration, and immigration, but we know relatively little of how demographic parameters vary during a cyclic phase (i.e. seasonally) or between phases (i.e. between years).

Lemmings mature early, have large litters, breed frequently, and have a short life span (Millar 2001). Early-born young mature and reproduce during their first summer and, in some species, reproduction starts during late winter, when snow cover reduces predation risk (Korpimaki et al. 2004). Predation is the main source of lemming mortality (Reid et al.

1995, Wilson et al. 1999, Gilg 2002, Korpimaki et al. 2003, 2004), and can be sufficient in some cases to prevent summer population growth and limit populations. In small mammals, life-history traits such as survival, reproduction and body mass are typically higher during the increase and peak years than during the decline phase, but this may result both from intraspecific density-dependent effects and predation (Chitty 1996, Wilson et al. 1999, Gilg 2002, Klemola et al. 2002, Norrdahl and Korpimaki 2002, Korpimaki et al. 2004).

Detailed demographic data on lemming populations in North America are mostly limited to studies in coastal areas of the Western Arctic (e.g. Krebs et al. 1995, Reid et al. 1995), with relatively few studies conducted in the Canadian Arctic islands (Fuller et al. 1975, Negus and Berger 1998). In this study, we analysed the demography of the brown (*Lemmus sibiricus*) and collared lemmings (*Dicrostonyx groenlandicus*) over a 2-year period at a high Arctic site, Bylot Island, Nunavut. Though sympatric, these two species are ecologically separated at the local level (Rodgers and Lewis 1986b, Stenseth et al. 1993).

Robust estimation of abundances and demographic parameters of secretive species like lemmings requires methods based on the recapture of marked animals (Williams et al. 2002). Estimation of abundance is traditionally done using closed population estimators, which can then be converted into density estimates using appropriate information on movements of animals (Williams et al. 2002, Parmenter et al. 2003). However, Efford (2004) recently proposed a new method to estimate density directly from capture-recapture data using spatial detection function (Efford 2004, Efford et al. 2005). Demographic parameters such as survival are traditionally estimated with capture-recapture methods for open populations although the robust design, which combines both open and closed populations methods, may allow for more robust estimation of such parameters (Kendall et al. 1997, Williams et al. 2002).

Our objectives were to (1) compare estimates of lemming density obtained with traditional models for closed populations with those obtained with Efford’s (2004) method, (2) examine seasonal variations in abundance, reproduction and survival of two sympatric lemming species during the summer and (3) compare reproduction and survival of these two species between different phases of their population cycle. We predicted that abundance, reproduction and survival decreased during the summer due to high predation rate, and that reproduction and survival were lower in the decline phase than in the peak phase of the cycle.

METHODS

Study species

The distribution of collared lemmings extends to the northernmost arctic islands whereas that of brown lemmings stops in the mid-Arctic (in the eastern Canadian Arctic, Bylot Island is the northern limit of its geographical range; Banfield 1974, Golley et al. 1975). Brown lemmings are found primarily in wet meadows of tundra lowlands whereas collared lemmings are mostly associated with upland dry heaths (Rodgers and Lewis 1986a, Stenseth et al. 1993). Brown lemmings eat graminoids during the summer and a mixture of graminoids and mosses in winter whereas collared lemmings feed on dicotyledons such as evergreen shrubs, herbs and forbs year round (Batzli and Jung 1980, Rodgers and Lewis 1986a). Demography also tends to differ between the two species. Generally, population fluctuations are of greater magnitude in the brown than in the collared lemmings (Stenseth et al. 1993), and the breeding season of collared lemmings generally starts earlier than that of the brown (Stenseth et al. 1993, Negus and Berger 1998).

Study area

Field work was carried out on the south plain of Bylot Island, Sirmilik National Park, Nunavut, Canada (73°N, 80°W) in the summers of 2004 and 2005. The landscape in the area is a mixture of wetlands in lowland areas, mesic tundra in both lowlands and hilly areas, and, at higher elevation, xeric tundra (Gauthier et al. 1996). Plant communities of mesic tundra are dominated by shrubs (e.g. *Salix arctica*, *Cassiope tetragona*, and *Vaccinium uliginosum*), grasses (e.g. *Arctagrostis latifolia*, *Alopecurus borealis*, and *Poa arctica*) and forbs (e.g. *Dryas integrifolia*, *Stellaria longipes*, *Oxytropis maydelliana* and *Oxyria digyna*) (Duclos 2002). In wetlands, graminoids are the most abundant plants (e.g. *Dupontia fisheri, Eriophorum scheuchzeri* and *Carex aquatilis*; Gauthier et al. 1996).

Trapping protocol

We trapped lemmings on two grids of 7.3 ha (270×270 m) located 1800 m apart, one in wet meadow habitat (wet grid) and one in mesic habitat (mesic grid; Annex 1). Trapping stations were at grid intersections every 30-m, for a total of 100 per grid. Within 15 m of each station, we set a Longworth® live-trap at a suitable trapping site such as active burrows or runways showing signs of recent use when possible. Trap positions were noted to the nearest meter. Traps were left on site throughout the summer (though not in winter) and were blocked open between trapping sessions. During trapping sessions, traps were constantly provided with clean and dry bedding material (fibre fill) and baited with apple quarters (Wilson et al. 1999). Apple baits do not affect body mass of trapped small mammals (Unangest and Wunder 2002).

We marked animals with electronic PIT tags (Gibbons and Andrews 2004) that were read with a 1002 AVID® mini tracker reader (www.avidcanada.com). Every time an animal was captured, we noted the date, time, trapping station, species, sex, and reproductive condition (females only). We weighed animals with a Pesola® spring scale (± 0.5 g). Females were considered reproductive when they had developed teats.

Our trapping schedule followed the robust design of Kendall et al. (1997), which requires two sampling periods. Primary periods were separated by ~14-day intervals without trapping. We had 3 primary periods in 2004 and 4 in 2005 (the first period is missing in 2004 because we arrived too late at the site). Each primary period had secondary sampling periods that consisted of 5 (in 2004) or 4 (in 2005) consecutive days of trapping. Even though traps were checked twice a day (or more often during adverse weather conditions), data were pooled on a daily basis (i.e. an individual captured twice on the same day counted for a single recapture on that day). Due to manpower limitation, each grid was trapped sequentially rather than simultaneously (Table 1).

Age determination

We categorized each individual captured as juvenile or adult according to its body mass when first caught. Brown lemmings weighing <33g and collared lemmings <40g were classified as juveniles, and those above these thresholds as adults (Stenseth et al. 1993).

Because eye lenses grow continuously through life, we also used their mass to estimate age of individuals (Ostbye and Semb-Johansson 1970, Mallory et al. 1981, Hansson 1983, Erlinge et al. 1999). We determined eye lens mass in brown lemmings from a sample of individuals that died accidentally or were obtained from a concurrent study using snap-traps (insufficient dead collared lemmings were available for such determination). We removed the eye lens of freshly dead individuals, fixed it in a formalin solution (4%) for one week, and then transferred it to 70% alcohol. In the laboratory, lenses were dried and weighed to the nearest 0.0001g, and age was determined using the equation $\ln(a) = 2.1 \ln(m) + 2.7$ where a represents the age in days and m the combined dry mass of both eye lenses (Erlinge et al. 1999). This allowed us to determine the relationship between whole body mass (M in g) and estimated age (a in day) among our sample of dead individuals. This relationship ($a = 0.26*M^{1.75}$, $R^2 = 0.81$, $n = 16$, $p < 0.0001$) was then used to estimate the age of all live lemmings based on body mass at first capture (Annex 2). We used this estimated age to determine the calendar-season of birth of all captured individuals (Ostbye and Semb-Johansson 1970, Erlinge et al. 1999).

Home range estimation

Converting abundance estimates into population density requires information on animal movements (Williams et al. 2002). Distance between recapture sites of the same individuals can provide such information (see below, under “Density estimations”). However, to verify if this information was reliable, we estimated home ranges of lemmings with radio-telemetry. We used Biotrack® radio collars weighing ca 1.6 g (Model Pip-2 with Ag392 cell) and no lemming received a radio representing more than 5% of its mass. Radios were fixed around the neck with replaceable cable-ties. Such transmitters do not seem to adversely influence survival, movement and reproduction during the summer (Reid et al. 1995). Lemmings were trapped with Longworth® and Sherman® live-traps between the primary sampling periods of our trapping protocol (Table 1). Traps were baited as previously described and set near active burrows or runways in similar habitats (i.e. wet meadow and mesic tundra) but not inside the trapping grids in order to avoid the additional stress of multiple captures on radio-tagged lemmings. The radio signal was detected at 70 m or more and exact position (± 1m) was recorded by homing on the signal using Lotek SRX_400 receivers. Animals were located 3 times daily following the recommendations of Agrell (1995) and we searched extensively for animals that could not be located. After about 10 days of tracking, lemmings were caught again and radio collars were recovered.

We calculated individual home ranges with the 95% minimum convex polygon (MCP) method, excluding the 5% outermost locations to reduce overestimation (White and Garrott 1990, Schmidt et al. 2002). We used only individuals for which we had enough data points based on the relationships between home range size and number of locations (Annex 3). We performed home-range analyses using the Animal Movement software Arcgis 9. We compared home ranges between species, sex, and habitat (wet meadow vs. mesic tundra) by means of *t*-test.

Analyses of trapping data

The estimation of abundance with closed capture models assumes that there is no birth, death, or migration so that the population size is constant over the trapping period. The assumption that the population is closed is usually valid for data collected over a relatively short period of time (a few days). Estimation of abundance, however, is sensitive to variations in probability of capture and thus we used the models proposed by Otis et al (1978) to test for these sources of variation. The four basic models considered are M_t, which allows capture probabilities to vary by time, M_b, which allows behavioural responses to capture (i.e. trap-happiness or trap-shyness), M_h, which allows heterogeneous capture probabilities, and M_0 without any variation. Various combinations of these three sources of variation in capture probabilities (i.e., models M_{tb}, M_{th}, M_{bh} and M_{tbh}) were also considered. We selected the most appropriate model for our data with the Akaike's information criterion (AIC; Burnham and Anderson 1998). We used the software CAPTURE (Otis et al. 1978) to adjust these models separately to each 4 or 5-day trapping session.

The robust design model combines the Cormack-Jolly-Seber (CJS) model for open populations with models for closed populations (Kendall et al. 1995, 1997). Closed population models are applied to secondary sampling periods whereas open ones are applied to primary periods. We used the robust design model implemented in program MARK 4.2 (White and Burnham 1999). Closed population models in the robust design are similar to those in CAPTURE except that the heterogeneity model is a simplified one (Pledger 2000). The CJS model in the robust design allows the estimation of the probability of survival (ϕ_i) between all primary periods i, as well as the probability of emigration from the trapping grid area (γ''_i) and the probability of staying away from the trapping area given that the animal has already left (γ'_i) (Kendall et al. 1997). Reduced models constraining parameters in either closed population or CJS models (e.g. models assuming no emigration, $\gamma'' = \gamma' = 0$) can be implemented. The most appropriate model for the data was also selected based on the AIC. If an animal died in a trap, his capture history was censored (which means that his capture history was used until time of death).

Trapping data on each grid usually consisted of individuals from the two species, both sexes, and young and adults. However, data was often too sparse to test for all these effects on capture probabilities, ϕ and γ. In the wet grid in 2004, only brown lemmings were captured and sample sizes were sufficiently large to examine both age and sex effects. In the mesic grid in 2004 and both grids in 2005, both species were captured; in these cases, species and age effects were modeled though not sex due to sample size limitation. When age, sex or species (*spp*) effects were included in open models, they were indicated by subscripts. In the case of closed capture models (*M*), these effects appeared in superscripts and always applied to the probability of capture. For instance, model $M_{tb}^{spp*age}$ would indicate that probability of capture changed over time, differed between newly-marked individuals (p) and previously marked ones (c; i.e. behavioural effect), and differed between species and age classes. Population size (N) was estimated for each species and age class separately, though sexes were pooled due to data sparseness.

As goodness-of-fit tests specific to the robust design do not exist, we only tested the fit of the CJS model to the data between primary periods in each year and grid using the program U-CARE (Choquet et al. 2005).

Density estimation

Because population density can be more easily compared among study sites than raw abundance, we converted our abundance estimates in density (*D*), defined as the number of animals (*N*) per unit area (*A*), $D = N/A$. However, since we can trap individuals whose home range mostly lies outside our trapping grid, we need to determine the spatial extent of the trappable population (i.e. the "effective trapping area"). The size of the effective sampling area is usually derived by adding to the grid area a boundary strip of width *W* around the grid from which some animals can come. We estimated the size of this boundary strip as half of the mean maximum distance moved by individuals trapped twice or more, excluding 0 values (i.e. individuals always recaptured in the same trap) as recommended by Williams et al. (2002). We calculated standard error of estimates using the delta method (Williams et al. 2002).

The method recently developed by Efford (Efford 2004, Efford et al. 2004, 2005) allows an estimation of density by fitting a simple spatial model directly to the animal trapping data. Thus, it does not require the determination of an effective trapping area using arbitrary criteria. Here is a brief summary of this method. During a closed-population sampling session, each animal is assumed to occupy a home range centered on an unknown location, whereas each trap is set at a known location. Considering only one animal and one trap, the probability of capture is a declining function of distance *d* between the range centre and the trap, directly analogous to a detection function $g(d)$ in distance analysis. The trap locations define an individual-based model of the capture process with parameters (D, g_0, σ), where σ is the spatial scale over which capture probability declines. The mean distance between recaptures of marked individuals (d) contains information on the scale of movements (σ), and information on D and g_0 is contained in conventional capture-recapture statistics (summarised as estimates of population size N and capture probability p). Simulated trapped samples with varying but known D, g_0 and σ are then generated and the statistics calculated from these samples (N, p, d) matched to those of the field data. For these estimations, we used the program DENSITY 3.2 (Efford et al. 2004) and we selected the best model for our data with the AIC.

For each trapping session (i.e. primary sampling periods), we thus obtained 3 density estimates (sometimes less due to sparse data) using different methods (from CAPTURE, the MARK robust design, and DENSITY). We used the reduced major axis regression (Sokal and Rohlf 1995) to compare these independent estimates because both were measured with errors. We estimated confidence intervals of parameters by bootstrapping and randomization tests.

Other data analyses

We compared the reproductive activity and distribution of birth dates between years and time periods with contingency tables (χ^2 tests). When sample size was too small at some time periods, we pooled data with adjacent time periods. As an index of reproductive activity, we used the proportion of lactating females among all captured females for each trapping session and the proportion of juveniles among all captured individuals. We compared mean adult body mass of each species between years with *t* tests. Finally, we examined the effects of species, age and sex on movements (i.e. the maximum distance moved by individuals trapped twice or more) using factorial ANOVA.

RESULTS

Model selection and comparison of methods

We captured 126 brown lemmings and 23 collared lemmings on our trapping grids in 2004, and 28 and 26 in 2005, respectively. In 2004, open-population models fitted well the data for both the wet and mesic grids (Global test: χ^2 = 2.60, df =3, p= 0.46 and χ^2 = 17.3, df = 13, p= 0.18, respectively), whereas in 2005 the test was not possible due to sparse data.

Preferred models for closed populations in MARK included both behavioural trap response and time variation on the capture probability in 2004, or no variation in 2005 when sample size were much smaller (Table 2). No effect of age or species on probability of capture was detected. In CAPTURE, the preferred model in 2005 was also model M_0 at all time periods, though with an age effect on probability of capture at period 2 and a species effect on the wet grid at period 4 (Annex 4). In 2004, preferred models differed more between periods.

On the wet grid, model M_t was preferred at period 1 and model M_b at periods 2 and 3, whereas in the mesic grid, model M_0 was preferred at period 1 and model M_b at periods 2 and 3, with a species effect on probability of capture at periods 1 and 2. Preferred models in DENSITY and CAPTURE were the same in 92% of the cases.

Despite differences in the models selected, closed population density estimates obtained in CAPTURE or in MARK were very similar (mean difference: -0.06 ± 0.02 (SE) n = 31). The slope of the relationship between pairs of estimates differed slightly from 1.0 (1.09, 95% CI: 1.02 - 1.27) but the intercept did not differ from 0 (0.003, 95%CI: -0.07 – 0.04, Fig. 1), indicating that CAPTURE estimates were slightly higher than those of MARK at large population size. Density estimates obtained with Efford' DENSITY were also well correlated with those obtained with either CAPTURE or MARK. The slopes of the relationships between DENSITY and CAPTURE or MARK estimates did not differed from 1.0 (1.09, 95%CI: 0.89 - 1.46; and 1.18, 95%CI: 0.92 – 1.80, respectively), and intercepts did not differ from 0 (-0.04, 95%CI: -0.26 – 0.08; and -0.03, 95%CI: -0.39 – 0.12). The mean difference between DENSITY and CAPTURE or MARK estimates was 0.05 ± 0.08 (SE) and 0.12 ± 0.10 n = 19, respectively, indicating that Efford's method gave similar population density estimates.

For the presentation of results, we used abundance estimates obtained with CAPTURE, except in 13 % of the cases where the CAPTURE algorithm did not converge properly and failed to provide an estimate (we then used estimates from MARK).

Population density

Density of brown lemmings was much higher in 2004 than in 2005 (Fig. 2). In the wet grid, mean brown lemming densities were 1.20 adults/ha and 1.53 juveniles/ha in 2004 compared to 0.20 and 0.13, respectively, in 2005. In the mesic grid, densities were 0.99 adults/ha and 1.14 juveniles/ha in 2004 compared to 0.50 and 0.08 in 2005. In contrast, density of collared lemmings varied much less between years (Fig. 2). On the wet meadow grid, surprisingly, almost no collared lemmings was trapped in 2004 whereas densities were 0.09 adults/ha and 0.22 juveniles/ha in 2005. On the mesic grid, collared lemmings densities were 0.34 adults/ha and 0.53 juveniles/ha in 2004 compared to 0.17 and 0.26, respectively, in 2005.

In both years, density of adult brown lemmings generally declined throughout the summer (Fig. 2). The only exception was in the mesic grid in 2005 where density increased at the last sampling occasion, from late July to mid-August. In 2004, density of juveniles in the wet grid increased considerably during the summer, a trend opposite to adults. In the mesic grid, juvenile density initially decreased but then stabilised or increased slightly in late summer. Juvenile density remained very low on both grids in 2005. For collared lemmings, adult density did not show clear trends throughout the summer (Fig. 2). Density of juveniles was often high shortly after snow-melt (e.g. mid-June 2005), decreased in mid-summer, and increased in late summer.

Reproductive activity

In brown lemmings, the proportion of lactating females tended to be higher in early than in late summer ($\chi^2 = 3.57$, df = 1, p = 0.06 Fig. 3), and higher in 2005 than 2004 ($\chi^2 = 3.94$, df = 1, p = 0.05). No significant effects were found in collared lemmings due to small sample sizes but proportion of lactating females tended to be higher in late than in early summer and higher in 2005 than 2004. The proportion of juveniles in the brown lemmings population increased throughout the summer ($\chi^2 = 31.6$, df = 3, $p < 0.001$) and was higher in 2004 (0.54) than in 2005 (0.29) ($\chi^2 = 24.0$, df = 1, $p < 0.001$). In collared lemmings, the proportion of juveniles was high in late summer and variable earlier ($\chi^2 = 20.5$, df = 3, $p < 0.001$), and similar between the 2 years ($\chi^2 = 0.64$, df = 1, p = 0.42) (Fig. 3).

The distribution of birth dates of brown lemmings captured in summer 2005 showed a decaying pattern over time, with the highest number of individuals being born in the current summer and the lowest in the previous summer (Fig. 4). This pattern is expected because the longer the time interval since birth, the lower the proportion of individuals surviving. Nonetheless, a surprisingly large number of individuals were estimated to be born during the previous winter. However, this pattern was drastically different in 2005 as, among individuals captured that summer, a higher proportion was born in the previous spring or winter than in the current summer (interaction year × time period: $\chi^2 = 8.68$, df = 3, p = 0.03).

Survival rates

Preferred models for open populations in MARK had an emigration rate fixed at 0 and no time, species, age, or sex effects on survival, except for the wet grid in 2004 (Table 2). In the latter case, survival rate of adult male brown lemmings was much lower than the one of adult females and juveniles in the wet grid (Fig. 5). In the wet grid, the survival rate of brown lemmings was similar in both years except for males, which was lower in 2004 than in 2005. However, in the mesic grid, the survival rate was much higher in 2005 than in 2004. When the two species were present in the same grid, their survival rate was found to be similar.

Body mass

The body mass of adult brown lemmings decreased by 12% between 2004 and 2005 (48.5 ± 1.3 (SE) vs 42.9 ± 2.3, respectively; $t = 2.08$, df = 80, $p < 0.05$). However there was no difference in average mass of adult collared lemmings (54.7 ± 2.8 g in 2004 vs 52.0 ± 2.8 in 2005; $t = 0.68$, df = 20, p = 0.50).

Home range

In 2005, 4 collared and 3 brown lemmings were fitted with radio collars. Among those, 4 were adult males (3 collared and 1 brown), and 3 were adult females (1 collared and 2 brown). Home range size determination was based on an average of 37.7 locations per individual (range: 21 to 46). Home range of collared lemmings (14.2 ± 4.0 (SE) ha) were on average twice the size as those of brown (7.5 ± 3.5 ha) but the difference was not significant ($t = 1.19$, df = 5, p = 0.29). The home ranges of males were larger than those of females (16.0 ± 2.7 ha vs. 5.1 ± 3.1 ha; $t = 2.66$, df = 5, p = 0.045). No difference was found between grids ($t = 0.04$, df = 5, p = 0.97).

Movement

In brown lemmings, maximum distance moved between capture locations did not differ between juveniles and adults (*F* = 0.23, df = 1, 63, p = 0.63), between sexes (*F* = 0.13, df = 1, 63, p = 0.72), and between years (*F* = 0.87, df =1, 63, p = 0.35; all interactions p > 0.53; Table 3). The mean maximum distance moved by brown lemmings was 81.8 ± 7.7 m. In collared lemmings, maximum distance moved also did not differ between juveniles and adults (*F* = 0.01, df =1, 6, p = 0.91), years (*F* = 0.94, df = 1, 6, p = 0.37) and sexes (*F* = 1.29, df =1, 6, p = 0.30, despite a trend for longer movements by males than females, (Table 3; all interactions, p > 0.54). The mean maximum distance moved by collared lemmings was 104.7 ± 7.6 m. Using these values, we estimated the effective area of the trapping grid at 12.2 ± 3.2 ha for brown lemmings and 13.8 ± 5.4 ha for collared lemmings.

DISCUSSION

Comparison of methods

Properly estimating population density with capture-recapture data is not a trivial task, and it is prone to several biases (Parmenter et al. 2003). In our study, we compared 3 different methods of density estimation: closed capture estimates implemented in CAPTURE and the MARK robust design, and Efford's DENSITY method. The similarity in the density estimates between CAPTURE and MARK is not surprising as both used the same basic models for estimating abundance (Kendall et al. 1997). However, CAPTURE is slightly more flexible because, unlike MARK, it allows selection of different models for each trapping session, which may explain some of the differences observed between the two methods. In 2005, the models selected were the simplest ones (model M_0) and did not include any temporal or/and behavioural effects on capture probabilities, presumably because sample size was too small to detect such effects.

Density estimates obtained with Efford's method were on average similar to those obtained with closed population models. Efford's method has the advantage of not requiring the estimation of a somewhat arbitrary effective trapping area (Efford 2004). Effective trapping area critically depends on the width of the boundary strip area. In our calculations, we used the mean maximum distance moved by individuals trapped twice or more divided by two as traditionnally used (Williams et al. 2002). However, Parmenter et al. (2003) suggested that not dividing this value by two may provide a better estimate of the boundary strip area. If we followed the latter recommendation, density estimates obtained with Efford's method were then 32 to 53% higher than those obtained with closed population models. We found that Efford's method required larger sample sizes as for several of our datasets it failed to converge on an estimate when CAPTURE or MARK did. Therefore, although our estimates based on traditional close capture methods may be biased by the size of the effective trapping area used, they have the advantage of being readily comparable to other studies using similar methods. Our analysis nonetheless suggests that Efford's method provides an interesting alternative to previous ones and should deserve consideration in future studies when sample sizes are sufficiently large.

Temporal and spatial variations in abundance

The density of brown lemmings differed markedly between the two years (density in 2004 was 6.2 times higher than in 2005 on average) whereas the density of collared lemmings was lower and similar between the two years (1.1 times higher in 2004 than in 2005 on the mesic grid). Thus, in 2005 the brown lemming population had declined to densities similar to those of collared lemmings. These changes in density between the two years are corroborated by long-term snap-trap data collected at our site (Chapter 1). This long term monitoring indicated that 2004 was a year of peak lemming abundance and 2005 a year of decline. This long term data set also indicated that brown lemmings are more abundant than collared lemmings and they show stronger oscillations, a pattern similar to the one reported by Krebs (1964) at Baker Lake, Nunavut, Canada. However, this pattern may not be ubiquitous because at other sites in Nunavut, collared lemmings are apparently more abundant than brown lemmings (Rodgers and Lewis 1986b, Wilson et al. 1999).

The pattern of abundance of each species in each grid is consistent with their known habitat and food preferences. Brown lemmings prefer wet meadows dominated by graminoids and mosses, whereas collared lemmings use mainly mesic tundra dominated by shrubs (Batzli and Jung 1980, Rodgers and Lewis 1986a, b, Stenseth et al. 1993). However, these basic patterns of habitat use may be modified by changes in the availability of preferred foods and by intra- and inter-specific interactions. Indeed, the brown lemmings is apparently a superior competitor than the collared lemmings and direct and indirect competition may occur in the use of runways and burrows in years when brown lemming is very abundant (Wilson et al. 1999, Morris et al. 2000, Predavec and Krebs 2000). This could explain why in 2004, when brown lemmings were most abundant in wet meadows, their preferred habitat, collared lemmings were totally absent from this habitat but were present in mesic tundra. In contrast, the decline in abundance of brown lemmings in 2005 may have allowed collared to move into areas normally used by browns, and thus explain their presence in both habitats that year (Rodgers and Lewis 1986a). Therefore, competitive interactions may be important in explaining patterns of habitat use by these two species. However, we must remain cautious with this conclusion because we only sampled one grid in each habitat, and thus we lack spatial replicates.

Comparing lemming densities across studies is difficult because trapping and analytical methods often differ. Nonetheless, our density estimates (average annual density, brown: 0.45 to 2.43 ind/ha, collared: 0.43 to 0.47) appear comparatively low for both species. For instance, in northern Greenland the density of collared lemmings (estimated in good habitats) ranged from <0.1 ind/ha to 11 ind/ha (Gilg 2002). Similarly, densities at Kent Peninsula, Nunavut ranged from 0.1 to 16 ind /ha (Blackburn et al. 1998, Wilson et al. 1999; values based on robust estimators in this case). However, at Pearce Point, NWT, collared lemmings densities remained constantly low (<3 ind/ha; Krebs et al. 1995, Reid et al 1995). In Atkasook (Alaska) where the two species are found in sympatry, densities averaged 0.3 to 1.4 ind/ha for each species, reaching a low of 0.1 ind/ha for collared lemmings and a high of 2.2 ind/ha for brown lemmings (Batzli 1980), a pattern similar to our study. Also, densities of brown lemmings ranging from <1 to >100 ind/ha have been reported in other studies from Alaska (Barrow; Pitelka 1973). However, the majority of studies of brown lemmings estimate an index of abundance instead of density (Stenseth et al. 1993). In the eastern Canadian Arctic, Bylot Island is the northern limit of geographical range for brown lemmings (Banfield 1974, Golley et al. 1975, Rodgers and Lewis 1986a), which may partly explain our observed low densities.

Summer declines in lemming densities are common and suggest that mortality (mostly due to predation), exceed recruitment during the summer (Wilson et al. 1999, Gilg 2002, Korpimaki et al. 2004). The absence of protective snow cover and the high abundance of predators (such as migratory birds) may explain higher predation rate in summer than in winter. We observed a decline in abundance through summer of brown lemmings but not collared lemmings. This could occur if the effect of predation differs between the two species. Angerbjorn et al. (1999) reported that Arctic foxes, a major lemming predator, act as a resident specialist predator for brown lemmings, and as generalist for collared lemmings. Under such condition, the density of collared lemmings was low and stable, whereas the population of brown lemmings showed oscillations (Turchin and Hanski 1997)

Variations in demographic traits

The higher proportion of individuals estimated to be born during the summer and juveniles captured in 2004 compared to 2005 suggest that recruitment of young brown lemmings was higher during the peak than the decline year. Poor recruitment and high predation rates are often reported to be the proximate causes of the summers declines (Gilg 2002b). A reduction in recruitment of young can be consequence of a fall in reproductive activity (Erlinge et al. 2000) and/or a reduced early survival of juveniles (i.e. before they can be caught; Krebs 1964). Because the proportion of lactating females tended to be higher during the decline years of 2005 than during the peak years of 2004, reduced early survival of juveniles may be the main reason for reduced recruitment in 2005.In contrast, reproductive parameters of collared lemmings did not change between the two years. The apparent constant reproductive activity fits with the low variation in abundance observed between 2004 and 2005. Collared lemmings are well known for reproducing under the snow in late winter (Krebs et al. 1995, Millard 2001), which could explain the relatively high proportion of juveniles observed early summer, soon after snow-melt, in comparison to brown lemmings. The estimated age of brown lemmings captured during summer nonetheless shows that many of them were born the previous winter, suggesting a significant winter activity in that species as well. The low proportion of juvenile brown lemmings captured in early summer is not incompatible with the previous conclusion because flooding of wetlands, their preferred habitat, during snow-melt would presumably interrupt their breeding activity in spring (Rodgers and Lewis 1986b). The increasing proportion of young recruiting in the population over the summer suggests that after snow-melt reproductive activity either resumed (in brown lemmings) or increased (collared lemming). The high proportion of collared lemming females still lactating in late summer in comparison to browns further suggests that the reproduction of the former species may extend later in summer (Negus and Berger 1998).

Our survival analyses have low power due to insufficient sample. The only emerging pattern was a lower survival of adult male brown lemmings compared to adult females and juveniles in the wet grid in 2004 (when sample sizes were largest). This difference may be explained by a greater exposure of males to predators. Males typically are active in summer as they search for reproductive females (Banks et al. 1975, Stenseth et al. 1993, Predavec and Krebs 2000). Consistent with this pattern, we found trough radio-tracking of adult brown lemmings that males had a larger home range than females.

Generally, survival rate of brown lemmings on the mesic grid were lower during the peak year (2004) than in the following year when density had declined, and also for males in the wet grid. Typically, survival rates of small mammals are higher in the peak phase than in the decline phase (Krebs 1964, Wilson et al. 1999), in contrast to our results. The relatively low survival observed in 2004 could explain why the annual population index obtained by snap-traps in late summer was low compared to previous peaks (Chapter 1). It is possible that the lemming population peaked earlier in spring or even in late winter under the snow (i.e. before we started trapping) and thus had already entered the declining phase during the summer. The strong decline of adult brown lemmings during the summer 2004 is consistent with this hypothesis. Finally, one has to remember that even though open-population models control for the probability of detection, they do not control for permanent emigration, which is confounded with mortality, and hence we can only estimate an apparent survival rate.

The decrease in body mass observed in brown lemmings between 2004 and 2005 may indicate a shift in individual quality. This did not occur in the collared lemmings. Again, this pattern is consistent with the change of abundance that we observed between years in the two species. In strongly fluctuating populations, individuals reach maximum size during peak abundance, apparently because animals born into rapidly expanding populations have high growth rates (Krebs et al. 1973, Stenseth et al. 1993, Chitty 1996). Conversely, animals born during declining populations grow more slowly, and usually fail to reach large sizes. (Mallory et al. 1981, Stenseth et al. 1993, Norrdahl et al. 2004)

Movement and home range

In small mammals, males typically have a larger home range than females (Banks et al. 1975, Predavec and Krebs 2000), a pattern that we also found despite small sample size. This pattern is associated with the polygamous mating systems of many small mammals such as lemmings (Banks et al. 1975, Rodgers and Lewis 1986b, Predavec and Krebs 2000, Schmidt et al. 2002). During the reproduction, males range widely searching for females whereas movements of the latter are restricted to a small area, especially in lactating females. This sex-difference was not detected in our estimates of maximum distance moved by individuals on our trapping grid, possibly because the latter measure is a coarser measure of movements than radio-tracking. This forced us to use the same mean distance moved for both sexes, which may be a source of heterogeneity in our estimates of density.

Although our live-trapping estimates of maximum distance moved were comparable to those obtained in other studies (Blackburn et al. 1988, Predavec and Krebs 2000), our estimates of home range size obtained by radio-telemetry were large compared to other studies (Rodgers and Lewis 1986, Schmidt et al 2002). For instance, in Igloolik Island (Nunavut), the home range of collared and brown lemmings (estimated by the mean maximum movement of all animals) ranged for 2.8 ±0.7 ha and 3.1 ±0.6 ha for brown and collared lemmings, respectively (Rodgers and Lewis 1986b). Similarly, home range at Kent Peninsula (Nunavut; estimated by radio telemetry) ranged from 2.4 ±1.3 ha for male and 3.5 ± 2.6 ha for female collared lemmings (Predavec and Krebs 2000). Comparing lemming home range across studies is difficult because measurement can be sensitive to habitat quality, the phase of the cycle (Gilg 2002), the number of relocations and the method used. For some individuals, we noticed an abrupt increase in home range size due to long-distance movements after a relatively large number of localisations (e.g. 25). This suggests a seasonal shift in the home range of some individuals, which may have lead to an over estimation of the home range size (Rodgers and Lewis 1986b). However, we must remain cautious in our interpretation because we only tracked 7 lemmings over periods not exceeding 2 weeks.

Conclusion

Our study revealed annual and seasonal differences in demographic parameters of lemmings. Overall, our results suggest that between the peak year of 2004 and the declining years of 2005, adult survival may have been the first parameter to decline, followed by a fall in juvenile recruitment, possibly due to a reduced early juvenile survival rather than a reduced reproduced activity. Both phenomenons presumably contributed to the decline of the population during that period. Abundance of adults declined during the summer whereas recruitment of juveniles into the population increased. Finally, fluctuations in demographic parameters were generally more pronounced in brown than in collared lemmings.

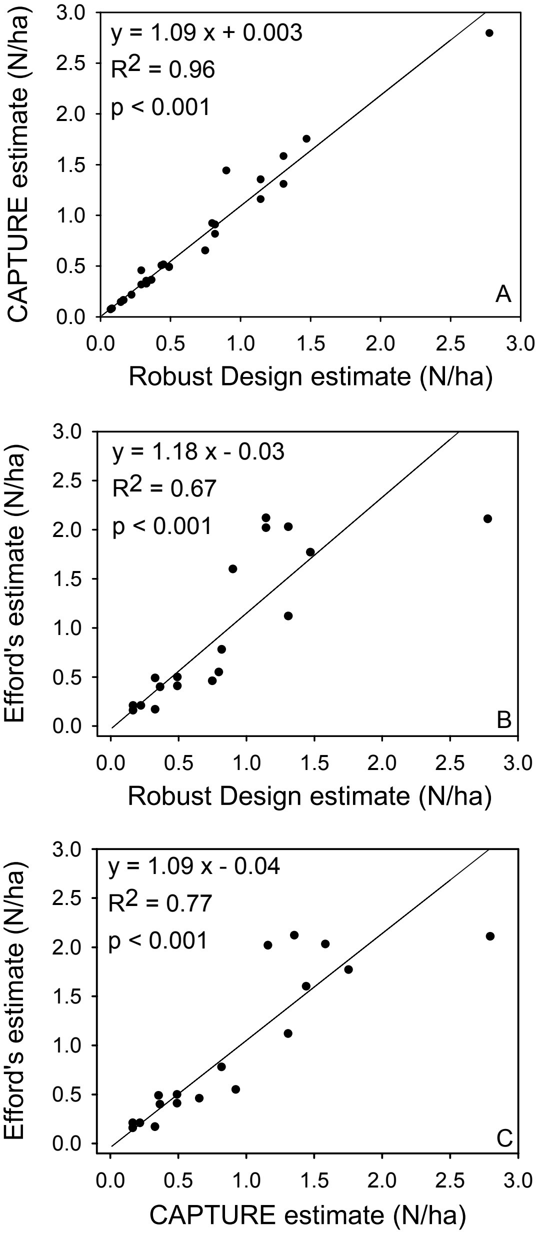

Figure 1. Relationship between density estimates (N/ha) obtained by various methods: closed population in CAPTURE vs closed population in the robust design in MARK (A), Efford's DENSITY vs closed population in the robust design in MARK (B), Efford's DENSITY vs closed population in CAPTURE (C). Each data point is an independent estimate for a unique combination of trapping grid, sampling period, species and age group. The regression line and associated parameters are the reduced major axis regression.

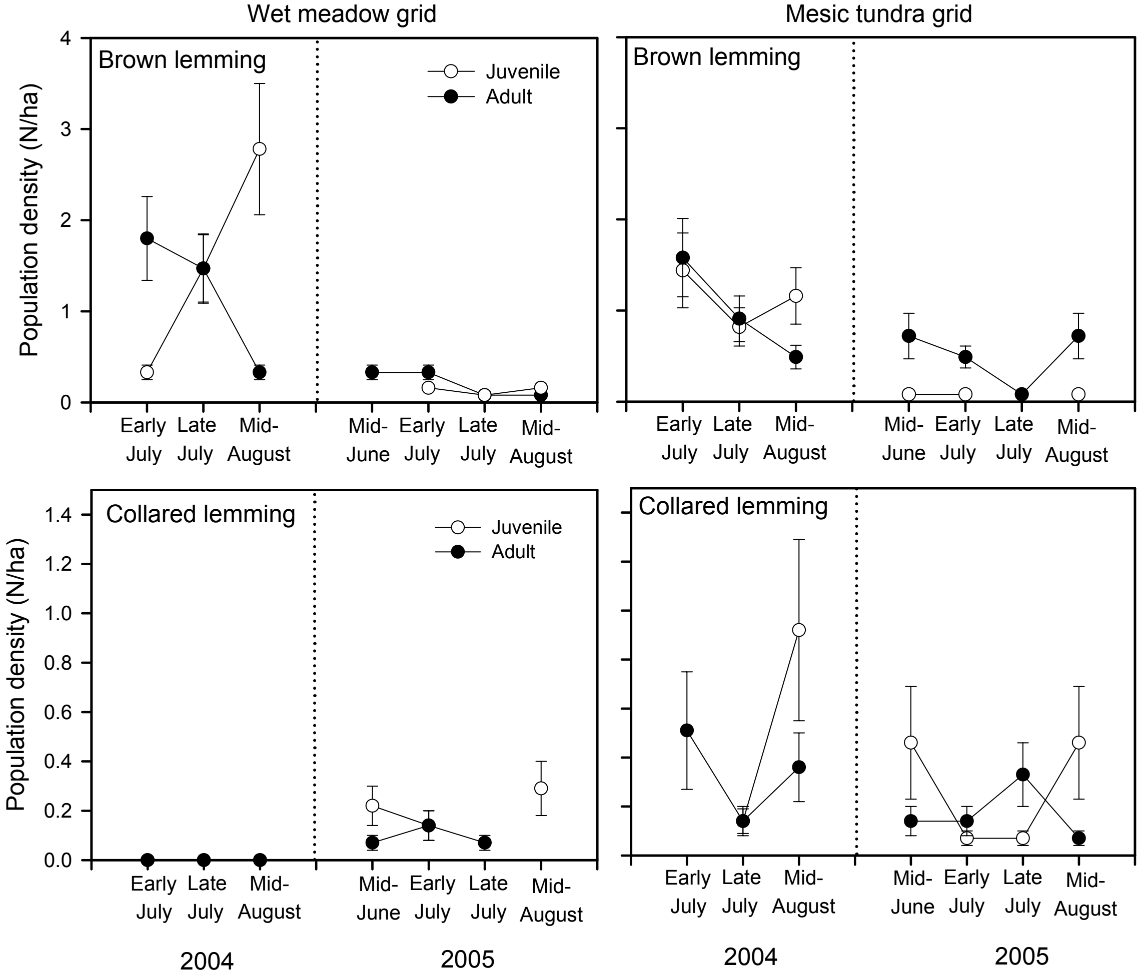

Figure 2. Population density estimates (± SE) of juvenile and adult brown and collared lemmings in different periods of the summer in two trapping grids (wet meadow and mesic tundra) on Bylot Island, 2004 and 2005. The dotted vertical line separates years.

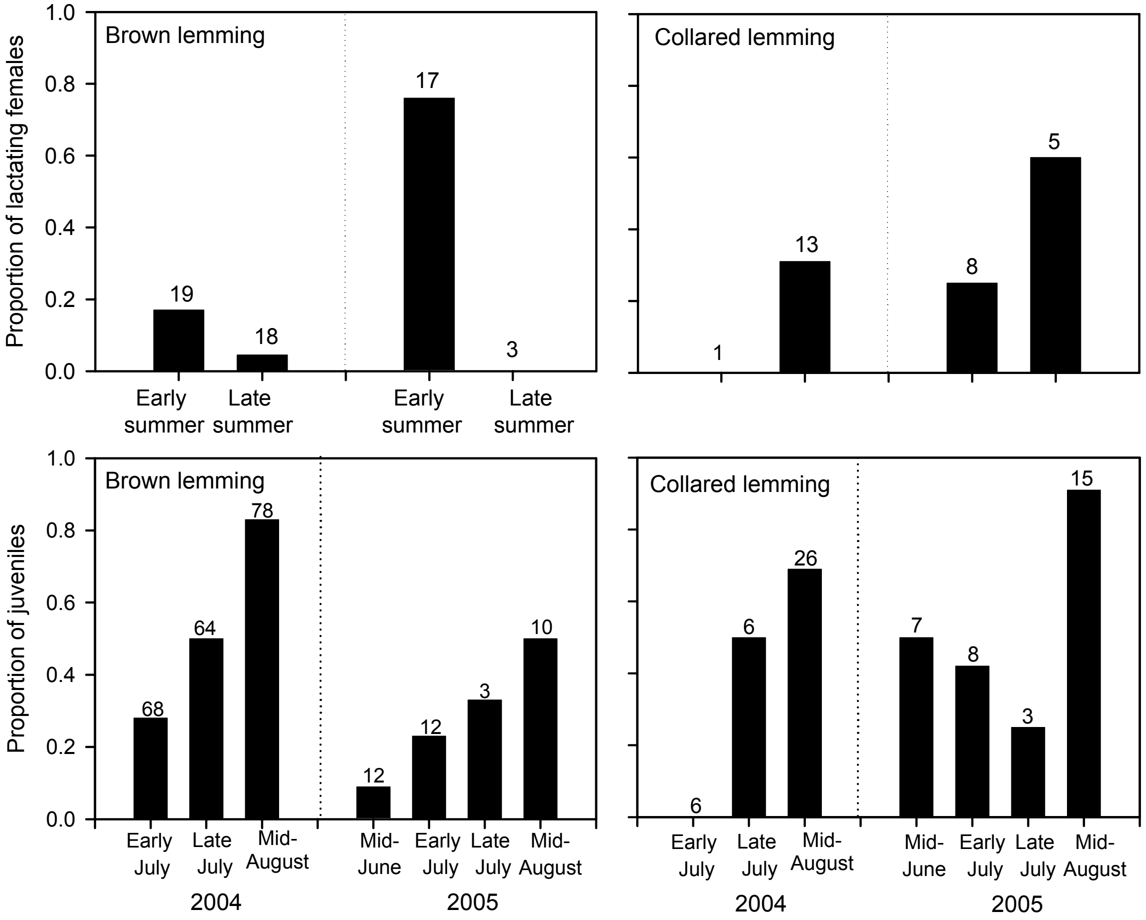

Figure 3. Proportion of lactating females among adult females and proportion of juveniles among all individuals trapped in brown and collared lemmings at different periods of the summer on Bylot Island, 2004 and 2005. Numbers above bars indicate sample size. The dotted vertical line separates years.

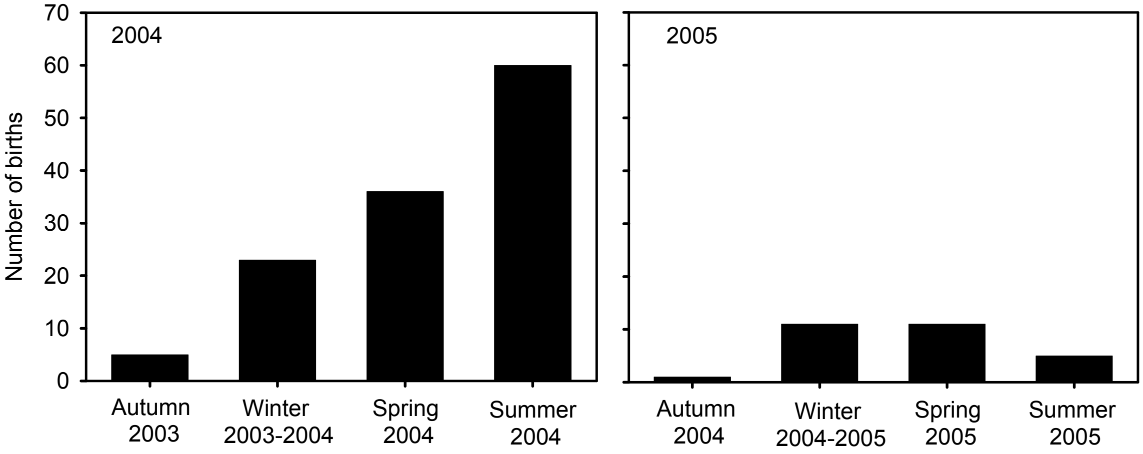

Figure 4. Distribution of inferred birth season of brown lemmings captured during summers 2004 and 2005 on Bylot Island based on a relationship between body mass at capture and age determined with eye lens on a sample of dead individuals (see methods).

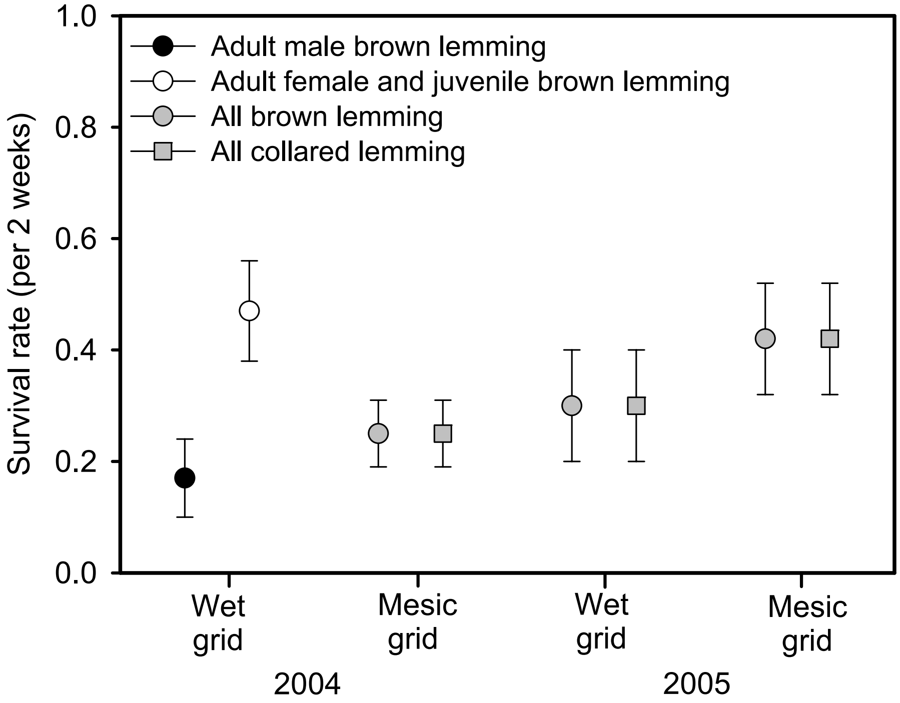

Figure 5. Robust Design estimates (±SE) of survival rate (per 2 weeks) of brown and collared lemmings on two trapping grids (wet and mesic grids) on Bylot Island, 2004 and 2005.

Table 1. Calendar of lemming live trapping on two grids using the Robust Design (see methods), and of radio telemetry for lemming home range estimation on Bylot Island, Nunavut, Canada.

Year	Primary period	Dates of secondary periods		Radio telemetry
		Mesic tundra grid	Wet meadow grid	
2004	II	2 - 7 July	8 - 13 July	-
2004	III	22 - 27 July	27 July - 1 August	-
2004	IV	11 - 16 August	16 - 21 August	-
2005	I	22 - 26 June	17 - 21 June	26 June - 5 July
2005	II	10 - 14 July	5 - 9 July	14 - 24 July
2005	III	29 July - 2 August	24 - 28 July	2 - 12 August
2005	IV	17 - 21 August	12 - 16 August	-

Table 2 Model selection in MARK for the robust design applied to the live-trapping data of brown and collared lemming on two trapping grids on Bylot Island, 2004 and 2005. For each model, we present the ΔAIC statistic (differences in AIC between the current and the best model), the AIC weights (ω), the number of estimated parameters (np) and the deviance. For closed population models (*M*), effects apply only to the probability of capture.

Model		Δ AICc	ω AICc	np	Deviance
Wet meadow grid 2004					
M_{tb}	$\Phi^{m},\Phi^{f, juv}, \gamma = 0$	0.00	0.70	31	121.97
M_{tb}	$\Phi^{m}\ \Phi^{f}\ \Phi^{juv}, \gamma = 0$	2.37	0.21	32	121.70
M_{tb}	$\Phi, \gamma = 0$	4.07	0.09	30	128.67
Wet meadow grid 2005					
M_0	$\Phi , \gamma = 0$	0.00	0.99	19	94.05
M_0	$\Phi^{br\text{-}juv,\ br\text{-}ad,\ col\text{-}ad}, \Phi^{col\text{-}juv}, \gamma = 0$	10.05	0.01	20	92.22
Mesic tundra grid 2004					
M_{tb}	$\Phi , \gamma = 0$	0.00	0.96	22	207.42
M_{tb}	$\Phi^{spp*age}, \gamma = 0$	6.48	0.04	25	205.72
Mesic tundra grid 2005					
M_0	$\Phi , \gamma = 0$	0.00	0.70	18	115.93
M_0^{age}	$\Phi , \gamma = 0$	3.18	0.14	19	114.65
M_0^{spp}	$\Phi , \gamma = 0$	4.35	0.08	19	115.82
M_0^{age}	$\Phi^{age}, \gamma = 0$	4.86	0.06	20	111.63
M_0^{spp}	$\Phi^{spp}, \gamma =0$	8.72	0.01	20	115.49

Model notation: ϕ = survival, γ = emigration; *t* = time, *b* = behavioural effect, 0 = no effect, *spp* = species effect, *m* = male, *f* = female, *juv* = juvenile, *ad* = adults, *br* = brown lemming, *col* = collared lemming, * = interaction.

Table 3. Mean (± SE) maximum distance moved (m) by individuals trapped twice or more for male and female brown and collared lemmings on two trapping grids on Bylot Island, 2004 and 2005. Sample sizes are shown in parentheses.

	2004		2005		All years and grids
	Wet grid	Mesic grid	Wet grid	Mesic grid	
Brown lemming					
Female	81.2 ± 13.5 *(8)*	76.6 ± 21.8 *(5)*	89.5 ± 8.9 *(2)*	78.9 ± 23.5 *(4)*	81.4 ± 8.2 *(19)*
Male	78.0 ± 8.3 *(32)*	78.1 ± 15.4 *(13)*	83.5 ± 15.1 *(4)*	131.9 ± 33.8 *(4)*	82.2 ± 7.1 *(52)*
Collared lemming					
Female	-	60.3 ± 13.1 *(3)*	-	46.6 ± 23.6 *(2)*	54.8 ± 11.0 *(5)*
Male	-	164.9 ± 47.1 *(4)*	165.2 ± 1.6 *(2)*	48.6 ± 7.0 *(2)*	135.9 ± 29.0 *(8)*

* (- : no data)

CONCLUSION GÉNÉRALE

Importance de l’étude dans la connaissance de l’écosystème arctique

Dans mon mémoire, j’ai voulu approfondir les connaissances sur deux espèces de lemmings, le lemming brun (*Lemmus sibericus*) et le lemming variable (*Dicrostonyx groelandicus*), vivant en sympatrie à l’Île Bylot, Nunavut, Canada. Les lemmings occupent une place centrale dans le réseau trophique arctique et leurs fluctuations d’abondance caractéristiques ont un effet sur l’écosystème tout entier. À notre site d’étude, les effets des fluctuations d’abondance des lemmings se font principalement ressentir sur les espèces de prédateurs, notamment au niveau de leurs succès reproducteurs, mais aussi sur d’autres espèces d’herbivores telles que la grande oie des neiges (*Chen caerulescens atlantica* ; Bêty et al. 2002, Gauthier et al. 2004). C’est pourquoi la compréhension des cycles, des variations démographiques et de la densité de chacune de ces deux espèces de lemming est nécessaire.

Dans le premier chapitre, j’ai utilisé les données à long terme de trappage mortel (de 1993 à 2005) afin d’avoir une vue d’ensemble sur les fluctuations interannuelles d’abondance des deux espèces. Puis, dans le deuxième chapitre, j’ai utilisé une approche de capture-marquage-recapture afin de connaître les variations annuelles (entre deux phases différentes du cycle) et saisonnières de la démographie et de la densité pour chacune des espèces. Ainsi, je désirais améliorer nos connaissances sur la dynamique des populations des deux espèces de lemming présentes à l’Île Bylot afin de participer à l’effort global de compréhension de cet écosystème arctique.

Implications des résultats

L’analyse des données à long terme nous a permis de mettre en évidence l’existence de fluctuations d’abondance régulières caractéristiques des petits rongeurs nordiques (les cycles) tels que les lemmings. Toutefois, ces fluctuations étaient différentes entre les deux espèces de lemming au site d’étude. En effet, le lemming brun a présenté des fluctuations d’abondance dont l’amplitude était très grande et caractéristique des populations cycliques. Les différentes phases d’abondance (pic, déclin et creux) se sont succédées à intervalle de temps régulier, périodiquement tous les 3-4 ans. Par contre, pour le lemming variable, l’amplitude des variations d’abondance était beaucoup moins marquée et ne suivait pas exactement le modèle de cyclicité des rongeurs nordiques. Notre hypothèse supporte nos observations pour le lemming brun mais seulement de manière partielle pour le lemming variable. Malgré cela, les deux espèces fluctuaient de manière synchrone dans le temps, ce qui appui une autre de nos hypothèses. Par contre, la synchronie des fluctuations entre les deux sites d'études, distant de 30 km, était relativement faible. Il a toutefois été difficile d'établir si cette absence apparente de synchronie spatiale dans les fluctuations était réelle ou était un artefact de la faible résolution temporelle de notre méthode de piégeage.

On a également remarqué une différence majeure d'abondance entre ces deux espèces, le lemming brun étant beaucoup plus abondant que le lemming variable, sauf durant la phase du creux d'abondance. Le modèle théorique développé par Hanski et al. (1996) a semblé s'ajuster à nos données. Ce modèle repose sur l'existence d'une compétition interspécifique entre les deux espèces, laquelle pourrait expliquer la différence d'abondance et de cyclicité entre les deux espèces. Cette compétition se ferait probablement au niveau de l'occupation de l'habitat et plus particulièrement dans l'utilisation des terriers, les régimes alimentaires des deux espèces étant différents. Toutefois, d'autres facteurs pourraient intervenir pour expliquer cette différence d'abondance, comme le plus haut taux de reproduction du lemming brun (Negus and Berger 1998).

Un aspect important de ce chapitre fut l'utilisation d'analyses spectrales et des transformations de la série temporelle en série de Fourier afin d'établir l'existence de cycles et de déterminer la période exacte du cycle de chacune des deux espèces. Les analyses spectrales demandent des séries temporelles assez longues afin de distinguer la présence d'un signal cyclique d'un bruit de fond. Notre série était à la limite pour pouvoir appliquer ces analyses. Toutefois, les analyses spectrales nous ont permis de générer des modèles prédictifs de cyclicité, modèles qui se sont avérés s'ajuster remarquablement bien avec nos données. De plus, les analyses spectrales ont non seulement permis de déterminer la périodicité des fluctuations, mais aussi de mettre en évidence des effets dépendants de la densité caractéristiques des populations de rongeurs nordiques cycliques, un indice de l'importance des interactions trophiques.

Après cette vue globale des variations interannuelles d'abondance, nous nous sommes intéressés à une échelle plus fine. Nous avons voulu mettre en évidence les variations annuelles et saisonnières de la démographie et de la densité, et ce, au cours de deux périodes estivales (2004 et 2005). Dans un premier temps, nous avons remarqué que la densité du lemming brun différait fortement entre ces deux années. L'année 2004, caractérisée par une densité élevée, a été considérée comme une année de pic, alors que l'année 2005, caractérisé par des densités plus faibles, a été considérée comme une année de déclin. Par contre, pour le lemming variable, la densité est restée basse et relativement constante entre ces deux années.

Pour le lemming brun, la population des individus adultes lors de la phase de pic a chuté au cours de l'été, alors que celle des juvéniles a augmenté. Ceci a suggéré une mortalité importante des adultes durant l'été, probablement à cause du nombre élevé de prédateurs durant cette période. Toutefois, après l'interruption causée par la fonte de la neige, nos résultats suggéraient un fort taux de reproduction pendant l'été, la proportion de juvéniles et de femelles lactantes augmentant alors dans la population, ce qui a supporté notre hypothèse initiale. Ainsi, la densité totale est restée élevée et relativement constante durant la période estivale de l'année du pic. Cependant, lors de la phase de déclin, le recrutement des juvéniles dans la population est apparu faible et insuffisant pour compenser la diminution de la population des adultes causée par la prédation confirmant ainsi une autre de nos hypothèses. Une baisse de survie adulte qui s'amorcerait dès que le pic est atteint pourrait contribuer à l'amorce du déclin, tel que suggéré au chapitre 2. La chute du recrutement des juvéniles dans la population a été responsable de la diminution de la densité lors de la phase de déclin. La démographie et la densité du lemming brun ont donc varié fortement entre les deux phases du cycle. Par contre, pour le lemming variable, les différences dans la démographie et la densité entre 2004 et 2005 ont été faibles, et aucune tendance n'est apparue. Toutefois, comme pour le lemming brun, les proportions de juvéniles et de femelles lactantes ont augmenté dans la population lors de la période estivale après l'interruption de la reproduction causée par la fonte de la neige. Bien qu'en apparence surprenant, il est en fait possible qu'en 2004 on ait été plutôt à la fin du pic/début du déclin, et dans ce cas la baisse de la survie adulte serait responsable de l'amorce du déclin. En 2005, peut être qu'on était à la fin de la phase de déclin, ce qui pourrait expliquer un début de remonter de la survie.

Nous avons observé que les mâles se déplaçaient plus que les femelles car d'après la littérature, ils recherchaient des femelles pour l'accouplement, et d'autre part parce que les femelles était plus sédentaires à cause de leurs portées (Schmidt et al. 2002). Ceci explique pourquoi la taille des domaines vitaux des mâles était plus grande que celle des femelles. Ce qui a confirmé notre dernière hypothèse.

Un autre aspect original de ce second chapitre était de comparer différentes méthodes d'estimation de la densité basées sur des modèles de capture-marquage-recapture pour population fermée, le design robuste et l'estimateur d'Efford. Nous n'avons pas été étonnés par les densités similaires obtenues pour population fermée et le design robuste. En effet, ces méthodes utilisent essentiellement les mêmes modèles pour estimer l'abondance. Toutefois, ces méthodes nécessitent des tailles d'échantillon relativement importante pour obtenir des estimés précis, surtout les modèles développés pour le design robuste et disponibles dans le logiciel MARK. De plus, selon les hypothèses retenues pour calculer la taille effective de la grille de piégeage, et ainsi transformer nos mesures d'abondance en mesures de densité, la différence entre les estimations de densité obtenues par les méthodes traditionnelles pour populations fermées et celles obtenues par l'estimateur d'Efford peuvent être plus ou moins grandes. Les estimations de densité de la méthode d'Efford sont plus directes que les précédentes, car il n'est pas nécessaire de déterminer la taille effective de la grille de trappage, mais elles nécessitent également une taille d'échantillon importante.

Considérations méthodologiques et directions futures

Je pense que certaines de mes analyses présentent quelques faiblesses, principalement dues au manque de données. En effet, dans le chapitre 1, les modèles autorégressifs ont semblé ne pas être assez robustes pour déterminer l'existence d'effets dépendants de la densité. Predavec et al. (2001) suggèrent un minimum de 30 ans pour appliquer certains de ces modèles aux populations qui ont des cycles de 3 à 4 ans. C'est pourquoi nous avons complété nos analyses avec les méthodes spectrales. Dans le chapitre 2, les modèles de capture-marquage-recapture, essentiellement les modèles issus du design robuste et de la méthode d'Efford, semblent nécessiter aussi des tailles d'échantillon plus importantes que les modèles pour population fermée développés par le logiciel CAPTURE afin d'obtenir la convergence des modèles et des estimés précis. En effet en 2005 (phase de déclin), les modèles sélectionnés étaient les plus simples (aucun effet du temps et/ou du comportement dans les probabilités de capture), sûrement dû à la taille trop faible de l'échantillon pour détecter des effets plus complexes.

En agrandissant la taille des grilles de piégeage, nous pourrions partiellement pallier à ce problème, surtout lors des épisodes de faible abondance comme l'année 2005. De plus, nos conclusions sont limitées à la période estivale (environ 10 semaines par an). La compréhension complète de la dynamique des populations de lemmings nécessite des connaissances étendues aux autres saisons, comme l'hiver et particulièrement au niveau de la reproduction hivernale qui semblerait primordiale.

En résumé, ce projet a permis une analyse approfondie des données à long terme de l'abondance (via le piégeage mortel) et de débuter une étude sur la démographie du lemming (via le piégeage vivant) à l'Île Bylot. J'ai pu ainsi démontrer une différence non seulement dans les fluctuations d'abondances mais aussi dans la démographie interannuelle et saisonnière des deux espèces présentes. J'espère ainsi que mon étude a contribué à la compréhension de la dynamique des populations du lemming brun et du lemming variable, mais surtout à l'effort global de compréhension de l'écosystème arctique de l'Île Bylot.

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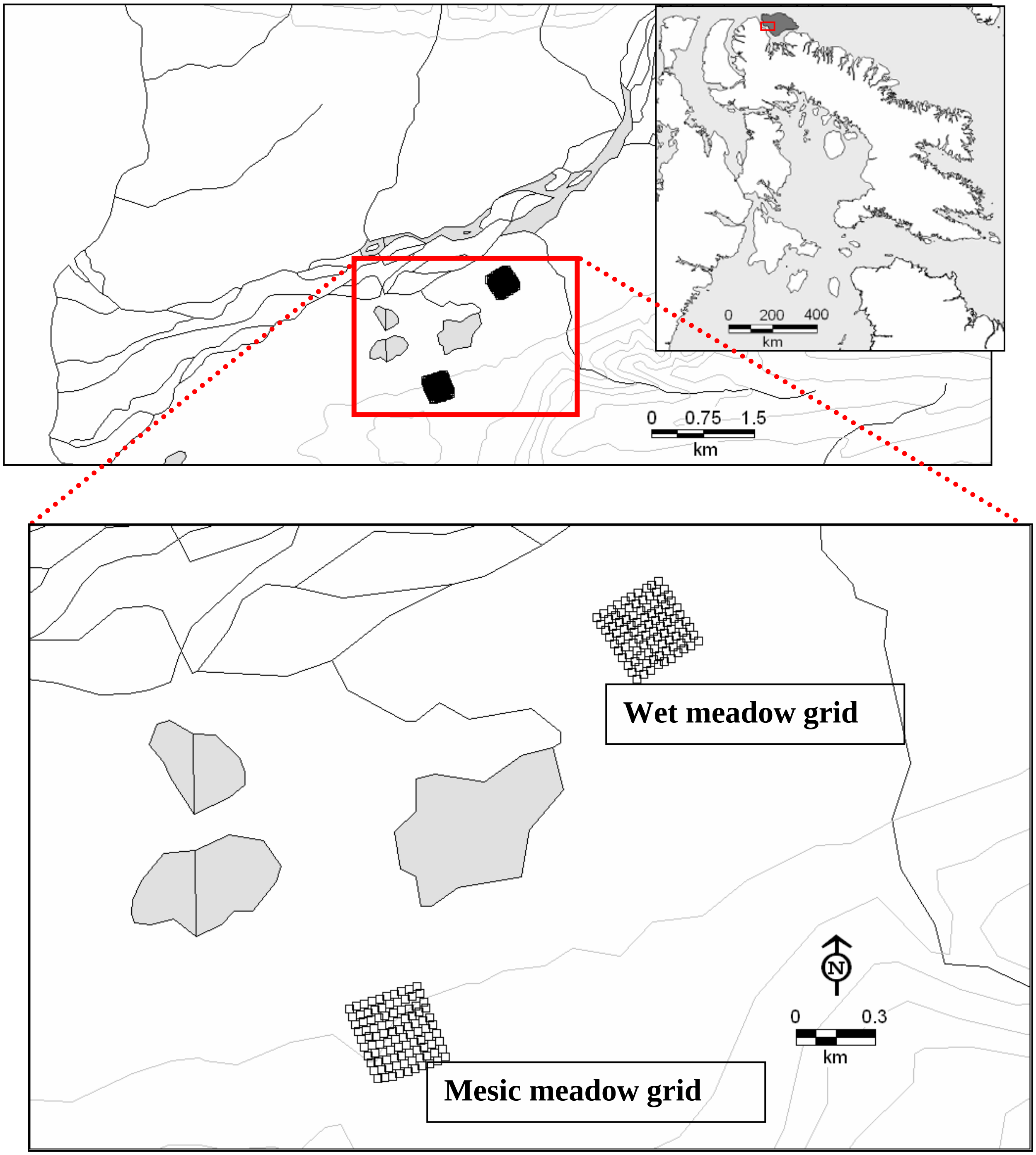
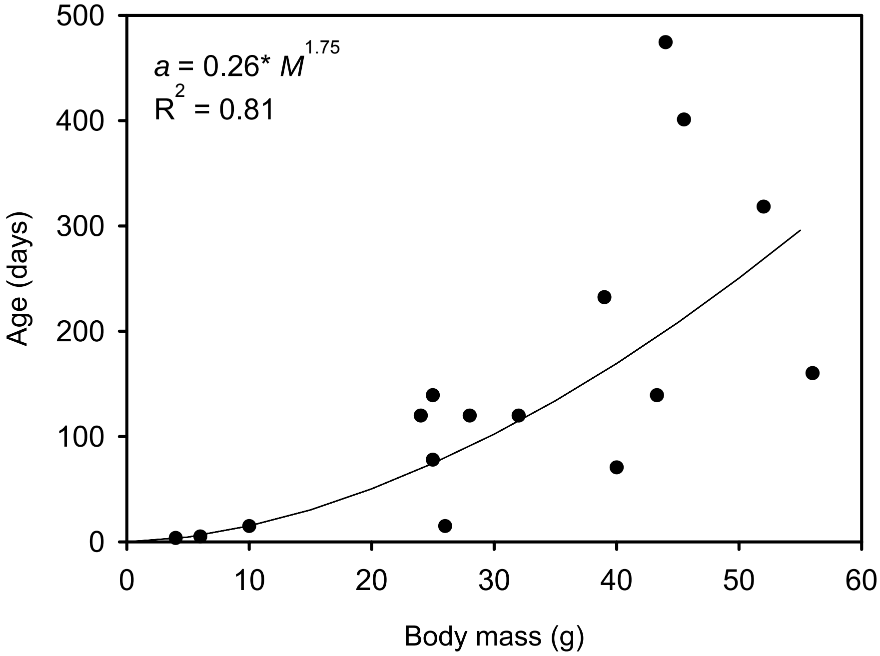
ANNEXES

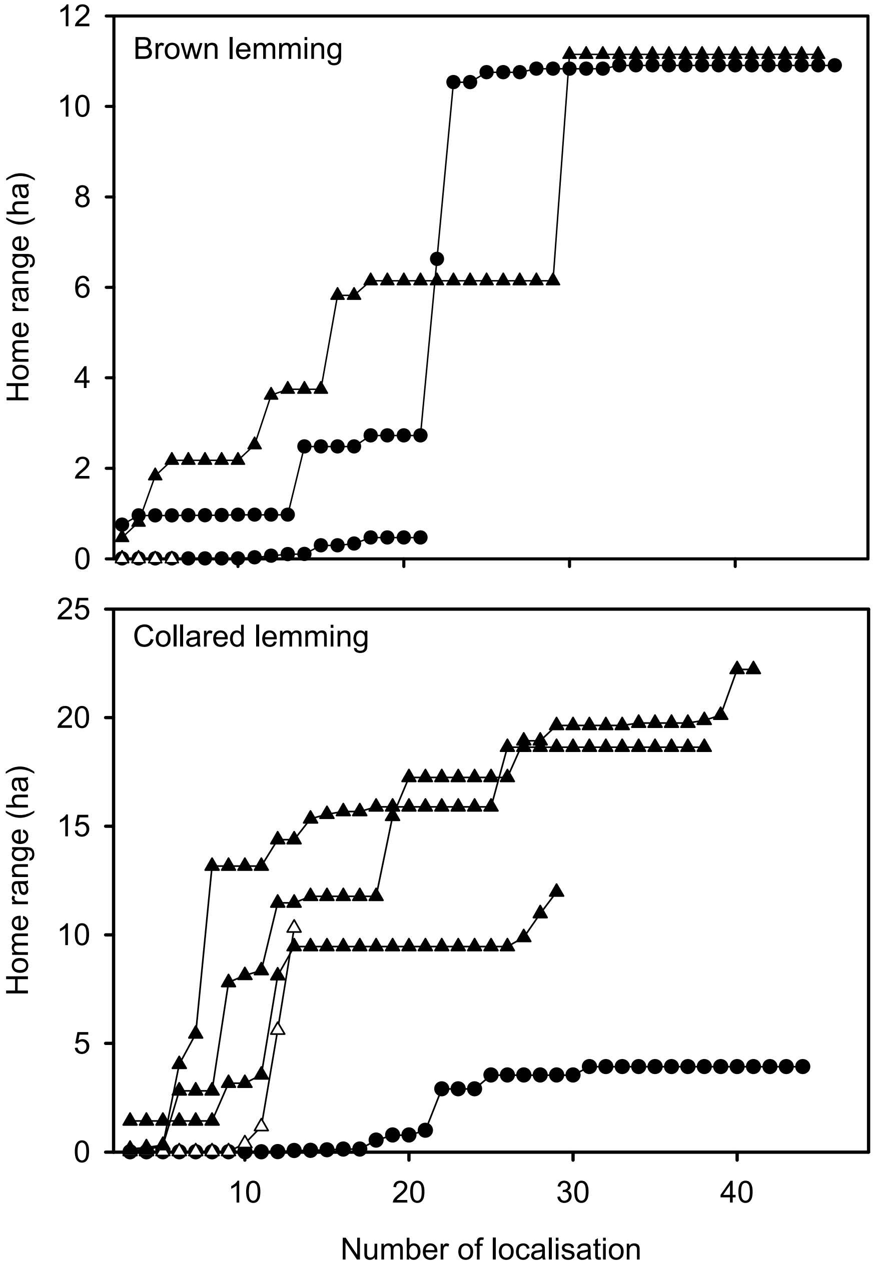
ANNEXE 1. Map showing the location of Bylot Island (in grey on the smallest inset) and the location of the two trapping grids on the study area. Lakes are shown in grey and each trapping station is represented by an open square within each trapping grid.



ANNEXE 2. Relationship between whole body mass (*M*., in grams) and age (*a*, in days) estimated with eye lens dry mass in dead brown lemmings (see methods) captured in 2005 on Bylot Island, Nunavut, Canada. Power regression line.



ANNEXE 3. Relationship between home range size and the cumulative number of localisations of female (circle) and male (triangle) lemmings tracked on Bylot Island, Nunavut, Canada (2005). The white dots are animals that did not show a plateau in the home range size determination and were excluded from the analysis.



ANNEXE 4. Model selection in CAPTURE for the closed population models applied to the live-trapping data of brown and collared lemming at different sampling periods on two trapping grids on Bylot Island, 2004 and 2005. For each model, we present the ΔAIC statistic (differences in AIC between the current and the best model), the AIC weights (ω), the number of estimated parameters (np) and the deviance. Model notation: M = closed population model, t = time, b = behavioural effect, 0 = no effect, *spp* = species effect, * = interaction. Effects apply only to the probability of capture

A. Wet meadow grid 2004

Model	Δ AICc	ω AICc	np	Deviance
Primary period II				
M_t	0.00	0.36	7	41.47
M_t^{age}	1.20	0.19	12	30.93
M_0	1.41	0.18	3	51.61
M_b	1.99	0.13	4	50.06
M_0^{age}	2.93	0.08	4	51.00
M_b^{age}	3.99	0.05	6	47.7
Primary period III				
M_b	0.00	0.70	4	41.15
M_t	2.82	0.17	6	39.64
M_b^{age}	3.64	0.11	6	40.47
M_t^{age}	8.24	0.01	10	36.03
Primary period IV				
M_b	0.00	0.63	4	64.87
M_0	2.15	0.21	3	69.10
M_0^{age}	2.93	0.14	4	67.80
M_b^{age}	9.87	0.00	12	57.20

B. Mesic tundra grid 2004				
Model	Δ AICc	ω AICc	np	Deviance
Primary period II				
M_0^{spp}	0.00	0.46	6	58.68
M_b^{spp}	1.21	0.25	8	55.50
$M_0^{spp*age}$	3.16	0.09	8	57.45
M_0	3.29	0.09	5	64.13
M_b	4.70	0.04	6	63.38
M_0^{age}	5.13	0.03	6	63.81
Primary period III				
M_b^{spp}	0.00	0.56	8	67.79
M_0^{spp}	2.72	0.14	6	75.07
M_b	3.55	0.09	6	75.90
M_b^{age}	4.75	0.05	8	72.54
M_0	5.26	0.04	5	79.82
$M_0^{spp*age}$	5.81	0.03	8	73.60
M_0^{age}	6.21	0.02	6	78.56
$M_b^{spp*age}$	6.51	0.02	12	64.68
M_t^{spp}	7.00	0.02	14	60.09
Primary period IV				
M_b	0.00	0.58	6	102.61
M_b^{spp}	2.43	0.17	8	100.68
M_b^{age}	4.06	0.08	8	102.32
M_t^{age}	4.34	0.07	14	88.89
M_t^{spp}	5.36	0.04	14	89.91

C. Wet meadow grid 2005

Model	Δ AICc	ω AICc	np	Deviance
Primary period I				
M_0	0.00	0.61	5	29.33
M_0^{spp}	1.92	0.23	6	28.19
M_0^{age}	2.84	0.15	6	29.12
$M_0^{spp*age}$	8.67	0.01	8	28.04
Primary period II				
$M_0^{spp*age}$	0.00	0.67	8	26.56
M_0^{age}	1.73	0.28	6	34.39
M_0	6.15	0.03	5	41.59
M_0^{spp}	7.25	0.02	6	39.91
Primary period III				
M_0	0.00	0.97	5	15.28
M_0^{spp}	8.61	0.01	6	15.08
M_0^{age}	8.61	0.01	6	15.08

D. Mesic tundra grid 2005				
Model	Δ AICc	ω AICc	np	Deviance
Primary period I				
M_0	0.00	0.62	5	29.11
M_0^{spp}	2.42	0.19	6	28.96
M_0^{age}	2.56	0.17	6	29.10
$M_0^{spp*age}$	7.42	0.01	8	28.49
Primary period II				
M_0^{age}	0.00	0.56	6	28.89
M_0	1.38	0.28	5	33.05
$M_0^{spp*age}$	3.90	0.08	8	26.69
M_0^{spp}	4.15	0.07	6	33.04
Primary period III				
M_0	0.00	0.57	5	9.55
M_0^{spp}	1.99	0.21	6	9.54
M_0^{age}	1.99	0.21	6	9.54
Primary period IV				
M_0^{spp}	0.00	0.46	6	30.72
M_0	0.76	0.31	5	34.17
M_0^{age}	1.80	0.19	6	32.52
$M_0^{spp*age}$	4.94	0.04	8	29.81