# Effets directs et indirects de la prédation sur les lemmings dans l'Arctique canadien

**Thèse**

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# Résumé de la thèse

Les populations caractérisées par des fluctuations cycliques ont fasciné et continuent de générer un grand intérêt chez la communauté scientifique en raison de la complexité des facteurs de régulation qui en sont responsables. Plusieurs hypothèses ont été proposées pour expliquer ces fluctuations cycliques mais aucun consensus n'a encore été atteint malgré près de 100 ans de recherche. La disponibilité de la nourriture et les effets sociaux (e.g. interactions compétitives) ont été proposés comme facteurs responsables de cycles de certaines espèces. Toutefois, la prédation est probablement le facteur le plus susceptible de causer des fluctuations cycliques chez les populations fauniques en raison de son effet dépendant de la densité avec délai. Un tandem circulaire de raréfaction et densification des prédateurs et des proies par des effets directs (i.e. mortalités) seraient à l'origine des cycles d'abondance. De plus, de récentes études montrent que les effets indirects (comme le stress) de la prédation pourraient être aussi importants que les effets directs pour générer les fluctuations cycliques. Cette thèse vise à identifier les effets directs et indirects de la prédation qui affectent la population de lemmings bruns de l'Île Bylot, Nunavut, caractérisée par des cycles d'abondance de 3-4 ans. Pour ce faire, nous avons d'abord comparé la plausibilité de l'hypothèse de la limitation par nourriture vis-à-vis l'hypothèse de la prédation en déterminant la chronologie saisonnière des cycles des lemmings. Ensuite, nous avons construit en 2012-2013 une clôture de 9 ha coiffée d'un filet anti-prédateur aviaire dans lequel nous avons piégé les lemmings de 2013 à 2015. Une deuxième grille de trappage sans clôture a été utilisée à des fins de comparaisons. Ces deux grilles étaient actives dès 2008, ce qui nous a permis d'avoir un contrôle pré-expérimental pour les données démographiques (effets directs). En 2014 et 2015, nous avons récolté les fèces des lemmings dans les deux grilles de trappage afin de quantifier les métabolites d'hormones de stress. Une validation de la mesure des métabolites fécales des glucocorticoïdes (i.e. hormones de stress) a été menée afin de mesurer le stress des lemmings de façon non-invasive. Les résultats sont clairs : (1) le déclin des lemmings se produit à la fin de l'été alors que les prédateurs sont au plus fort de leur abondance et pas à la fin de l'hiver, supportant ainsi l'hypothèse de la limitation par la prédation. Nos résultats suggèrent aussi (2) que les lemmings à l'intérieur de la clôture avaient une survie plus élevée qu'à l'extérieur, favorisant ainsi une croissance plus forte de la population. Ensuite, (3) les

lemmings ont montré des niveaux de stress plus faibles sans prédation sans toutefois que cela ait un impact sur leur reproduction. À la lumière des résultats de cette thèse et en les comparant avec deux autres études ayant aussi réduit expérimentalement l'abondance des prédateurs dans la toundra arctique, nous pouvons conclure que la prédation est la force trophique dominante de régulation de l'abondance des lemmings. Cette étude montre également que le stress induit par la prédation est insuffisant pour avoir un impact sur la dynamique des lemmings en été, soit pendant la saison où la prédation est maximale. Il est possible que cette absence d'effet soit une réponse adaptative des lemmings pour maintenir une reproduction élevée face à une prédation élevée, et ainsi maximiser leur aptitude phénotypique.

## Summary of the thesis

Populations characterised by cyclic fluctuations have fascinated and continue to generate a great interest among the scientific community because of the complexity of the regulating factors. Several hypotheses have been proposed to explain these cyclical fluctuations but no consensus has yet been reached despite nearly 100 years of research. The availability of food and social effects (e.g. competitive interactions) has been proposed as factors responsible for cycles in certain species. However, predation is probably the factor most likely to cause cyclical fluctuations in wildlife populations due to its delayed density-dependence. A circular tandem of rarefaction and densification of predators and prey caused by direct effects (i.e. mortalities) can cause cycles of abundance. Moreover, recent studies show that indirect effects of predation such as stress could be as important as direct effects in generating cycles. This thesis aims to identify direct and indirect effects of predation that affect the cyclic brown lemming populations of Bylot Island, Nunavut, which is characterized by 3-4 yr cycles. To do this, we first compared the plausibility of the food limitation hypothesis vs. the predation limitation hypothesis by determining the seasonal timing of lemming cycles. We then we built a 9-ha fence in 2012-2013 covered by an anti-avian predator net in which we trapped lemmings from 2013 to 2015. A second control trapping grid was used for comparisons. These two grids were active since 2008, allowing us to have a pre-experimental control for demographic parameters (direct effects). In 2014 and 2015, we collected lemming feces in the two trapping grids to quantify stress hormone metabolites. A validation of the measurement of fecal glucocorticoid metabolites (i.e. stress hormones) was conducted to measure stress non-invasively. The results are clear: (1) the decline of lemmings occurs in late summer when predators are at their peak abundance and not in late winter, thereby supporting the predator-limitation hypothesis. Our results also suggest (2) that lemmings within the fence had higher survival than outside, thus promoting a higher growth of the population. Then, (3) even though lemmings had lower stress levels without predation, stress had no impact on their reproduction. In light of the results of this thesis and according to two other studies during which predator abundance was also reduced experimentally in the Arctic tundra, I conclude that predation is the dominant trophic force that regulates the abundance of lemmings. This study also shows that the stress induced by predation is insufficient to affect the dynamics of lemmings in summer,

when predation is maximum. It is possible that this lack of an effect is an adaptive response by lemmings to maintain high reproductive rate despite high predation, and thus maximize their fitness.

# Table des matières

# Liste des tableaux

CHAPITRE 2



CHAPITRE 3



CHAPITRE 4

# Liste des figures

CHAPITRE 1



CHAPITRE 2



CHAPITRE 3

ANNEXE S3

*À 'Ma, 'Pa, Annie et Thomas*

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# Avant-propos

Cette thèse est divisée en six chapitres, incluant l'introduction et la conclusion générale. Les autres chapitres sont présentés sous forme d'articles scientifiques révisés par les pairs. Ces articles sont présentés dans la langue de Shakespeare. Le chapitre 2 est présentement publié, les chapitres 3 et 4 sont en révision et le chapitre 5 sera soumis prochainement.

La référence du chapitre 2 est : Fauteux, D., Gauthier, G. et Berteaux, D. (2015). Seasonal demography of a cyclic lemming population in the Canadian Arctic. *Journal of Animal Ecology*, 84, 1412-1422. Des informations supplémentaires sont disponibles en Annexe S1. Cet article a été accepté le 26 avril 2015.

Le chapitre 3 est présentement en révision pour le journal *Ecology* : Fauteux, D., Gauthier, G. et Berteaux, D. (2016). Top-down limitation of lemmings revealed by experimental reduction of predators. Des informations supplémentaires sont disponibles en Annexe S2. Cet article a été soumis le 2 avril 2016.

Le chapitre 4 est aussi en révision pour le *Journal of Comparative Physiology B* : Fauteux, D., Gauthier, G., Berteaux, D., Bosson, C., Palme, R. et Boonstra, R. (2016). Assessing stress in Arctic lemmings: plasma and fecal signatures sing the same song. Des informations supplémentaires sont disponibles en Annexe S3. Cet article a été soumis le 5 février 2016.

Le chapitre 5 est présentement en rédaction et sera soumis à un journal avec comité de lecture pendant l'été 2016 : Fauteux, D., Gauthier, G., Berteaux, D., Palme, R. et Boonstra, R. (2016). Predator-induced stress does not suppress reproduction in High Arctic lemmings. Des informations supplémentaires sont disponibles en Annexe S4. Cet article sera soumis à *Ecology Letters* à l'été 2016.

Pour chacun de ces articles, j'ai identifié les objectifs des chapitres, j'ai participé à la récolte des données pour le chapitre 1 et j'ai récolté la totalité des données pour trois autres chapitres avec l'aide d'aides de terrain. De plus, j'ai mené les analyses statistiques et j'ai rédigé le texte pour tous les chapitres. J'ai participé à toutes les étapes de la construction de l'exclos à prédateur utilisé pour les chapitres 3 et 5. Mon directeur, Gilles Gauthier, a participé activement à chacune de ces étapes. Dominique Berteaux (Université du Québec à

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J'ai également participé à l'écriture de deux documents scientifiques publiés durant mon doctorat mais non inclus dans la thèse dont les références sont :

Bilodeau, F., Gauthier, G., Fauteux, D. et Berteaux, D. (2014). Does lemming winter grazing impact vegetation in the Canadian Arctic? *Polar Biology*, 37, 845-857.

Cadieux, M.-C., Fauteux, D., et Gauthier, G. (2015) Technical manual for sampling small mammals in the Arctic. Centre d'Études Nordiques, 55 pp. URL: http://www.cen.ulaval.ca/bylot/files/Small_Mammal_Sampling_v1.pdf

# CHAPITRE 1. Introduction générale

## 1.1 Problématique

### *1.1.1. Limitation et régulation des populations*

Les fluctuations d'abondance des populations qu'on observe dans le temps et dans l'espace sont régies par des facteurs biotiques (e.g. interactions trophiques) et abiotiques (e.g. météo; Krebs, 2009). Ces facteurs peuvent être limitants s'ils réduisent l'abondance moyenne d'une population ou encore ils peuvent la réguler en augmentant la proportion de mortalités ou en réduisant le taux de reproduction per capita lorsque l'abondance augmente. Les facteurs biotiques peuvent impliquer un seul niveau trophique (Menge et Sutherland 1987; Polis et Strong 1996). Par exemple, la compétition intraspécifique par exploitation des ressources implique que chaque individu a le potentiel de réduire la quantité de ressources disponibles aux autres individus. Ceci a pour conséquence d'augmenter le risque de mortalité ou de diminuer la fécondité des individus et donc de réduire le taux de croissance de la population (Polis et Strong 1996). D'autre part, les interactions trophiques impliquant plusieurs espèces ou niveaux trophiques ont souvent été mises en cause comme facteurs limitant la croissance des populations (Polis et Strong 1996; Oksanen et Oksanen 2000; Sinclair et Krebs 2002).

La régulation des populations via des interactions trophiques peut se faire par le haut (top-down) et/ou par le bas (bottom-up). La régulation par le bas suppose que le taux de croissance des consommateurs est réduit par un apport énergétique insuffisant provenant de la nourriture. L'hypothèse de la régulation par le haut implique plutôt l'effet inverse alors que les prédateurs réduisent le taux de croissance de la population de proies (Polis et Strong 1996; Sinclair et Krebs 2002). Puisque les écosystèmes sont composés de plusieurs niveaux trophiques, ces deux types de régulations peuvent interagir pour moduler les fluctuations d'abondance des populations (Meserve *et al.* 2003; Krebs 2013).

L'hypothèse du «green-world» (Hairston *et al.* 1960) suggère que la force trophique la plus forte est la consommation (ou prédation) car la quasi omniprésence de végétation serait le résultat d'un fort effet limitant des prédateurs sur les populations d'herbivores. Plus spécifiquement, l'hypothèse de l'exploitation des écosystèmes (EEH; Oksanen et Oksanen, 2000) stipule que la limitation par le haut se produit là où la productivité (efficacité écologique) est suffisamment élevée pour assurer la subsistance des populations de

consommateurs des niveaux trophiques supérieurs. En effet, la forte productivité de certains écosystèmes assurerait un transfert d'énergie (*i.e.* efficacité écologique) suffisamment élevé pour soutenir les populations de prédateurs au sommet de la chaîne alimentaire (Post 2002). Au contraire, quand la productivité primaire d'un milieu est trop faible, les populations d'herbivores seraient trop faibles pour supporter des populations viables de prédateurs, empêchant un contrôle par le haut. Toutefois, cette hypothèse a été remise en question par plusieurs chercheurs car de plus en plus d'études montrent que la prédation est une force trophique majeure dans des milieux peu productifs, tels que l'Arctique et les déserts (Gilg *et al.* 2003; Meserve *et al.* 2003; Legagneux *et al.* 2012).

### *1.1.2. Fluctuations cycliques et dynamique des populations*

Une population dont la croissance est indépendante de la densité augmentera de façon exponentielle. Toutefois, il est plus réaliste que la croissance soit dépendante de la densité et se stabilise au niveau de la capacité de charge (i.e. densité maximale pouvant être supportée par l'habitat) du milieu, dénotée par *K*. Toutefois, cette stabilité est compromise par des effets dépendants de la densité avec délai. Un effet de densité qui n'exerce pas son effet de façon immédiate sur la croissance de la population permettra à la population de dépasser la capacité de charge (Krebs 2009). Éventuellement, les mortalités dépassent la capacité de croissance de la population et la font décliner à un niveau inférieur à *K*, encore une fois en raison du délai du facteur de régulation. La répétition constante de cet effet de délai et des réponses démographiques positives et négatives crée des fluctuations autour de la capacité de charge, une condition suffisante pour créer des «cycles» d'abondance. Toutefois, ces fluctuations peuvent se produire sans dépasser *K* en raison de son instabilité (e.g. augmentation soudaine de la productivité primaire lors d'épisodes de pluie dans des milieux xériques; Meserve *et al.* 2003) et des facteurs limitants.

Charles Elton a été le premier auteur à documenter empiriquement la présence de fluctuations cycliques chez plusieurs taxons (Elton 1924). Depuis ce temps, d'autres études ont décrit des cycles chez plusieurs espèces fauniques dont les lagopèdes (Cattadori *et al.* 2005), les lièvres (Krebs *et al.* 1995), les porcs-épics (Klvana *et al.* 2004) et les campagnols (Stenseth 1999; Fauteux *et al.* 2015a). La période de ces fluctuations cycliques semble

varier entre 8-10 ans pour certaines espèces, dont les lièvres d'Amérique (*Lepus americanus*, Krebs et al. 1995), alors que pour d'autres, comme les petits rongeurs, elle varie souvent entre 3 et 5 ans (Stenseth 1999; Gilg *et al.* 2003; Gruyer *et al.* 2008). La période des cycles est dépendante des traits d'histoire de vie des espèces et des facteurs environnementaux (Krebs 2013). Par exemple, les lièvres d'Amérique fluctuent selon des périodes plus longues que les lemmings ou les campagnols probablement en raison de leur plus grande longévité et parce que leur prédateur principal (i.e. lynx du Canada, *Lynx canadensis*) prend plus de temps à croître en abondance que les prédateurs des petits rongeurs (Krebs 2011). L'amplitude des fluctuations peut aussi varier d'une population à l'autre chez une même espèce, souvent selon un gradient latitudinal (Johnson *et al.* 2000; Angerbjorn *et al.* 2001). Les fluctuations cycliques des populations sont souvent caractérisées par une certaine synchronie spatiale. Les conditions climatiques ainsi que les effets indirects causés par celles-ci seraient à l'origine d'une synchronie à grandes distances alors que la compétition et la prédation seraient davantage susceptibles de causer une synchronie sur de courtes distances (Krebs *et al.* 2002; Cattadori *et al.* 2005; Ims et Andreassen 2005; Elmhagen *et al.* 2011). Les différentes composantes des cycles complexifient leur étude mais la manipulation expérimentale est une méthode puissante pour tester l'effet limitant et de régulation des facteurs externes sur les populations cycliques (Krebs 1996; Klemola *et al.* 2000; Salo *et al.* 2010).

Les cycles de lemmings en Arctique sont remarquables par leur grande amplitude (Stenseth 1999; Krebs 2013) et bien qu'ils soient connus depuis près de 100 ans (Elton 1924), les causes de ces cycles restent débattues en écologie (Gauthier *et al.* 2009; Oksanen *et al.* 2009). En effet, certains écologistes invoquent un effet régulateur par les plantes (effet par le bas), tout particulièrement pour les lemmings de Norvège (*Lemmus lemmus*; Oksanen et Oksanen, 2000; Turchin *et al.* 2000). Le manque de nourriture en hiver ou l'augmentation des composés peu digestes chez les plantes excessivement broutées (e.g. catéchines, silices et inhibiteurs de protéinase) seraient à la base d'un effet limitant par la nourriture (Seldal *et al.* 1994; Berg 2003; Massey *et al.* 2008). Par contre, chez les lemmings bruns (*Lemmus trimucronatus*) et variables (*Dicrostonyx groenlandicus*), il semble que ce serait plutôt un effet régulateur par les prédateurs qui seraient en cause (effet par le haut; Wilson et al. 1999; Gilg *et al.* 2003; Legagneux *et al.* 2012; mais voir Pitelka et

Batzli 2007). Des manipulations expérimentales de la prédation menées en Scandinavie ont également montré que plusieurs populations de campagnols boréaux sont limitées par la prédation (Klemola *et al.* 2000; Huitu *et al.* 2003). De récentes études montrent de plus que les effets indirects de la prédation (e.g. peur) pourraient même être responsables de certaines phases des fluctuations de petits mammifères (Norrdahl *et al.* 1995a; Sheriff *et al.* 2009b; Bian *et al.* 2015). L'hypothèse EEH tente d'unifier ces deux hypothèses avec la productivité des écosystèmes. Plus spécifiquement, les populations les plus nordiques de petits mammifères, là où la productivité primaire est trop faible pour maintenir des densités d'herbivores suffisantes pour supporter des populations de prédateurs (Lindeman 1942; Oksanen et Oksanen 2000; Post 2002), devraient être régulées par les plantes (*i.e.* par le bas). La faible disponibilité des nutriments maintiendrait les plantes à de faibles biomasses et les herbivores seraient donc limités par la nourriture. D'autre part, les populations de petits mammifères qui habitent les écosystèmes avec une plus forte productivité et où l'efficacité écologique est élevée seraient plutôt régulés par les prédateurs. Toutefois, plusieurs exceptions viennent contredire les prédictions de l'hypothèse EEH, notamment chez les lemmings vivant dans des régions peu productives de la toundra au Groenland (Gilg *et al.* 2003) et au Canada (Reid *et al.* 1995; Wilson *et al.* 1999; Legagneux *et al.* 2012).

Les conditions climatiques sont un autre facteur invoqué pour expliquer les fluctuations d'abondance des lemmings (Kausrud *et al.* 2008). Puisque les lemmings passent la majorité de l'hiver sous le couvert nival, une faible qualité de la neige aurait un impact direct sur leurs populations (Gilg *et al.* 2009; Ims *et al.* 2011). Par exemple, un hiver doux et humide favorisant l'accumulation d'une neige dense et lourde et la formation de couches glacées au sol réduirait l'accès à la végétation et le pouvoir isolant de la neige. Ces conditions dégradées de neige pourraient affecter la survie des petits mammifères de façon importante en rendant plus difficile l'accès aux plantes servant de nourriture (Aars et Ims 2002; Kausrud *et al.* 2008; Ims *et al.* 2011). À l'inverse, une couche nivale épaisse et peu dense combinée à une absence de couches de glace favoriseraient une croissance plus élevée des populations en hiver (Bilodeau *et al.* 2013a). Certains auteurs soupçonnent d'ailleurs que la perturbation du couvert nival par le réchauffement climatique serait une des causes probables de la disparition récente de irruptions chez certaines populations de

lemmings (Hornfeldt *et al.* 2005; Ims *et al.* 2008; Gilg *et al.* 2009). Cependant, Brommer *et al.* (2010) montrent que certaines populations dont les fluctuations avaient cessé au cours de la dernière décennie sont redevenues cycliques et ce, malgré des hivers toujours plus doux. Une étude menée récemment au Canada montre que l'épaisseur de neige seule, une variable importante affectant les températures sous-nivales auxquelles les lemmings sont exposés, ne serait peut-être pas suffisante pour modifier les fluctuations cycliques des populations de lemmings (Reid *et al.* 2012; Bilodeau *et al.* 2013c). Davantage d'études seront nécessaires pour déterminer quels sont les liens entre les conditions climatiques et les fluctuations cycliques des petits mammifères.

### *1.1.3. Effets directs de la prédation sur les fluctuations cycliques de petits mammifères*

L'effet direct de la prédation sur une population est une augmentation de la mortalité menant à une réduction de l'abondance moyenne de la population des proies. Plusieurs études montrent que la prédation est un facteur prépondérant des fluctuations cycliques de certaines populations de proies (Krebs 1996; Gilg 2002; Therrien *et al.* 2014). Dans la toundra arctique, l'hermine (*Mustela erminea*), le renard arctique (*Vulpes lagopus*), le harfang des neiges (*Bubo scandiacus*), les labbes (*Stercorarius* spp.) et la buse pattue (*Buteo lagopus*) sont les principales espèces qui composent la guilde de prédateurs dont le régime alimentaire est partiellement ou totalement composé de lemmings (Gauthier *et al.* 2011). Au cours de l'été, leur abondance augmente énormément lorsque les lemmings sont en phase d'abondance élevée (Gilg *et al.* 2006; Therrien *et al.* 2014). De récentes études montrent que leur impact direct serait suffisant pour réguler les populations de lemmings en les décimant en été (Gilg *et al.* 2003; Bilodeau 2013; Therrien *et al.* 2014). D'autre part, Reid *et al.* (1995) ont étudié une population de lemmings variables qui fluctue très peu et suggèrent que ces faibles variations seraient dues à une plus grande abondance de prédateurs résidents pendant toute l'année. Les auteurs suggèrent que la présence de proies alternatives en hiver permettrait à plusieurs prédateurs de persister pendant les années de faibles abondances de lemmings. Krebs (2011) a suggéré qu'en hiver, il doit y avoir un relâchement de la pression de prédation pour permettre un recrutement positif chez les

lemmings, ceux-ci étant capables de se reproduire sous la neige. Sans ce relâchement saisonnier, les populations ne pourraient pas croître et avoir une dynamique cyclique.

L'hermine, un prédateur spécialiste, pourrait exercer une pression de prédation suffisamment forte pour générer les cycles des lemmings (Gilg *et al.* 2003). De plus, la prédation des hermines est dépendante de la densité avec un délai de un an, une situation souvent représentée par le tandem cyclique des lièvres et des lynx du Canada (*Lynx canadensis*; Krebs *et al.* 2001). En plus d'une réponse numérique élevée, les hermines modulent leur réponse fonctionnelle en augmentant leur consommation per capita lorsque les lemmings abondent (Gilg *et al.* 2006). D'autres études montrent un impact majeur des mustélidés sur la survie de plusieurs espèces de campagnols et de lemmings (Henttonen *et al.* 1987; Norrdahl et Korpimäki 1995b; Sittler 1995; Johnson *et al.* 2000). Pourtant, nous devons rester prudents par rapport à l'importance du rôle des prédateurs spécialistes car les effets seuls ou combinés des généralistes pourraient aussi jouer un rôle dans l'initiation de cycles chez les petits mammifères (Gilg *et al.* 2003; Korpimaki *et al.* 2005; Therrien *et al.* 2014).

Afin de vérifier l'hypothèse de la prédation comme facteur de régulation des populations de lemmings, deux manipulations expérimentales de la prédation ont été menées dans le bas Arctique canadien à Pearce Point, Territoires du Nord-Ouest et sur la Péninsule de Kent, au Nunavut (Reid *et al.* 1995; Wilson *et al.* 1999). Les chercheurs ont clôturé des parcelles de 9 et 11 ha pour exclure les prédateurs. Ces expériences ont permis l'exclusion expérimentale complète de tous les prédateurs des lemmings variables sauf l'hermine dont l'exclusion n'a été que partielle. Reid *et al.* (1995) indiquent que la survie des adultes et le recrutement des jeunes dans la population de lemmings étaient plus élevés à l'intérieur de la parcelle d'exclusion que dans les sites témoins. Les auteurs suggèrent également que la mortalité par la prédation n'est pas compensatoire en période de faible abondance, ce qui indique une régulation par le haut. Toutefois, la réduction de la prédation n'a pas favorisé la croissance des populations de lemmings, probablement parce que les jeunes qui se dispersaient étaient rapidement capturés par les prédateurs en dehors de la parcelle clôturée (Krebs 1996). Wilson *et al.* (1999) ont pour leur part aussi montré que la survie des adultes était plus élevée à l'intérieur de la parcelle d'exclusion des prédateurs

que dans le site témoin et que la population des lemmings était plus abondante dans la parcelle d'exclusion. Ces dernières expériences ont été menées dans le bas Arctique où la productivité végétale est plus faible comparativement aux forêts boréales mais relativement élevée comparée aux autres régions de la toundra arctique (Oksanen *et al.* 2008). Aucune expérience de ce genre n'a encore été menée dans le haut Arctique, là où la productivité primaire est plus faible que dans le bas Arctique.

### *1.1.4. Effets indirects de la prédation*

En plus d'avoir un impact direct via la mortalité, la prédation est susceptible d'induire des effets non-létaux qui peuvent aussi affecter les paramètres démographiques (Sheriff *et al.* 2011b). En plus de changer le comportement de quête alimentaire en favorisant d'autres activités comme la vigilance (Verplancke *et al.* 2010), le risque de prédation perçu par les proies peut affecter leur comportement reproducteur (Apfelbach *et al.* 2005). Certaines études en milieu semi-naturel (i.e. enclos soumis à différents traitements) ont montré que l'exposition de petits mammifères aux odeurs de mustélidés induit des changements comportementaux pouvant résulter en une réduction de la proportion d'individus en état reproducteur ou un évitement de la copulation (Ronkainen et Ylönen 1994; Jochym et Halle 2012). Toutefois, la pertinence de ces résultats en milieu naturel a été mise en doute (Norrdahl et Korpimäki 2000), notamment parce que les expériences controlée exagéraient grandement l'exposition chronique des individus aux indices olfactifs. Pour clarifier si la prédation peut effectivement avoir un impact sur la reproduction de leurs proies, certains chercheurs ont commencé à examiner les mécanismes qui pourraient moduler de tels effets, notamment la réponse au stress via le système endocrinien (Boonstra et Boag 1992; Boonstra *et al.* 1998a). Parallèlement, d'autres chercheurs ont proposé que les effets maternels puissent être un facteur engendrant une densité-dépendance avec délai souvent caractéristique des cycles (Inchausti et Ginzburg 1998). Selon eux, des femelles stressées offriraient un environnement stressant à leur progéniture durant la gestation, créant ainsi un effet multigénérationnel. Aujourd'hui, les idées de ces chercheurs font partie des hypothèses principales pour expliquer les cycles des populations animales (Krebs 2011; Sheriff 2015). En somme, ces idées représentent une

modernisation de l'hypothèse de John Christian (1950) stipulant que le stress est un facteur suffisant pour amener les populations à fluctuer cycliquement.

### *1.1.5. Le stress et la dynamique des populations*

Suite à un évènement stressant, tel que la détection d'un prédateur, le système nerveux central d'un mammifère s'active rapidement pour répondre physiquement au danger. Plus spécifiquement, lorsqu'un animal détecte un danger, un stimulus sensoriel active l'hypothalamus qui produit des facteurs d'activation de l'hypophyse qui sécrète alors la corticotrophine (ACTH), une hormone agissant sur les glandes surrénales (Sapolsky *et al.* 2000). Ce sont ces dernières qui sécrètent les glucocorticoïdes dans le sang, communément appelés hormones de stress. Chez les rongeurs, les glucocorticoïdes sont principalement sous forme de corticostérones (Palme *et al.* 2005). Récemment, de nouvelles méthodes ont été développées afin de mesurer le stress de façon non-invasive chez les populations animales, notamment grâce aux métabolites fécaux des glucocorticoïdes (Sheriff *et al.* 2011a).

Lorsque l'axe hypothalamus-hypophyse-surrénale est activé par l'événement stressant, la concentration de glucocorticoïdes sanguins augmente très rapidement. Si le stress est chronique, des réponses physiologiques à long-terme et parfois délétères peuvent se produire (Sapolsky *et al.* 2000; Wingfield et Sapolsky 2003). Ce stress chronique peut par exemple inhiber le système immunitaire, digestif, reproducteur ou encore la croissance des individus. Certaines pathologies ont été associées au stress dont des niveaux de glucose sanguin anormalement élevés (Fletcher et Boonstra 2006b) qui pourraient favoriser le diabète et la myocardite (Andrews *et al.* 1975; Niklasson *et al.* 2006). Toutefois, les effets délétères du stress sur la reproduction sont ceux les plus susceptibles d'avoir un impact sur la démographie (Crespi *et al.* 2013). De tels effets pourraient se répandre à l'échelle d'une population si un événement externe (e.g. risque de prédation élevé ou manque de nourriture) se produit à grande échelle. Par exemple, Sheriff *et al.* (2009b) ont récemment montré que les niveaux de glucocorticoïdes d'une population cyclique de lièvres étaient élevés pendant la phase de déclin où les prédateurs abondent. Selon les auteurs, les lièvres développent un stress chronique, forçant ainsi des niveaux de glucocorticoïdes élevés qui

réduisent le succès reproducteur des femelles par l'action inhibiteur des hormones sur la fécondité, le développement normal des embryons et les soins parentaux.

Les effets maternels sont un mécanisme par lequel les effets délétères du stress sur la physiologie des individus pourraient se propager à travers une population et ainsi affecter sa dynamique cyclique (Sheriff *et al.* 2011b). En effet, les femelles stressées par leur environnement pourraient en quelque sorte « léguer » leur stress à leur progéniture soit par des modifications dans leur comportement (e.g. soins aux jeunes; McGowan *et al.* 2011) ou en exposant les fœtus à un environnement utérin dont les concentrations d'hormones de stress sont anormalement élevées (Lesage *et al.* 2001).

Inchausti et Ginzburg (2009) avaient déjà souligné que les études d'exclusion expérimentale des prédateurs menées dans le Nord-Ouest canadien n'ont pu totalement supprimer les fluctuations cycliques des populations de lièvres. Ils avaient suggéré que les effets directs de la prédation ne pouvaient à eux seuls générer des fluctuations cycliques malgré qu'ils puissent fortement affecter leur amplitude. Par contre, la prédation pouvait aussi avoir un effet indirect et négatif sur l'activité reproductrice des femelles qui serait transmis aux jeunes par effet maternel, engendrant ainsi un effet de densité avec délai; ce délai serait le temps nécessaire pour que les femelles retrouvent un succès reproducteur élevé dans la population. Cette hypothèse a été testée expérimentalement par Sheriff *et al.* (2009b) et leurs résultats démontrent de façon convaincante que le stress induit par un risque de prédation élevé et transmis aux jeunes par les mères pourrait être l'effet maternel suggéré par Inchausti et Ginzburg (2009). Boonstra *et al.* (1998b) avaient aussi suggéré que les effets maternels pourraient causer la persistance d'un faible recrutement suivant un déclin de populations de campagnols. Il est donc possible que les fluctuations cycliques des lemmings soient en partie causées par un niveau de stress élevé induit par une forte abondance de prédateurs et maintenu pendant plusieurs générations via des effets maternels.

### *1.1.6. Le cas de la population des lemmings de l'Île Bylot*

L'Île Bylot est un site du Haut Arctique canadien occupé par deux espèces sympatriques de lemmings (le lemming brun et le lemming variable) dont les populations

sont caractérisées par des fluctuations cycliques avec des périodes de 3-4 ans (Gruyer *et al.*, 2008). Pendant un cycle, l'abondance des lemmings bruns peut être multipliée par 100 d'un été à l'autre. Les lemmings variables, quant à eux, fluctuent selon des cycles dont les amplitudes sont faibles, soit selon un facteur d'environ 4. Une modélisation récente du réseau trophique de l'île Bylot suggère que la prédation pourrait être suffisante pour réguler le lemming variable à faible densité mais il est encore incertain qu'elle serait suffisante pour réugler le lemming brun (Legagneux *et al.* 2012). Toutefois, les lemmings ne consomment qu'une faible proportion de la productivité primaire, ce qui suggère qu'ils ne sont pas limités par l'abondance de nourriture (Legagneux *et al.* 2012; Bilodeau *et al.* 2014). En été, les lemmings bruns (Figure 1.1) sont généralement associés à la toundra humide/mésique alors que les lemmings variables sont plutôt associés à la toundra mésique/xérique (Morris *et al.* 2000). En hiver, les deux espèces de lemmings utilisent surtout la toundra mésique et sélectionnent généralement des sites avec une topographie hétérogène et où l'épaisseur de neige est élevée (Duchesne *et al.* 2011b). Les bords de cours d'eau et les sites dont la pente est abrupte sont alors recherchés.

La prédation estivale des lemmings arà l'Île Bylot est exercée par plusieurs espèces d'oiseaux (*e.g.* harfang des neiges; labbe à longue queue, *S. longicaudus*; buse pattue; goéland bourgmestre, *Larus hyperboreus*) et de mammifères (*e.g.* hermine; renard arctique; Gauthier *et al.* 2011). En hiver, l'hermine et le renard sont les seuls prédateurs des lemmings (Bilodeau *et al.* 2013b). La présence d'une population dense de grandes oies des neiges (*Chen caerulescens atlantica*) pendant la période estivale pourrait aussi intervenir dans l'effet de la prédation sur les lemmings. En effet, une compétition apparente semble affecter les interactions entre ces deux espèces via certains prédateurs, tels que le renard arctique et les labbes, qui s'alimentent à la fois sur les lemmings et les oies (Bety *et al.* 2002). La présence des oies pourrait donc contribuer à maintenir des niveaux de populations plus élevés de certains prédateurs qu'il ne serait possible en l'absence de celles-ci.

## 1.2. Objectifs de la thèse

De façon générale, cette thèse vise à documenter comment les prédateurs affectent la démographie et la dynamique des populations de lemmings dans le haut Arctique. Elle sert à élucider les facteurs de régulation prédominants dans l'Arctique et vérifier si le contrôle par le haut (prédateurs) est suffisant pour induire les fluctuations de population observés chez les lemmings. Cette étude est principalement basée sur une manipulation à grande échelle de la prédation par la construction d'un exclos à prédateurs. Il s'agit de la troisième expérience de réduction des prédateurs de lemmings dans l'Arctique, augmentant ainsi le nombre de réplicas disponibles pour tester cette hypothèse qui n'a toujours pas été résolue malgré des recherches pendant près de 100 ans. Mon étude se distingue toutefois de façon importante des précédentes par le fait que notre site d'étude se trouve dans le haut Arctique (i.e. milieu moins productif que le bas Arctique), nous étudions une nouvelle espèce (i.e. lemmings bruns) dont les fluctuations sont très grandes, nous étudions l'effet de la prédation sur la démographie hivernale grâce aux nids d'hiver et nous quantifions les effets indirects induits par la prédation. Ce dernier point servira à déterminer si les effets indirects de la prédation peuvent aussi affecter la dynamique de population des lemmings, une hypothèse qui a été confirmée chez une autre espèce cyclique (i.e. lièvres d'Amérique).

Le chapitre 2 présente une analyse à long terme de la démographie saisonnière des lemmings bruns à travers les différentes phases de leurs cycles de population. Cette analyse nous permet d'évaluer les deux hypothèses les plus courantes pour expliquer les cycles des petits mammifères. La première hypothèse est que si le manque de nourriture et la famine sont responsables des déclins des lemmings, ceux-ci devraient se produire surtout en hiver alors que la nourriture est plus difficile d'accès et les plantes sont en dormance. La deuxième hypothèse est que si la prédation est responsable des déclins, ceux-ci devraient se produire à l'été et à l'automne lorsque les prédateurs atteignent leur maximum d'abondance avec notamment la présence des rapaces. Grâce au trappage et au marquage d'individus qui durent depuis 2004 sur l'Île Bylot, Nunavut, ainsi qu'à l'échantillonnage des nids d'hiver, nous avons déterminé quels paramètres démographiques (i.e. survie ou reproduction) sont à l'origine des phases de déclin et de croissance des lemmings. Ces résultats nous permettent

de vérifier si le calendrier des fluctuations saisonnières d'abondance supporte l'hypothèse de la prédation ou la réfute.

Le chapitre 3 permet de tester plus directement l'hypothèse de régulation de la population des lemmings par la prédation grâce à une réduction expérimentale des prédateurs. Pour cette étude, nous avons construit une clôture de 9 ha coiffée d'un filet fait de monofilaments à pêche pour exclure tous les prédateurs mammaliens et aviaires. Nous y posons l'hypothèse que la réduction de la prédation augmente la densité, la survie, la proportion de juvéniles et la masse corporelle des lemmings pendant l'été. En hiver, la densité des nids devrait également être plus élevée à l'intérieur de la clôture. Ce chapitre utilise une approche puissante (i.e. manipulation expérimentale à grande échelle) afin de clarifier si la prédation limite les lemmings et, si c'est le cas, de préciser les mécanismes en cause.

Afin de vérifier si la prédation est une source de stress importante pour les lemmings et si elle pourrait ultimement affecter la dynamique de leurs populations, nous devions valider une méthode non-invasive permettant de récolter des échantillons sans perturber le niveau de stress basal car le stress augmente au moment d'une capture. Le chapitre 4 décrit et valide une méthode de dosage immunoenzymatique des métabolites fécaux de la corticostérone chez le lemming brun. Ce chapitre repose sur l'hypothèse de l'hormone libre, c'est-à-dire que seule la corticostérone libre est biologiquement active et est excrétée dans le tractus digestif (Breuner *et al.* 2013). Pour cette validation, nous avons prélevé du sang et des fèces chez plusieurs lemmings bruns capturés à la main afin d'obtenir rapidement des échantillons sanguins (<3 min). Ces mêmes lemmings ont été gardés en captivités pour établir leur profil de réponse de stress détecté grâce aux métabolites fécaux. Ce chapitre était essentiel afin de valider la méthode de quantification du stress utilisée au chapitre suivant et de déterminer le temps maximal que les lemmings peuvent rester dans les trappes avant que le stress artificiel lié à la capture ne commence à apparaître dans les échantillons fécaux.

Pour le cinquième et dernier chapitre principal, nous analysons les niveaux de stress des lemmings capturés dans la grille de trappage protégée des prédateurs et dans la grille témoin exposée aux prédateurs. Les niveaux de stress ont été mesurés grâce à une visite

fréquente des pièges et à l'échantillonnage des fèces dans ceux-ci. La méthode développée au chapitre 4 a été utilisée pour quantifier les métabolites fécaux de la corticostérone et ainsi obtenir les niveaux de stress. Nous vérifions ici deux hypothèses principales : (1) la prédation stresse les lemmings et (2) le stress induit par la prédation a un effet délétère sur la fécondité des lemmings. Ce chapitre est la première étude documentant l'effet d'un retrait expérimental à grande échelle des prédateurs sur le niveau de stress de mammifères en milieu totalement naturel. Il s'agit également du premier test de l'hypothèse que la prédation naturelle (i.e. non simulée en laboratoire) peut réduire la fécondité des petits rongeurs en les stressant.

Enfin le sixième et dernier chapitre présente la portée des résultats issus de cette thèse sur mon domaine de recherche et discute du rôle de régulation de la prédation des populations d'herbivores dans le haut Arctique comparativement aux autres milieux nordiques. Des perspectives futures de recherche sont également abordées afin de mettre en lumière les lacunes et besoins de recherche identifiés dans les quatre chapitres principaux de la thèse.

Figure 1.1. Photo d’un lemming brun sur l’Île Bylot.

# CHAPITRE 2. Seasonal demography of a cyclic lemming population in the Canadian Arctic

*Référence de la publication*:

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## 2.1. Résumé

Les causes des fluctuations cycliques dans les populations animales demeurent un sujet controversé en écologie. Les facteurs de limitation démographiques dont l'alimentation et la prédation sont deux hypothèses de premier plan pour expliquer la dynamique des populations des petits mammifères dans les environnements nordiques. Nous avons documenté le calendrier saisonnier des phases de déclin et les paramètres (survie et reproduction) associés aux changements démographiques des lemmings, nous permettant ainsi d'évaluer certaines prédictions de ces deux hypothèses. Nous avons étudié la démographie des lemmings bruns (*Lemmus trimucronatus*), une espèce suivant des cycles de population de 4 ans dans l'Arctique canadien, en combinant les analyses de capture-marquage-recapture issues du trappage vivant estival et le suivi des nids d'hiver sur une période de 10 ans. Nous avons également examiné les effets de certaines variables climatiques sur la survie. Nous avons constaté que le déclin de la population qui suit le pic d'abondance a lieu entre la période estivale et l'hiver et non pas pendant l'hiver. Pendant l'été, la croissance de la population était positivement associée aux changements de survie, mais pas par la fécondité ou la proportion de juvéniles. À l'opposé, la croissance hivernale était principalement associée aux changements reproductifs à la fin de l'été et en hiver. Nous n'avons pas trouvé de densité-dépendance directe sur les paramètres démographiques estivaux, mais notre analyse a été limitée par le manque de données au cours de la phase de faible abondance. Cependant, la masse corporelle était plus élevée au cours des années de pic d'abondance. Des effets météorologiques ont été détectés seulement au début de l'été alors que la survie des lemmings était positivement associée à la profondeur de la neige au début de la fonte et négativement à la pluie. Nos résultats montrent que la mortalité élevée provoque le déclin des populations de lemmings pendant l'été et l'automne, ce qui suggère que la prédation est suffisante pour décimer la population, alors que la fécondité élevée en hiver est le principal facteur menant aux irruptions de la population. L'association positive entre la profondeur de la neige et la survie au début de l'été peut être due au couvert protecteur de la neige contre les prédateurs. On ignore encore pourquoi la reproduction reste faible au cours de la phase de faible abondance.

*Mots clés : Île Bylot, fécondité, Lemmus, cycles des populations, limitation des populations, probabilité de survie, couvert nival, nids d'hiver.*

**2.2. Summary**

The causes of cyclical fluctuations in animal populations remain a controversial topic in ecology. Food limitation and predation are two leading hypotheses to explain small mammal population dynamics in northern environments. We documented the seasonal timing of the decline phases and demographic parameters (survival and reproduction) associated with population changes in lemmings, allowing us to evaluate some predictions from these two hypotheses. We studied the demography of brown lemmings (*Lemmus trimucronatus*), a species showing 3- to 4-year population cycles in the Canadian Arctic, by combining capture–mark–recapture analysis of summer live-trapping with monitoring of winter nests, over a 10-year period. We also examined the effects of some weather variables on survival. We found that population declines after a peak occurred between the summer and winter period and not during winter. During the summer, population growth was driven by change in survival, but not by fecundity or proportion of juveniles, whereas in winter population growth was driven by changes in late summer and winter reproduction. We did not find evidence for direct density dependence on summer demographic parameters, though our analysis was constrained by the paucity of data during the low phase. Body mass, however, was highest in peak years. Weather effects were detected only in early summer when lemming survival was positively related to snow depth at the onset of melt, but negatively related to rainfall. Our results show that high mortality causes population declines of lemmings during summer and fall, which suggests that predation is sufficient to cause population crashes, whereas high winter fecundity is the primary factor leading to population irruptions. The positive association between snow depth and early summer survival may be due to the protective cover offered by snow against predators. It is still unclear why reproduction remains low during the low phase.

*Key-words: Bylot Island, fecundity, Lemmus, population cycles, population limitation, probability of survival, snow cover, winter nests.*

## 2.3. Introduction

Cyclic fluctuations in northern small mammal populations have been the focus of extensive research for almost 100 years (Krebs 2013), but a consensus on the predominant factors generating these cycles has not been reached (e.g. Gauthier et al. 2009). Although numerous long-term time series of fluctuations in small rodent abundance are available, detailed temporal changes in demographic parameters such as reproduction and survival remain scarce. Yet, such information is crucial to fully understand factors driving the dynamics of these populations (Krebs 2011).

Although social interactions may play an important role in the population dynamics of microtine species, the two most popular hypotheses for explaining lemming cycles are the bottom-up (i.e. food) and top-down (i.e. predators) limitation (Krebs 2013). According to the first hypothesis, population cycles should be controlled by variations in food abundance or quality due to a delayed response of plants to grazing. High concentration of plant defensive compounds such as catechins, proteinase inhibitors or silica can affect food consumption and digestion of small mammal (Seldal *et al.* 1994; Berg 2003; Massey *et al.* 2008), but a link between grazing- induced levels of these compounds and population fluctuations was not found in several lemming and northern vole populations (Lindgren *et al.* 2007; Dahlgren *et al.* 2009; Erlinge *et al.* 2011). Alternatively, overgrazing of plants during population peaks may cause the decline of small mammal populations, and low food abundance may limit subsequent population growth as plants need time to recover. Evidence for the food abundance hypothesis was found in both lemming and northern vole populations (Moen et Oksanen 1998; Turchin *et al.* 2000; Pitelka et Batzli 2007). According to the second hypothesis, delayed density-dependent effects of predation and the inability of the prey to compensate for the resulting high mortality could limit small rodent populations (Hanski *et al.* 2001; Gilg *et al.* 2003).

One important difference exists between the predation and food abundance hypotheses as applied to the control of small tundra herbivores, namely the period of the year when conditions should be most limiting. Strong seasonality forces small herbivores like lemmings to survive on a limited food supply during the 9-month-long arctic winter when plants are dormant (Billings et Mooney 1968), and the accessibility may be hindered

by ice crusts formed by melt–freeze events (Aars et Ims 2002; Korslund et Steen 2006). Thus, if food abundance is limiting, population decline should occur in winter, when food depletion will be most severe, as empirically shown in voles (Huitu *et al.* 2003; Ergon *et al.* 2004). In contrast, the predation rate on small mammals increases dramatically during the summer when birds of prey migrate to the Arctic to breed and the disappearance of snow increases access to prey for resident predators like foxes (Gilg *et al.* 2006; Bilodeau *et al.* 2013b; Therrien *et al.* 2014). Therefore, if predation is the limiting factor, population decline should occur mostly during the snow-free period and especially in late summer when predator populations should be highest after the fledging/weaning of young. Determining the seasonal timing of each phase of lemming population cycles (i.e. growth and declines) and seasonal changes in vital rates is thus critical to establish what the most likely limiting factors are.

The demography of lemming and vole populations may differ between the phases of the cycle (Goswami *et al.* 2011). For instance, reproduction declined when lemmings were abundant at Barrow, Alaska (Pitelka et Batzli 2007), the proportion of juvenile collared lemmings (*Dicrostonyx groenlandicus*) was relatively low during the decline phase in Greenland (Gilg 2002), and the proportion of lactating Siberian brown lemmings (Lemmus sibiricus) was higher during the increase than the peak phase (Erlinge *et al.* 2000). As discussed by Goswami *et al.* (2011) for voles, phase-dependent demographic parameters may be indicative of future changes in densities. Other characteristics may also be associated with population density such as body mass, which is often highest during high abundance phases (Krebs 1964; Gilg 2002; Krebs *et al.* 2011b).

Snow quality affects both the amplitude and spatial synchrony of small mammal population cycles in Fennoscandia and eastern Greenland (Aars et Ims 2002; Kausrud *et al.* 2008; Gilg *et al.* 2009). Even in northern Canada where the snow is dry, snow depth and density explain part of the annual variation in brown lemming (*Lemmus trimucronatus*) abundance, presumably because survival is higher under deep snow cover (Bilodeau *et al.* 2013a). High summer rainfall may also negatively affect lemming survival through increased thermoregulation costs and burrow flooding, especially during snow melt

(Shelford 1943; Reid *et al.* 1995). However, few studies have analysed variations in lemming survival in relation to climatic factors.

On Bylot Island in the Canadian Arctic, annual summer trapping of brown lemmings has revealed large amplitude fluctuations of abundance with a 3- to 4-year periodicity (Gruyer *et al.* 2008). Since 2004, we have studied lemming summer demography with live-trapping data and their winter demography with winter nests (Duchesne *et al.* 2011b). Lemming winter nests sampled after snow melt can provide an estimate of spring densities (Krebs *et al.* 2012), whereas the presence of small faeces in those nests can be used to infer winter reproduction (Duchesne *et al.* 2011a). Thus, a combination of long time series of summer and winter demographic data can be used to pinpoint more accurately when population increases and declines occur, and determine which demographic factors are associated with seasonal population changes.

We had three objectives. First, we studied the seasonal timing of lemming population changes over three population cycles to determine whether declines occurred between the winter and early summer (as predicted by the food abundance hypothesis) or between summer and winter (as predicted by the predation hypothesis). Because lemmings consume a small proportion of the plant biomass at our study site in winter (Legagneux *et al.* 2012; Bilodeau *et al.* 2014) and summer predation is high (Therrien *et al.* 2014), we predicted that declines should occur mostly between the summer and winter periods. Our second objective was to identify changes in demographic parameters that are recurrent and associated with population fluctuations. We examined whether summer population growth was mostly related to change in survival, fecundity or proportion of juveniles and whether winter growth was related to fecundity and proportion of juveniles. We also investigated whether changes in demographic parameters and body mass could be due to direct density-dependent effects. Our third objective was to study the effects of selected weather variables on summer survival of lemmings. Based on the study of Bilodeau *et al.* (2013a), we hypothesized that a deep snow cover in spring should increase early summer survival by extending the period during which lemmings are protected from predation under the snow. In contrast, we hypothesized that heavy summer rainfall should reduce summer survival, especially during spring thaw.

## 2.4. Materials and methods

### *2.4.1. Study area*

Our study area was located in the Qarlikturvik valley (~50 km2) on Bylot Island, Nunavut, Canada (73°080 N; 80°000 W). Two main habitats dominate the valley and are used by lemmings (Duchesne *et al.* 2011b). The wet habitat consists primarily of a mosaic of tundra polygons, ponds and thaw lakes and is common in the valley bottom. The surrounding slopes and hills as well as higher grounds in the valley are characterized by mesic tundra, the dominant habitat. The vegetation of the wet habitat is composed of sedges (*Eriophorum* spp., *Carex aquatilis*), grasses (*Dupontia fisheri*) and brown mosses (such as *Limprichtia cossonii* and *Campylium stellatum*), while prostrate shrubs (*Salix* spp., *Cassiope tetragona*), grasses (*Arctagrostis latifolia*, *Alopecurus alpinus*), forbs (*Saxifraga* spp., *Ranunculus* spp.) and some mosses (such a *Polytrichum swartzii*) are dominant in the mesic habitat (Bilodeau *et al.* 2014). The average annual temperature is 15°C, and the ground is generally covered by snow from early October to mid-June.

Only two rodent species are present on Bylot Island: brown and collared lemmings. Here, we focus on the former species because it is the most abundant and its abundance fluctuates >40-fold between the low and peak phases of its cycle (Gruyer *et al.* 2008). Other herbivores include the snow goose (*Anser caerulescens*; during the summer only) and arctic hare (*Lepus arcticus*) and rock ptarmigan (*Lagopus muta*) at very low densities. The main predators are the ermine (*Mustela erminea*), arctic fox (*Vulpes lagopus*), snowy owl (*Bubo scandiacus*) and long-tailed jaeger (*Stercorarius longicaudus*).

### *2.4.2. Small mammal trapping*

From 2004 to 2013, we live-trapped lemmings in two 11-ha permanent grids, one located in wet habitat and one in mesic habitat. Each grid was laid out in a 12 x 12 Cartesian plane (10 x 10 from 2004 to 2006) with 144 trapping stations (100 from 2004 to 2006) separated by 30 m. From 2007 to 2013, a third trapping grid of 7.3 ha (10 x 10) was located in mesic habitat and used for a snow fencing experiment (2008–2011). Although

the enhanced snow depth on that grid increased the density of winter nests, it had no effect on summer population density (Bilodeau *et al.* 2013c). We thus used data from this grid to estimate summer demographic parameters, but not winter parameters. All trapping grids were separated by >500 m to minimize spatial dependence.

Trapping stations had one Longworth trap baited with a piece of apple and stuffed with a 10-cm ball of cotton batting to provide warmth and bedding material. Lemmings were trapped during four primary periods (mid-June, beginning and end of July and mid-August) from 2004 to 2007 and three periods afterwards (mid-June, mid-July and mid-August) according to Pollock's robust design (Williams *et al.* 2002). During each primary period, we visited traps twice a day at 12-h intervals for three consecutive days (4 days from 2004 to 2006), for a total of six (or eight) secondary occasions. We activated one grid at a time and trapping was done consecutively on the three grids at each primary occasion. Traps remained in the field between primary periods for pre-baiting. All captured lemmings were identified to species, weighed, sexed, marked with a Passive Integrated Transponder (PIT, AVID®; Avid Identification Systems, Inc., Norco, CA, USA) tag, and the reproductive condition of females was noted. Females were noted as lactating or gravid when their mammary glands were visible or when foetuses were palpable. From 2010 to 2013, males were noted as reproductive if their scrotum was visible. All subsequent recaptures were noted. Manipulations were approved by the Animal Welfare Committee of Université Laval and Parks Canada (SIR-2013-13953).

### *2.4.4. Estimation of summer demographic parameters*

We estimated five demographic parameters during the summer: population density (*D*), apparent survival (*S*), fecundity (*B*), proportion of juveniles (*J*) and body mass (*M*). In contrast with true survival, mortalities and permanent emigration are not distinguished when estimating survival probabilities. To simplify the text, we will use the term "survival" to designate "apparent survival" throughout the text. Three separate estimates of each parameter were calculated for lemmings trapped on each grid in June, July and August, except for survival which was calculated for the two intervals. From 2004 to 2007, lemmings trapped during both periods of July were pooled as one July group for *B*, *J* and *M*

estimations. Demographic parameters (except *D*, see below) could not be estimated at periods with <5 lemming captures, which frequently occurred during the low phases of the cycle. Sample sizes are provided in Annexe S1.1 (Supporting Information).

Population density was modelled with spatially explicit capture– recapture (SECR) analyses with the package 'secr' implemented in the R software (Efford 2015). This inferential approach uses the spatial structure of the trapping grids and the location of each trapped animal in the grids to estimate densities (lemming $ha^{-1}$) using a maximum-likelihood approach (Efford et Fewster 2013). We used the null SECR model with a 100-m buffer and the half-normal detection function to estimate densities and their standard errors (Krebs *et al.* 2011a). If <4 lemmings were trapped on a grid during a primary period, we used the minimum number of animals alive.

Capture–mark–recapture analyses (Williams *et al.* 2002) were used to estimate survival probabilities between the primary periods (see Annexe S1.2, Supporting Information for methodological details). We estimated the fecundity of females as the proportion of adult females that were lactating or gravid, and the proportion of juveniles among all captured individuals. Females and males were considered adults if they weighed ≥28 g and ≥30 g, respectively (see Annexe S1.3, Supporting Information for criteria used to determine this threshold), and juveniles below these values (individuals became trappable at ~12 g).

### *2.4.5. Estimation of winter demographic parameters*

Starting in 2007, we sampled winter nests after snow melt. During winter, lemmings are most abundant in mesic tundra and especially in small gullies along intermittent streams, which are conducive to deep snow accumulation (Duchesne *et al.* 2011b). We sampled winter nests along forty 500-m long permanent transects (evenly split between mesic tundra and stream gullies) randomly distributed over 40 $km^2$. While walking along each transect, we removed all winter nests found and recorded the perpendicular distance from the transect. Nests are easy to detect at our site due to the low vegetation height. All nests were classified as belonging to brown or collared lemmings according to the size, shape and colour of the faeces (Duchesne *et al.* 2011a; Soininen *et al.* 2015). We eliminated

from the analysis the small number of nests containing faeces of both species. We used the line transect method (Buckland 2001) and the software DISTANCE 6.0 (Thomas *et al.* 2009) to estimate overall densities of brown lemming nests and the associated variance.

The proportion of brown lemming nests with signs of reproduction (based on the presence of small faeces using the criteria of Duchesne *et al.* 2011a) among those found across all transects, provided an overall index of their reproductive activity during winter (a single value per year). To increase sample size in years of low lemming abundance, we also used nests collected along transects run in the wet areas (used to study winter habitat selection; Duchesne *et al.* 2011b) and those found while walking on our trapping grids or opportunistically, to determine reproductive activity.

*2.4.6. Weather variables*

We collected snow and rainfall data at the study site every year. Spring snow depth was monitored annually from ca 25 May to 3 June until disappearance (around 20 June). Snow depth was measured every two days at 50 stations spaced out by 10 m along two 250-m transects running parallel to each other and separated by 100 m. The transects encompassed the two main habitats, wet and mesic. We used the average snow depth observed between 5 and 7 June to obtain an annual measure in spring because these dates were available through all years of the study. Daily rainfall (mm $day^{-1}$) was measured with a rain gauge from early June until 20 August, annually. We averaged daily rainfall for two periods: early (6 June–20 July) and late summer (21 July–20 August). The date of 20 July corresponds to the end of our mid-summer live-trapping period.

2.4.7. Statistical analyses

We used linear mixed-effects models (LMMs) to estimate the relationships between change in population density and demographic parameters. Trapping grids were used as a random factor because the same grids were sampled repeatedly. Coefficients and their standard errors (which are reported throughout the paper) were obtained with the packages 'lme4' (Bates *et al.* 2014) and 'contrast' (Kuhn *et al.* 2013) within the R software. When

appropriate, population growth rates and densities were ln-transformed to respect normality and homoscedasticity was determined visually by plotting the residuals in relation to fitted values. We checked for collinearity among independent variables with Pearson correlations and we avoided including highly correlated variables ($|r| \geq 0.7$) simultaneously in models. Relationships were considered statistically significant when the 95% confidence interval of the slope excluded 0. To assess the amount of variation explained by our models, we report the marginal $R_g^2$ (for fixed effects) and conditional $R_m^2$ (for fixed and random effects) calculated with the method proposed by Nakagawa and Schielzeth (2013) for mixed-effects models.

We used two time units to study changes in population density: intraseasonal (between months, *m*) for summer analyses and interannual (*w*) for winter analyses. We first examined the relationships between the population growth rate ($\lambda$) on each trapping grid and various demographic parameters to verify which ones could explain changes in numbers. To study the effect of winter demography on $\lambda$, we examined the relationship between changes in population density from August of year *y* to June of year *y* + 1, and nest density (M1) or the fecundity index observed in winter nests (M2; Table 2.1). We also examined the relationships between winter $\lambda$ and late summer demographic parameters (fecundity and proportion of juveniles, models M3–M4). We used separate models because several of these independent variables were highly correlated (see Results). We further assessed the relationship between annual change in winter nest density and population density measured in August (model M5). For intraseasonal analyses, we examined the relationship between $\lambda$ during the summer months and demographic parameters observed during the interval (for survival, model M6) or at the start of the interval (for fecundity and proportion of juveniles, models M7 and M8) on each trapping grid.

In simple linear regressions between two variables measured with an error, such as survival and population density, the uncertainty associated with the slope should consider variance components of both variables. We thus used ranged major axis regressions to estimate the slope and its 95% confidence intervals when an error was present on both axes (models M1, M5 and M6) using the package 'lmodel2' (Legendre 2014) implemented in

the software R. Coefficients estimated with ranged major axis regressions assume that the response and explanatory variables are correlated, which was verified.

We tested for direct density dependence on summer survival, proportion of juveniles, adult body mass (both sexes combined) and fecundity (i.e. relationships between demographic parameters and monthly population density on each trapping grid, models M9–M12, Table 2.1). We conducted analyses on fecundity if we had ≥5 adult females and on proportion of juveniles if we had ≥5 lemmings, regardless of age and sex. Post hoc multiple comparisons were conducted using Tukey's tests to determine whether there were differences between months.

We used LMMs to assess potential effects of weather variables on demographic parameters, also using trapping grid as a random variable. We examined the relationships between June–July survival (dependent variable) and spring snow depth or June–July rainfall, and between July–August survival and July–August rainfall.

## 2.5. Results

### *2.5.1. Fluctuations in lemming abundance*

Brown lemmings showed large fluctuations in abundance (Fig. 2.1). During summer 2004, population density was high but declined to very low values in early summer 2005 until summer 2007. Nest density increased in winter 2007–2008 compared to the previous year. Population density was high in early summer 2008 but winter nest density indicated that it had declined to low levels by the following winter and remained low in summer 2009. Nest density increased in winter 2009–2010 as well as population density in summer 2010, compared to the previous year. Nest and population densities remained high during winter 2010–2011 and early summer 2011. Population density declined in summer 2011, and nest density was very low during the following winter. Lemming abundance was very low during summers 2012 and 2013 and the winter in between.

*2.5.2. Estimation of demographic parameters*

Sample size allowed an estimation of summer survival only in years of high abundance (2004, 2008, 2010 and 2011). The most parsimonious models for estimating probabilities of survival differed between years (see Annexe 1.2, Table S1.3 for model selection). In 2004 and 2008, models with constant survival between months and trapping grids were preferred, but survival probabilities differed between trapping grids in 2010 and trapping grids and months in 2011. Model-averaged survival estimates in 2010 and 2011 were higher in the mesic trapping grids compared to the wet grid, and higher in June–July than July–August (Table 2.2).

Estimation of summer fecundity was also possible only in years of high abundance. The average proportion of females with signs of reproduction was lowest in August 2008 ($B$ = 0.07, $n$ = 13) and highest in July 2010 ($B$ = 0.69, $n$ = 60). In winter, the proportion of nests with signs of reproduction averaged 0.25 ($n$ = 1534). The lowest value occurred in 2007 ($B^{WN}$ = 0.12, $n$ = 76) and the highest in 2010 ($B^{WN}$ = 0.41, $n$ = 497). The proportion of juveniles could be estimated in most years except in 2013 and a few periods in 2006, 2009 and 2012. The lowest proportion of juveniles occurred in June 2005 with no juvenile being captured ($J$ = 0.0, $n$ = 11) and the highest proportion was in August 2008 ($J$ = 0.72, $n$ = 80). The average body mass of adult lemmings could not be estimated in 2006, 2013 and some periods in 2007, 2009 and 2012. The lowest average body mass was observed in June 2012 ($M$ = 35.4 g, $n$ = 5) and the highest in July 2011 ($M$ = 56.8 g, $n$ = 230).

*2.5.3. Covariate effects of demographic parameters.*

Growth rate of lemming populations over winter was positively related to winter nest density (M1) and to reproductive activity in winter nests (M2, Table 2.3). Winter nest density and fecundity index were highly correlated ($r$ = 0.89). Thus, when density of winter nests and reproductive rates were high, the population increased, but it decreased when these parameters were low (Fig. 2.2A). Similarly, population growth rate over winter was positively related to the proportion of reproductive females in August (M3, Fig. 2.2B), but not to the proportion of juveniles (M4, Table 2.3). Fecundity in August and in nests during

the following winter were also positively correlated ($r$ = 0.75). In contrast, annual change in winter nest density was negatively related with population density in late August (M5).

During the summer, monthly growth rate of lemming populations was positively related to their survival rate (M6, Fig. 2.3), but not to fecundity (M7) or proportion of juveniles (M8, Table 2.3). Although demographic parameters were variable during the summer, we found no direct density-dependent effect on survival, recruitment or fecundity (M9, M10 and M11, Table 2.3). The proportion of juvenile lemmings was higher (M10) in August (0.54) compared to June (0.25) and July (0.20), but fecundity of adult females was similar (M11) between months (June: 0.37, July: 0.44, August: 0.35). The only significant direct density-dependent effect was on body mass (M12, Table 2.3). Adult lemmings were heavier during high abundance years than in low years and heavier in July (57.5 g) than in June (36.8 g) or August (46.7 g; Fig. 2.4).

#### 2.5.5. Weather effects

The snow depth observed at the beginning of melt and total rainfall in June–July had opposite effects on early summer lemming survival ($R_g^2$ = 0.74, $R_c^2$ = 0.85); survival probability increased with snow depth ($\beta$ = 0.008, SE = 0.002) but decreased with daily rainfall ($\beta$ = -0.39, SE = 0.08; Fig. 2.5). Daily rainfall did not have any effect on late summer survival ($\beta$ = 0.00, SE = 0.02).

## 2.6. Discussion

### *2.6.1. Timing of population change*

Our results show that lemming population declines occurred between the late summer and winter periods on Bylot Island. Indeed, a large population decline between late summer and the following spring was associated with a very low abundance of winter nests and was further confirmed by the negative relationship between annual change in winter nests and late summer density. This is likely a general pattern as Krebs *et al.* (2012) reported that winter nest abundance was more strongly correlated with spring than late summer population size across several sites in the Canadian Arctic. In contrast, population

build-ups during our study occurred in winter as high density of winter nests was associated with peak lemming densities in the following summers. Finally, periods of peak density were short-lived and were followed by a population decline before the onset of winter as evidenced by the low density of nests in winters following peak summer abundance.

Winter nests provide shelters for lemmings under the snow and are important for thermoregulation, rearing young, and survival (Casey 1981; Duchesne *et al.* 2011b). Our results show that reproductive activity in those nests can be very high in some years. In certain areas, lemmings can apparently overwinter in natural sites with a high accumulation of litter, such as in tussock tundra in northern Alaska (Krebs *et al.* 2012). However, these features are absent from most of the Canadian High Arctic due to the sparse vegetation cover. Therefore, as the ground freezes in the fall and snow sets in, these nests become important shelters. The strong positive relationship between winter population growth rate and reproductive activity substantiates previous suggestions that lemming population growth is conditional upon high winter reproduction (Millar 2001; Krebs 2011).

The seasonal pattern in brown lemming population changes that we document here differs from that reported in northern Alaska. At this site, high winter nest density is generally associated with low population density at snow melt, which suggests that population crashes occur mostly during winter, possibly due to winter food limitation (Pitelka et Batzli 2007). Interestingly, peak lemming densities in northern Alaska can reach 100-200 ind $ha^{-1}$, which is much higher than peak densities reported elsewhere in the Canadian Arctic or Greenland, usually 10-15 ind $ha^{-1}$ (Wilson *et al.* 1999; Gilg *et al.* 2003; this study). Experimental and observational studies conducted at the latter sites suggest that delayed density-dependent effects of specialist predators (e.g. weasels) and direct density-dependent effects of generalist predators cause population declines (Wilson *et al.* 1999; Gilg *et al.* 2003) or else maintain populations at low density (Reid *et al.* 1995). In northern voles, an experimental removal of predators allowed peak populations to exceed 150 ind $ha^{-1}$, compared to <50 ind $ha^{-1}$ on the control, which then prompted a population crash due to winter food limitation (Huitu *et al.* 2003).

Recent evidence shows that, unlike what has been reported for *Lemmus* elsewhere, brown lemmings on Bylot Island consume willows (*Salix* spp.) in high proportion during

winter (56% of their diet), along with mosses (Soininen *et al.* 2015). They can take advantage of the high abundance of prostrate willows at our study site during the critical winter period without negatively affecting its biomass in snow beds, even during years of high abundance (Bilodeau *et al.* 2014). Thus, a lack of food during winter, as predicted by the food abundance hypothesis, is unlikely to explain the periodic declines of brown lemmings in the Canadian Arctic.

### *2.6.2. Demography and population changes*

We found a highly interesting contrast between summer and winter in the demographic factors associated with lemming population changes. During the summer, population growth was apparently driven by change in survival, but not in fecundity or proportion of juveniles, whereas in winter it was driven by changes in late summer and winter reproduction. Even though we used capture–recapture methods to estimate survival, we recognize that mortality is here confounded with permanent emigration, which includes dispersal, and could vary with phases of the cycle. However, given that survival could only be estimated in years of moderately high abundance, variations in dispersal rate with cycle phase should not be a serious issue here. Although we could not measure survival probability during winter, the contrasting effects of fecundity on summer and winter population growth rates indicate that factors limiting lemmings vary seasonally.

During summer, it is safe to say that predation is the main cause of mortality due to the high abundance of birds of prey, foxes and ermines (Reid *et al.* 1995; Therrien *et al.* 2014). Because survival was the only demographic parameter related to summer population change, predation may thus be the main factor driving lemmings into a summer decline, as found in Greenland (Gilg *et al.* 2006). Young born in winter will have matured and should be able to reproduce during the summer, which could explain why the proportion of juveniles in the population peaked in late summer. Nonetheless, high reproductive activity did not prevent the summer population from declining. Although we have no data from mid-August until the onset of snow in October, predation is likely to remain high as the population of predators should increase with the addition of recently-fledged and weaned juveniles.

At the beginning of winter, lemmings move under the snow and become less vulnerable to predation (Duchesne *et al.* 2011b; Bilodeau *et al.* 2013c). Furthermore, most avian predators have migrated southwards (Gilg *et al.* 2009; Therrien *et al.* 2014). Thus, lemming survival should improve as soon as the snow cover settles, which may explain why fecundity then becomes a driver of lemming population change, unlike in the summer. Interestingly, winter population growth rate was also positively associated with fecundity in August. The reproductive output of lemmings during winter may thus be dependent upon their condition in late summer, as also reported by Wilson *et al.* (1999) and Krebs *et al.* (2011b). Nonetheless, we recognize that we have no data on winter survival, and nests only provide information on overall reproduction during the 9-month-long winter period. For instance, we have no information on the timing of winter reproduction, whereas breeding onset can be important in some vole population dynamics (Ergon *et al.* 2011).

We did not find any evidence for direct density dependence on summer demographic parameters, which indicates that density had little direct effect on summer growth. However, a limitation of our analysis was that these parameters, and especially survival, could only be estimated in years of moderate to high densities due to small sample sizes in other years. Therefore, density-dependent effects could still be present when considering all phases of the cycle (Goswami *et al.* 2011). The strong effect of weather on summer survival may also have weakened our ability to detect density dependence. Body mass of adult lemmings was the only density-dependent parameter, which supports the hypothesis that lemmings are generally larger during years of peak density (Krebs 1964; Gilg 2002).

If reproduction is driving population growth in winter, it is surprising that populations do not recover more quickly after a population crash. Clearly, the population must be exposed to delayed density dependence that prevents its quick recovery (Boonstra *et al.* 1998b; Barraquand *et al.* 2014). A possible mechanism may be a delayed, negative neuro-endocrinological effect on fecundity, as recently shown in the snowshoe hares (*Lepus americanus*; Boonstra et al. 1998; Sheriff, Krebs et Boonstra 2009) and root voles (*Microtus oeconomus*; Bian et al. 2015). Chronic stress induced by high predator density or social interactions, either alone or in interaction with predation risk, may cause breeding

suppression in small mammals and be carried over to the winter period due to maternal effects (Jochym et Halle 2012). However, we note that we did not find any density-dependent effect on fecundity, and Ylönen *et al.* (2006) found no change in corticosterone levels in bank voles (*Myodes glareolus*) exposed to weasel odours. In some vole populations, it has been suggested that a delay in the initiation of spring breeding due to grazing-induced change in plant quality (e.g. phenolic compounds or silica content) could be a mechanism leading to delayed density dependence (Massey *et al.* 2008; Ergon *et al.* 2011). However, considering that lemming reproduction occurs in winter when plants are dormant (Billings et Mooney 1968), it is difficult to imagine how such mechanisms could operate. It is also possible that poor snow condition limits access to food in some winters (Korslund et Steen 2006).

### *2.6.3. Effects of weather on summer survival*

Our analysis suggests that climatic factors may also affect summer survival of lemmings. However, it is possible that the high early summer survival in years of deep snow cover is actually an indirect effect mediated through predation. Although deep snow cover in winter may provide benefits to lemmings in terms of improved insulation (Duchesne *et al.* 2011b), this is unlikely at snow melt when temperatures are milder above the snow pack than underneath (Bilodeau *et al.* 2013a). A deep snow cover will delay snow melt and could allow lemmings to move for a longer period of time under the protective cover offered by snow during the melt period (Gilg *et al.* 2009). The result is also consistent with the positive correlation between snow depth and the amplitude of lemming population cycles shown by Bilodeau *et al.* (2013c).

High rainfall was another climatic factor that negatively affected early summer survival of lemmings. High precipitation during spring should accelerate the melting of snow, increase run-off, and cause streams to overflow. On one hand, this could reduce the period during which snow still offers a protective cover. On the other hand, high rainfall may flood lemming habitats in lowlands, including burrows, thereby increasing mortality. This could also force individuals to move more in search of drier grounds, thereby increasing their vulnerability to predators (Shelford 1943).

## 2.7. Conclusion

Our study presents for the first time a detailed analysis of the seasonal (summer and winter) demography of a lemming species over multiple cycles. We show that mortality, likely due to predation, drives summer population growth and is the major factor causing fall population crashes during peak years in brown lemmings. High winter reproduction appears to be the main driver of the increase phase of the population cycle, but it is still unclear why reproduction does not increase immediately after the decline (i.e. the low phase remains unexplained). A neuro-endocrinological response through maternal effects is a candidate factor, though a limited access to food in years of poor snow condition is another potential explanation. Experimental manipulations will be required to fully decipher the causal effects of predation or food on these demographic parameters (Huitu *et al.* 2003; Krebs 2011). Our results support a multifactorial hypothesis to explain lemming population growth and decline phases, where changes in survival and reproduction may be caused by both biotic (i.e. direct and possibly also indirect effects of predators) and abiotic (i.e. snow cover and rainfall) factors. The general decline of snow cover observed in the Canadian Arctic (Derksen et Brown 2012) may be of particular concern for lemming populations because it may extend their period of vulnerability to predators during the snow-free period, while reducing their potential for population growth under the snow.

## 2.8. Acknowledgements

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### 2.9. Data accessibility

All data used in this manuscript are available at the NordicanaD website: http://dx.doi.org/10.5885/45400AW-9891BD76704C4CE2 (Gauthier 2015).

### 2.10. Suplementary material

Annexe S1.1. Sample size.

Annexe S1.2. Methods and model selection for the estimation of survival probabilities.

Annexe S1.3. Body mass criteria used to determine maturity.

## 2.11. Tables

Table 2.1. Candidate models for determining the effects of demographic parameters on lemming population growth rate and density-dependent effects on demographic parameters.

| Model ID | Response variables | Independent variables | Model description |
|---|---|---|---|
| M1 | $\lambda_w$ | $D^{WN}$ | Effect of winter nest density on winter population growth rate |
| M2 | $\lambda_w$ | $B^{WN}$ | Effect of winter reproduction on winter population growth rate |
| M3 | $\lambda_w$ | $B^{A}$ | Effect of August fecundity on winter population growth rate |
| M4 | $\lambda_w$ | $J^{A}$ | Effect of proportion of juveniles in August on winter population growth rate |
| M5 | $\lambda^{WN}$ | $D^{A}$ | Effect of August population density on change in winter nest density |
| M6 | $\lambda_m$ | $S_m$ | Effect of monthly survival (from $m$ to $m$+1) on monthly population growth rate |
| M7 | $\lambda_m$ | $B_m$ | Effect of monthly fecundity on monthly population growth rate |
| M8 | $\lambda_m$ | $J_m$ | Effect of monthly proportion of juveniles on monthly population growth rate |
| M9 | $S_m$ | $D_m$ | Direct density-dependence on monthly survival (from $m$ to $m$+1) |
| M10 | $J_m$ | $D_m$, $m$ | Direct density-dependence on monthly proportion of juveniles |
| M11 | $B_m$ | $D_m$, $m$ | Direct density-dependence on monthly fecundity |
| M12 | $M_m$ | $D_m$, $m$ | Direct density-dependence on monthly body mass |

Note: $\lambda_w = D_{w+1}^{Jn}/D_w^A$; $\lambda_m = D_{m+1}/D_m$; $\lambda^{WN} = D_{w+1}^{WN}/D_w^{WN}$; $\lambda$ = population growth rate; $D$ = population density, $D^{WN}$ = winter nest density; $S$ =survival; $B$ = fecundity; $J$ = proportion of juveniles; $M$ = body mass; $Jn$ = June; $A$ = August; $m$ = month; $w$ = winter.

Table 2.2. Monthly survival probability estimates (*S*) of brown lemmings trapped on three different grids on Bylot Island. Periods extend from the middle of each month except in 2004. Survival was obtained by capture-mark-recapture analysis, which controls for capture probabilities, and mean and standard errors were averaged across models (see Annexe S1.2).

| | | Mesic 1 | | Mesic 2 | | Wet | |
|---|---|---|---|---|---|---|---|
| Year | Period | *S* | SE | *S* | SE | *S* | SE |
| 2004 | July-July[a] | 0.32 | 0.06 | –[b] | – | 0.30 | 0.06 |
| | July-August[c] | 0.31 | 0.06 | – | – | 0.29 | 0.05 |
| 2008 | June-July | 0.26 | 0.07 | 0.27 | 0.06 | 0.26 | 0.05 |
| | July-August | 0.28 | 0.07 | 0.28 | 0.06 | 0.27 | 0.05 |
| 2010 | June-July | 0.56 | 0.24 | 0.56 | 0.19 | 0.38 | 0.15 |
| | July-August | 0.41 | 0.07 | 0.45 | 0.09 | 0.31 | 0.08 |
| 2011 | June-July | 0.61 | 0.09 | 0.59 | 0.10 | 0.44 | 0.10 |
| | July-August | 0.28 | 0.06 | 0.34 | 0.09 | 0.13 | 0.07 |

[a†]Survival estimates for the period of early July to end of July.

[b]Grid «Mesic 2» did not exist in 2004.

[c]Survival estimates for the period of end of July to mid-August.

Table 2.3. Slope parameters and their 95% confidence intervals (CI) for all variables tested in the models described in Table 1. Variables and coefficients in bold have confidence intervals that exclude 0. Marginal $R^2$ for mixed-effects models are shown and were identical to conditional $R^2$ for all models except M9 ($R_c^2 = 0.07$).

| Model ID | Response variable | Explanatory variable | $\beta$ | Low CI | High CI | $R_g^2$ |
|---|---|---|---|---|---|---|
| M1† | $\ln(\lambda_w)$ | $\boldsymbol{D^{WN}}$ | **1.58** | **0.94** | **2.54** | 0.55 |
| M2 | $\ln(\lambda_w)$ | $\boldsymbol{B^{WN}}$ | **25.6** | **17.3** | **33.9** | 0.70 |
| M3 | $\ln(\lambda_w)$ | $\boldsymbol{B^{A}}$ | **7.53** | **3.76** | **11.3** | 0.69 |
| M4 | $\ln(\lambda_w)$ | $J^A$ | -2.18 | -6.96 | 2.60 | 0.07 |
| M5[a] | $\ln(\lambda^{WN})$ | $\boldsymbol{\ln(D^A)}$ | **-1.23** | **-3.28** | **-0.41** | 0.29 |
| M6[a] | $\ln(\lambda_m)$ | $\boldsymbol{S_m}$ | **4.95** | **0.33** | **14.8** | 0.18 |
| M7 | $\ln(\lambda_m)$ | $B_m$ | -0.50 | -1.43 | 0.44 | 0.02 |
| M8 | $\ln(\lambda_m)$ | $J_m$ | 0.61 | -2.13 | 3.35 | 0.01 |
| M9 | $S_m$ | $\ln(D_m)$ | -0.01 | -0.08 | 0.06 | 0.00 |
| M10 | $J_m$ | $\ln(D_m)$ | -0.00 | -0.05 | 0.04 | 0.49 |
| | | $\boldsymbol{m_{Jl}}$ | **-0.39** | **-0.53** | **-0.26** | |
| | | $\boldsymbol{m_{Jn}}$ | **-0.37** | **-0.52** | **-0.22** | |
| M11 | $B_m$ | $\ln(D_m)$ | 0.14 | -0.05 | 0.33 | 0.11 |
| | | $m_{Jl}$ | 0.08 | -0.15 | 0.32 | |
| | | $m_{Jn}$ | 0.00 | -0.29 | 0.29 | |
| M12 | $M_m$ | $\boldsymbol{D_m}$ | **1.02** | **0.34** | **1.70** | 0.34 |
| | | $\boldsymbol{m_A}$ | **-4.90** | **-9.26** | **-0.55** | |
| | | $\boldsymbol{m_{Jn}}$ | **-6.66** | **-11.28** | **-2.04** | |

$\lambda$ = population growth rate; $D$ = population density; $WN$ = winter nest density; $S$ = survival; $B$ = fecundity; $J$ = proportion of juveniles; $M$ = body mass; $m$ = month; $w$ = winter; $A$ = August; $Jl$ = July, $Jn$ = June

[a]Slope estimated with a ranged major axis regression.

## 2.12. Figures

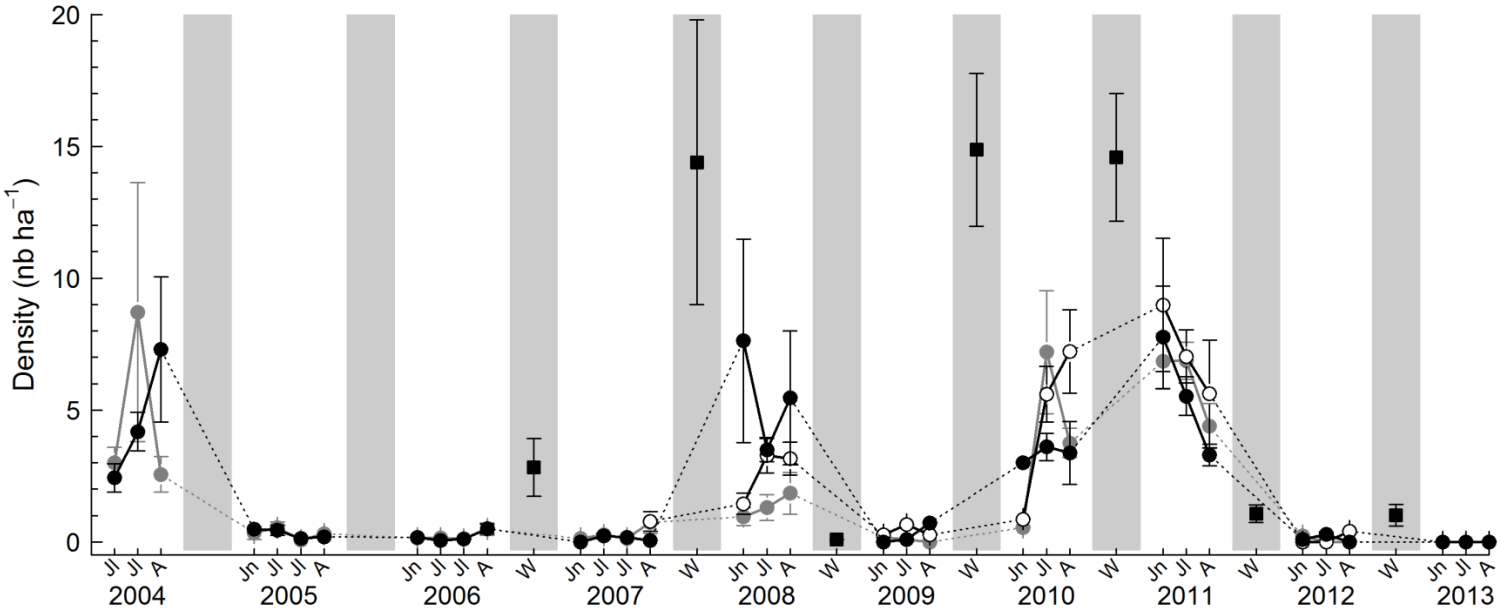


Fig. 2.1. Temporal fluctuations in brown lemming populations represented by monthly population densities in summer (circles) and nest densities in winter (squares) with their standard error on Bylot Island, NU, Canada. Population densities are presented for three trapping grids: wet (black circles), mesic 1 (grey circles), and mesic 2 (open circles, starting in 2007 only). Winter nest densities (black squares) are averaged values across the study area. Gray areas represent winters and stippled lines link late summer population density of year *y* with early summer population density of year *y* + 1. Jn = June, Jl = July, A = August, W = winter

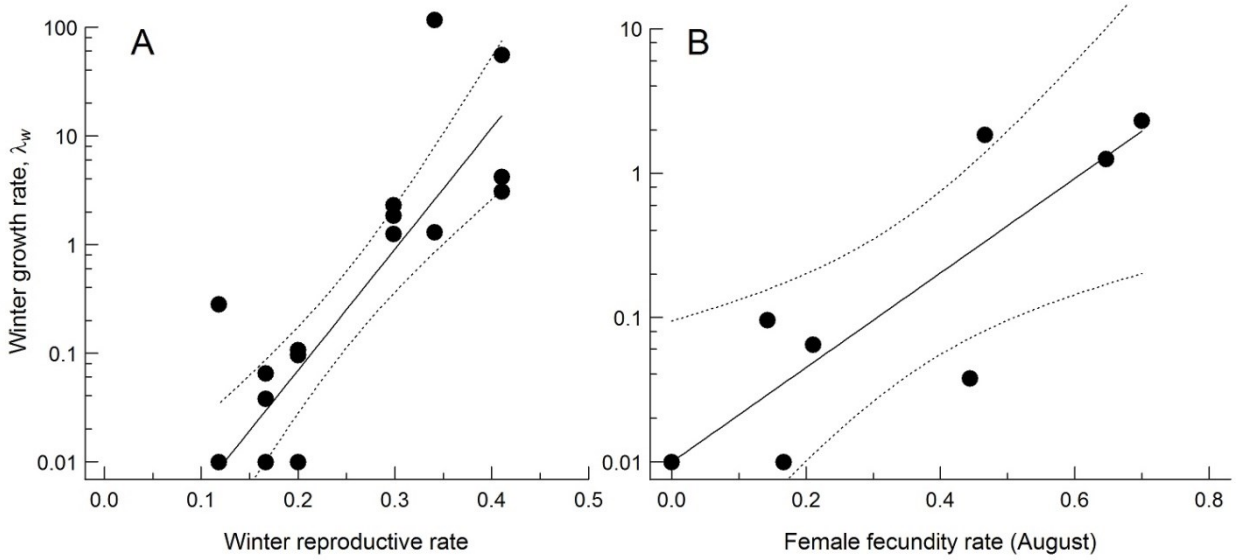


Fig. 2.2. Relationships between winter population growth rate ($\lambda_w$, from August of year $y$ to June of year $y$+1) of brown lemmings on each trapping grid and reproductive rate in winter nests (A) as well as fecundity of adult females measured in August (B). The regression (solid lines) and 95% confidence intervals (dotted lines) are presented.

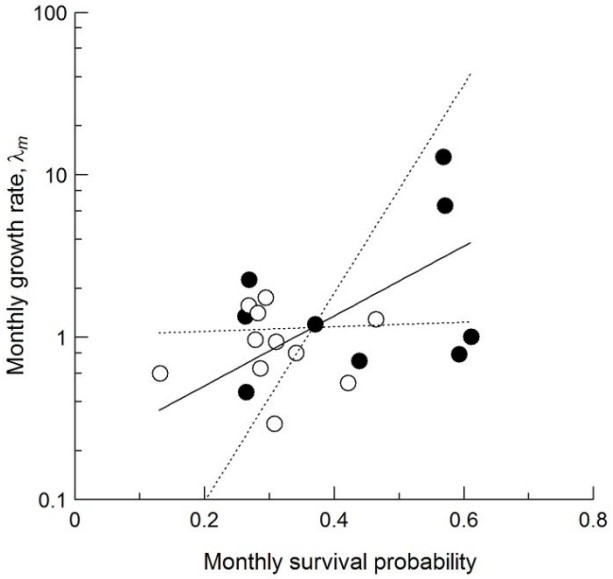


Fig. 2.3. Relationship between monthly population growth rate ($\lambda_m$) of brown lemmings and survival probability over the same period on each trapping grid. Monthly survival estimates are shown for the periods June-July (filled circles) and July-August (open circles). Regression (solid line) and 95% confidence interval (dotted lines) were estimated with a ranged major axis regression.

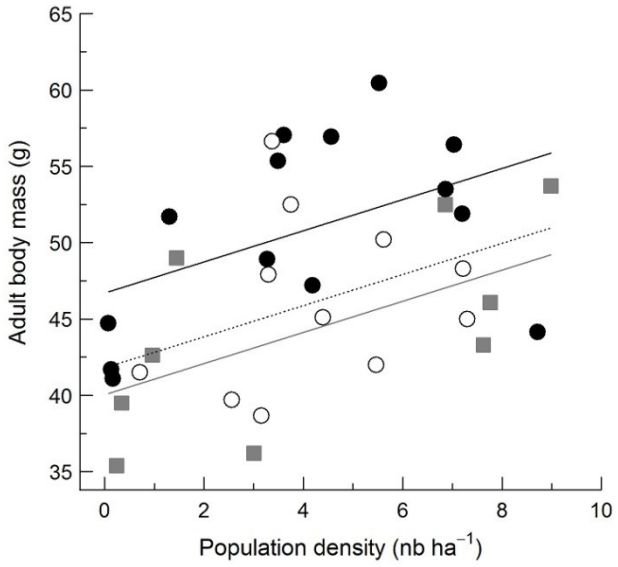


Fig. 2.4. Relationship between adult body mass of brown lemmings and population density measured in June (grey squares and line), July (black circles and solid line), and August (open circles and stippled line) on each trapping grid.

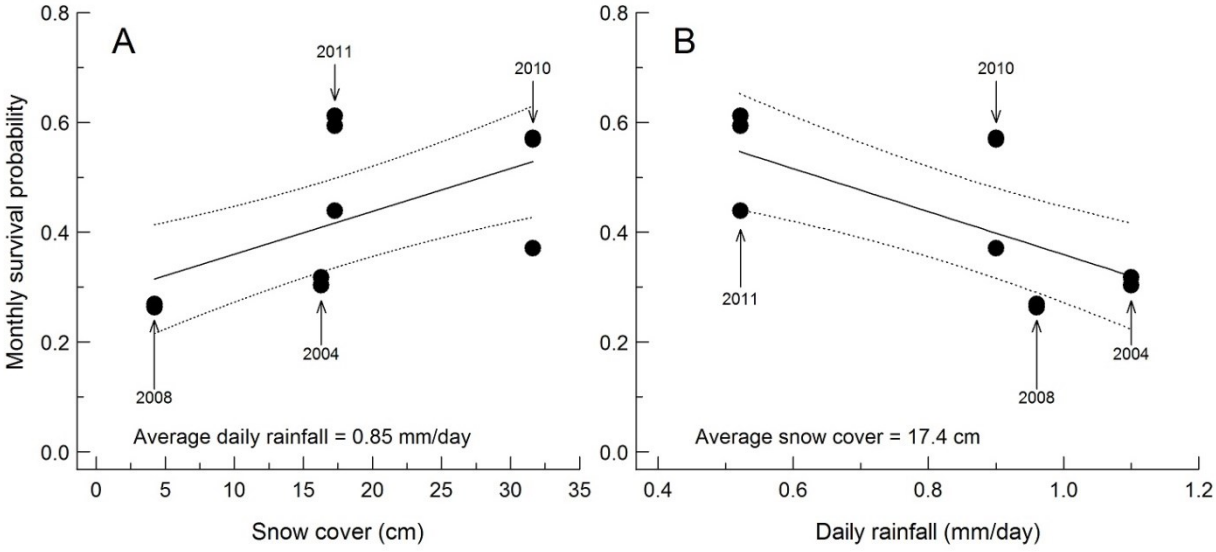


Fig. 2.5. Relationships between early summer (June to July) survival probability of brown lemmings on each trapping grid and spring snow depth (A) and mean daily rainfall (B). The regression (solid lines) and 95% confidence intervals (dotted lines) are presented.

# CHAPITRE 3. Top-down limitation of lemmings revealed by experimental reduction of predators

*Soumis :*

Fauteux, D., Gauthier, G. et Berteaux, D. (2016). Top-down limitation of lemmings revealed by experimental reduction of predators. *Ecology.*

### 3.1. Résumé

Il est généralement reconnu que la densité-dépendance avec délai est responsable de la dynamique des populations cycliques. Cependant, il est encore incertain si un seul facteur peut expliquer pourquoi certaines populations de rongeurs fluctuent selon une périodicité de 3-4 ans. Il y a de plus en plus de preuves que la prédation peut jouer un rôle au niveau des cycles des populations de lemmings, bien que cette relation puisse varier selon les saisons. Nous avons mené une expérience où nous avons construit un grand exclos (9 ha) pour protéger les lemmings bruns de prédateurs aviaires et terrestres. Nous avons testé l'hypothèse que la prédation est un facteur limitant pour lemmings en mesurant les conséquences démographiques de la réduction de prédateurs et ce, pendant les phases du cycle de croissance et de pic d'abondance. De 2008 à 2015, nous avons évalué la démographie des lemmings pendant l'été (méthodes de capture-marquage-recapture) et en hiver (hiver nid échantillonnage) sur deux grilles situées sur l'île Bylot, Nunavut, Canada. L'exclos à prédateur est devenu pleinement efficace en Juillet 2013, ce qui nous a permis de comparer les paramètres démographiques entre la grille témoin et expérimentale. Avant le traitement expérimental, l'abondance des lemmings, leur survie et la proportion de juvéniles étaient similaires entre les deux grilles. Au cours de l'expérience, les densités estivales étaient en moyenne 1,9× plus élevées à l'intérieur de la grille expérimentale que le témoin et cet effet était plus grand pour les femelles et les juvéniles (densités de 2,4× et 3,4× plus élevée, respectivement). La survie estivale des lemmings était 1,8× plus élevée sur la grille expérimentale que sur la grille témoin alors que la masse corporelle et la proportion de juvéniles étaient aussi légèrement plus élevées. Suite à l'été de forte abondance, la densité des nids d'hiver est restée élevée à l'intérieur de l'exclos, mais a diminué dans la grille témoin. Ces résultats confirment que la prédation limite la croissance de la population des lemmings au cours de l'été en raison de son impact négatif sur la survie. Toutefois, il est possible que pendant l'hiver la prédation interagisse avec d'autres facteurs qui influent sur la reproduction et ultimement sur les cycles de la population.

*Mots clés : interactions trophiques, saisonnalité, interactions prédateur-proie, régulation des populations, capture-marquage-recapture, cycles des populations.*

### 3.2. Summary

It is generally recognised that delayed density-dependence is responsible for cyclic population dynamics. However, it is still uncertain whether a single factor can explain why some rodent populations fluctuate according to a 3-4 yr periodicity. There is increasing evidence that predation may play a role in lemming population cycles, although this effect may vary seasonally. To address this issue, we conducted an experiment where we built a large exclosure (9 ha) to protect brown lemmings (*Lemmus trimucronatus*) from avian and terrestrial predators. We tested the hypothesis that predation is a limiting factor for lemmings by measuring the demographic consequences of a predator reduction during the growth and peak phases of the cycle. We assessed summer (capture-mark-recapture methods) and winter (winter nest sampling) lemming demography on two grids located on Bylot Island, Nunavut, Canada, from 2008 to 2015. The predator exclosure became fully effective in July 2013, allowing us to compare demography between the control and experimental grids before and during the treatment. Lemming abundance, survival and proportion of juveniles were similar between the two grids before the treatment. During the predator-reduction period, summer densities were on average 1.9× higher inside the experimental grid than the control and this effect was greatest for adult females and juveniles (densities 2.4× and 3.4× higher, respectively). Summer survival was 1.8× higher on the experimental grid than the control whereas body mass and proportion of juveniles were also slightly higher. Winter nest densities remained high inside the predator reduction grid following high summer abundance but declined on the control grid. These results confirm that predation regulates lemming population growth during the summer due to its negative impact on survival. However, it is possible that in winter, predation may interact with other factors affecting reproduction and ultimately population cycles.

*Key words: trophic interactions, seasonality, predator-prey interactions, population regulation, capture-mark-recapture, population cycle.*

## 3.3. Introduction

Cyclic populations are known since the pioneer work of Charles Elton in rodents (1924) but factors responsible for such dynamics have remained elusive in many instances (Sinclair et Krebs 2002, Krebs 2013, Barraquand *et al.* 2014). Collapsing cycles in several boreal and arctic environments and taxa have been suggested to be a consequence of climate change (Ims *et al.* 2008, Gilg *et al.* 2009, Cornulier *et al.* 2013), which emphasizes the critical need to identify the mechanisms driving these cycles.

Several hypotheses have been proposed to explain why some populations of small rodents fluctuate according to a 3-5 yr periodicity (Stenseth 1999). It is generally recognized that delayed density-dependence is required to force populations into decline once the potential for growth is overcome by opposing forces (Royama 1992). These forces can be both extrinsic (Krebs 2013) and intrinsic (e.g. maternal effects; Inchausti et Ginzburg 2009). Predation and food availability are two leading hypotheses to explain vole and lemming cycles (Krebs 2011, Prevedello *et al.* 2013). Other hypotheses such as parasites (Forbes *et al.* 2014) and intrinsic factors like stress (Boonstra et Boag 1992) have also been proposed but even if they may negatively affect population growth, there is still no evidence that they can be solely responsible for population cycles in small mammals.

Single factor hypotheses, however, have often failed to fully explain cyclic dynamics (Boonstra *et al.* 1998, Huitu *et al.* 2003, Gauthier *et al.* 2009, Krebs 2013), which has spurred new interest into the phase or seasonal dependency of population growth processes (Barraquand *et al.* 2014). For instance, population growth may be mainly limited by mortality during periods of high predation rate while it may be limited by reproduction (i.e. resource availability) during periods of low predation rate such as when individuals are protected from predators by the snow (Fauteux *et al.* 2015). Predation and food availability may thus both play a role as the strength of trophic interactions can vary through time at a single site (Sinclair *et al.* 2000). In this context, field experiments are critical to identify the causal relationships between hypothesised factors and population growth.

There is increasing evidence that predation may be a key factor in the cyclic dynamics of lemmings in Arctic Canada and Greenland (Reid *et al.* 1995, Gilg *et al.* 2003, Therrien *et al.* 2014, Fauteux *et al.* 2015). Manipulating predation in the field, however, is a

daunting task and previous studies have reported multiple potential problems such as mechanical failures of exclosures (e.g. predators going through fences, Reid *et al.* 1995) or indirect manipulation of non-target factors (e.g. fence-effect, Ostfeld 1994). Another caveat of several predator manipulation experiments is the paucity of empirical evidence that predators were effectively excluded from protected areas or the potential attraction of predators to the neighborhood of the exclusion area (Salo *et al.* 2010). The lack of replication has also been presented as a limitation for large-scale predator manipulation experiments. However, as the number of experimental studies increases in the literature, meta-analyses can successfully identify general patterns (Salo *et al.* 2010, Prevedello *et al.* 2013). Manipulative field experiments remain the most powerful method to test clearly defined hypotheses, even when they involve the manipulation of a single factor due to logistic constraints (Krebs 2011).

On Bylot Island, Nunavut, Canada, brown lemmings (*Lemmus trimucronatus*) show large amplitude fluctuations in abundance (up to 100-fold) according to a 3-4 yr periodicity (Fauteux *et al.* 2015). Because previous studies at this site suggested that food availability was not limiting for lemmings (Legagneux *et al.* 2012, Bilodeau *et al.* 2014), our manipulation focused on predation. Our study is the first to assess experimentally the effects of predation on brown lemming population dynamics in the High Arctic. Moreover, our long-term dataset included pre-experiment trapping surveys spanning several years, thereby providing a rare opportunity to compare our treatment effect with the pre-treatment situation at the same site, in addition to comparison with a control site (Smith 2013). Our main goal was to determine the demographic consequences of a reduction in predator abundance on brown lemmings in both summer and winter, during the growth and peak phases of the cycle. We hypothesised that predation is a limiting factor that reduces the realised growth rate of lemming populations. We tested the following predictions: (1) population densities and survival will be higher in our predator reduction grid compared to the control, (2) the proportion of juveniles captured will also be higher in the predator reduction grid due to a higher survival of juveniles, and (3) average body mass of adults will be higher in the predator reduction grid due to a longer life expectancy resulting from a reduced mortality rate. Population densities were assessed during both summer and winter

but survival and proportion of juveniles could not be assessed during winter due to the difficulties of trapping lemmings under the harsh High Arctic winter conditions.

## 3.4. Methods

### *3.4.1. Study area*

Our study was conducted on Bylot Island, Nunavut, Canada (73°08'N; 80°00'W) in the Qarlikturvik valley. The valley is surrounded by gentle slopes and hills mostly covered by mesic tundra vegetation while the bottom of the valley consists of a mosaic of wet habitat (i.e. tundra polygons, ponds and lakes) and mesic tundra. The mesic tundra is dominated by prostrate shrubs (*Salix* spp., *Cassiope tetragona*) with a sparse cover of grasses (*Arctagrostis latifolia, Alopecurus alpinus*), forbs (*Saxifraga* spp., *Ranunculus* spp.) and some mosses (such a *Polytrichum swartzii*) (Bilodeau *et al.* 2014). In contrast, sedges (*Eriophorum* spp., *Carex aquatilis*), grasses (*Dupontia fisheri*) and brown mosses (such as *Limprichtia cossonii* and *Campylium stellatum*) dominate in the wet tundra. In the mesic tundra, numerous small streams running down the slopes form small gullies, which are conducive to the formation of snow banks and are heavily used by lemmings in winter (Duchesne *et al.* 2011b). Snow covers the ground from October to mid-June and the average annual temperature is -15°C with a warming trend in recent decades (Gauthier *et al.* 2013).

Both brown and collared lemmings (*Dicrostonyx groenlandicus*) are present in our study area but we focused only on the former species because it is the most abundant and the only one clearly showing large, cyclical fluctuations in abundance. Lemming predators consist mainly of the ermine (*Mustela erminea*), arctic fox (*Vulpes lagopus*), snowy owl (*Bubo scandiacus*), rough-legged hawk (*Buteo lagopus*), long-tailed jaegers (*Stercorarius longicaudus*) and glaucous gull (*Larus hyperboreus*). All of these species are major predators of lemmings in the Canadian Arctic (Bilodeau 2013, Therrien *et al.* 2014, Gauthier *et al.* 2015b; Ruffino *et al.* 2015).

*3.4.2. Experimental design*

We used a Before–After Control-Impact design (Smith 2013), with the control and experimental trapping grids set in relatively homogenous patches of mesic tundra. The two grids were 600 m apart, a distance much larger than the average 15-30 m movements of individuals within each grid (see results). The control grid (11 ha) was set up in 2004 and consisted of 12 × 12 trapping stations every 30 m. The experimental grid was set up in 2007 and originally consisted of 10 × 10 stations (7.3 ha), also every 30 m, but changed in 2012 to 8 x 12 stations (6.9 ha) to better fit inside the predator exclosure (see more details below). From 2008 to 2011, the experimental grid was used for a snow fencing experiment but snow enhancement had no effect on summer density or other demographic parameters (Bilodeau *et al.* 2013b). Each station consisted of a single Longworth trap and trapping grids were surveyed in mid-June, mid-July, and mid-August (primary occasions). Primary occasions consisted of three consecutive days of trapping and grids were visited twice per day. Trapping was conducted sequentially on both grids. Each captured lemming was identified to species, sexed, weighed, and tagged with a passive integrated transponder (PIT) or a uniquely numbered ear-tag (see Fauteux *et al.* 2015 for details). For the purpose of the current study, we focused on the 2008-2015 period, when live trapping data were collected on both trapping grids.

We started the construction of a fence delimiting an area slightly larger than the experimental trapping grid, approximately 240 × 360 m (8.6 ha; see Fig. 3.1 for details), in July 2012. In order to prevent foxes from entering the protected area, the perimeter was made of chicken wire (1-inch mesh) 1.4 m high (2.0 m high when crossing snow drift areas) attached to T-shaped steel bars. This mesh size allowed movements of lemmings in and out of the grid. To exclude avian predators, we built a "roof" made of criss-crossing nylon fishing line 0.5 m apart in order to completely cover the 8.6 ha area. The roof was completed in July 2013. Both the fence and the roof sustained well weather conditions although some minor repairs (e.g. bent rods, broken fishing lines, loose nylon cords) were made every summer. Similar experimental designs were successfully used in previous studies in the Canadian tundra and proved effective against all predators except small mustelids (Reid *et al.* 1995, Wilson *et al.* 1999).

*3.4.3. Estimation of demographic parameters*

We estimated four demographic parameters of lemmings during the summer: density (*D*), survival (*S*), proportion of juveniles (*J*), and body mass (*M*). In addition, movements (σ) were also estimated within spatially-explicit capture-recapture (SECR) analyses for densities (see below). Parameters were estimated for each trapping grid at monthly occasions except survival, which was estimated for two time intervals (June-July, July-August). When sample size allowed, we separated lemmings into three groups to estimate those parameters: adult males, adult females, and juveniles (disregarding the sex). However, σ, *S*, *J,* and *M* were not analysed when sample size was too low (<5 ind., which happened in the low phase of the cycle; Annexe S2.1, Table S2.1). Because inter-annual recapture of marked lemmings is extremely rare (Fauteux *et al.* 2015), we calculated parameters separately for each year.

Monthly lemming densities and movements were estimated annually for each trapping grid by combining monthly occasions into a single model with SECR models using the package "secr" implemented in the R software (Borchers et Efford 2008, Efford 2015). When lemmings were in very low abundance (<5 lemmings captured per month per grid), we used the known minimum number alive divided by the average effective sampling area of the respective trapping grids determined with SECR models in other years. We report densities as the number of individuals per ha. Statistical details are presented in Annexe S2.2. Survival was estimated with the RMark package implemented in R (Laake *et al.* 2013). Our sampling corresponded to Pollock's robust design and we used the Huggins parameterisation to minimise the number of parameters per model (Williams *et al.* 2002). More details on survival estimation are presented in Annexe S2.3.

We determined the proportion of juveniles (*J*) among all individual captured at each occasion. Females <28 g and males <30 g were considered juveniles (Fauteux *et al.* 2015). The average body mass was calculated for adults of both sexes separately.

Nests built by lemmings under the snow during the cold season can be used to obtain an estimate of winter densities ($D^W$) (Duchesne *et al.* 2011a, Krebs *et al.* 2012). Winter nest densities were obtained by searching thoroughly trapping grids with several

persons walking side by side along parallel lines set 10 m apart. Winter nests are easily detected on the Arctic tundra (Krebs *et al.* 2012), so we assumed that observers had a 100% probability of detecting nests located within 5 m of their walking path. For each nest found, the species using it was recorded based on the size, shape and color of faeces (Duchesne *et al.* 2011a, Soininen *et al.* 2015). Nest density was calculated as the total number of nests occupied by brown lemmings divided by the size of the searched grid. The presence of a snow fence on our experimental grid from 2008 to 2011 affected winter nest density but the effect was mostly concentrated within 10 m from the snow fences (Bilodeau *et al.* 2013). Results from our analyses did not differ if we included or not winter nests located within 10 m from the snow fence, hence we present the results including all winter nests.

### *3.4.4. Predator activity*

We conducted observations of predator activity at trapping grids every two to three days in 2014 and 2015. No observations were conducted in 2013 due to the complete absence of lemmings and the scarcity of predators (no long-tailed jaeger, rough-legged hawk or snowy owl nest was found in our study area; Gauthier *et al.* 2014). Observations were conducted during predetermined periods of time (~1 h) one grid at a time from lookout points that offered good visibility. Presence of predators was also noted opportunistically when walking the grids during trapping sessions or during other activities (time spent doing these activities were considered as observation periods). All mammalian predators passing nearby or inside the trapping grids were noted as well as their behavior: hunting, digging, running, or vocalising. Similarly, avian predators and their behavior were noted as flying above the grids, vocalising, hovering (e.g. jaegers), or perching. The number of predators seen divided by the total length of observation periods yielded the frequency of observations by species. In early July 2015, we placed 7 artificial bird nests made of 4 quail eggs inside the experimental grid while 40 were placed outside the exclosure (<5 km) as part of a long-term monitoring of predation risk in the area (McKinnon *et al.* 2014). Nests were monitored daily for the first 3 days and weekly thereafter. Field manipulations were approved by the Animal Welfare Committee of Université Laval (2014-061) and Parks Canada (SIR-2013-13953).

*3.4.5. Statistical analyses*

Our long-term dataset allowed us to compare the experimental and control grids before (2008-2012) and during (2013-2015) the treatment but with no replicate during the predator reduction experiment (we return to this topic in the Discussion). Quantitative comparisons of densities, movements, and survival estimates obtained with the capture-recapture data were conducted using 90% and 95% confidence intervals (CI). Estimates with overlapping 90% CI between the control and experimental grids were considered statistically similar while non-overlapping 95% CI were considered statistically different. Overlapping 95% but non-overlapping 90% CI were considered marginally different.

We analysed the effects of the period (before and during predator reduction) and trapping grids on $J$ using a generalised linear mixed model with a binomial distribution and on $M$ using a linear mixed model (LMM) with a Gaussian distribution. An interaction between both variables was included in all models to consider that predator reduction on the experimental grid started in 2013 and year and months nested in year were used as random variables to consider potential temporal variations. We also used a LMM with a Gaussian distribution to compare $D^W$ between trapping grids and periods in interaction using year as a random variable. We used the coefficient of determination ($R^2$) of Nakagawa et Schielzeth (2013) to estimate the variance explained by the mixed-effects models with and without the random variables.

## 3.5. Results

Before the predator exclosure became effective in 2013, we had three years of high abundance (2008, 2010, and 2011) and two years of low abundance (2009 and 2012; Fig. 3.2). The low phase persisted in 2013 as no brown lemming was captured that year. Populations built up during the winter 2013-2014, as shown by the high winter nest density (Fig. 3.3). Populations peaked in summers 2014 before declining in 2015 (Fig. 3.2).

*3.5.1. Demographic response*

During 2014 and 2015, densities of brown lemmings were higher in the predator-reduction grid compared to the control grid at all times, with slightly overlapping to non-overlapping 95% CI, except in June 2015, when there was no difference (Fig. 3.2). The difference was especially marked in July 2014 and July-August 2015 for juveniles and June 2014 and August 2015 for adult females (densities were >2.4× higher on the predator-reduction grid). Densities of adult males, however, were similar between the 2 grids at most occasions. During the two previous peaks (2008 and 2010-2011) before establishment of the predator exclosure, we found no consistent difference in densities between the two grids as densities were slightly higher (no 95% CI overlap) in the experimental grid compared to the control grid at only 1 out of 15 occasions (July 2008, Fig. 3.2).

There were no systematic differences in distances moved by lemmings between the predator-reduction grid and the control either before or after the treatment, although males generally had longer movements than females or juveniles (Fig. S2.1). Similar inconsistent differences were observed during the pre-experimental period.

In 2014 and 2015, survival of adult females and males were 1.4× and 1.6× higher inside the predator exclosure than outside, although all 90% CI overlapped slightly (Fig. 3.4). Similarly, survival of juveniles was 1.6× and 1.8× higher inside the predator exclosure compared to the control grid in 2014 and 2015, respectively, but all 90% CI overlapped. Model selection, however, provided strong support for a grid effect on survival in both years (Table S2.2). Prior to the predator exclosure, survival was similar between both trapping grids (Fig. 3.4) and model selection provided weak (2008) or no (2010 and 2011) evidence for a grid effect (Table S2.2). Survival generally did not differ between periods or lemming groups except in 2011, when adult female survival was lower in July-August compared to June-July.

The proportion of juveniles was similar in the 2 grids before the treatment period (control: $J = 0.23 \pm 0.06$, experimental: $J = 0.23 \pm 0.07$), but was lower in the control ($J = 0.16 \pm 0.06$) compared to the experimental grid ($J = 0.25 \pm 0.08$) during predator reduction (significant interaction grid*period; Table 3.1, Fig. 3.5).

Adult body mass differed between the 2 grids and the 95% CI of the interaction with period almost excluded 0 (Table 3.1). Adult lemmings were generally heavier inside the exclosure ($M_{exp}$ = 52.2 ± 2.5 g) than in the control grid ($M_{con}$ = 46.8 ± 2.6 g) during the predator-reduction period, whereas body mass was more similar between the 2 grids ($M_{exp}$ = 51.3 ± 2.2 g v.s. $M_{co}$ = 49.0 ± 2.2 g) before that period.

Winter nest densities ($B^W$) were not statistically different between the experimental and control grids or the periods although the 95% CI of the grid effect nearly excluded 0 (Table 3.1). We note a trend for higher nest density on the experimental grid in winter 2008 (a year when the snow fence was present) and especially in 2015 during the predator-reduction experiment (Fig. 3.3).

### *3.5.2. Predator activity*

During behavioral observations conducted in summer, predators were observed on 22 occasions ($n$ = 127 h of observations) above and near the predator-reduction grid and on 44 occasions ($n$ = 143 h) for the control grid. All predator species were seen more often at the control than at the experimental grid except parasitic jaegers (Table 3.2). Among the 161 long-tailed jaegers observed (commonest predator), most were just passing by in flight or vocalising from a short distance (<200 m). We observed jaegers attempting to catch lemmings 3 times in the control grid, and two were successful. Four snowy owls were seen flying above the control grid and a single one sitting <100 m from the experimental grid in 2014. An arctic fox that was tagged for another study was observed inside the control grid five times during June-August 2014. Fecal deposits found before snow-melt were the only evidence that foxes entered inside the exclosure during winter 2014. In 2015, arctic fox digging under the anti-predator fence was found soon after snow melt and small holes were dug inside the exclosure, apparently to catch lemmings. It is unclear when a fox breached the fence (i.e. spring or fall 2015) but potential entry points were blocked in June 2015 and the fence was reinforced. In 2015, all artificial bird nests placed within the predator exclosure remained intact after 48 d ($n$ = 7) whereas all 40 nests placed outside the exclosure were depredated within 72 h. In 2014, none of the winter nests sampled had signs

of predation by ermine ($n$ = 120) and in 2015 a single nest on the control grid ($n$ = 78) had signs of predation.

## 3.6. Discussion

### *3.6.1. Predation was sufficient to limit population size*

In accordance with our first prediction, brown lemming densities were generally higher in the experimental than in the control grid during the peak and initial phase of the decline (2014-2015). Indeed, the average densities of adult females and juveniles were 2.4× and 3.4× more abundant inside the experimental than in the control grid, respectively. In contrast, comparisons of densities between the experimental and control grids did not reveal any consistent pattern during the pre-experimental period (2008-2012). Therefore, the higher density of brown lemmings in the predator-reduction grid supports the limitation by predation hypothesis (Krebs 2011). Interestingly, predator reduction had a negligible effect on adult males as their average density in the experimental grid was only 1.4× higher than in the control during the experiment.

Previous predator-removal experiments conducted in the low Arctic of Canada reported positive numerical responses of collared lemmings similar to ours (Table 3). In Scandinavia, predator removal experiments also yielded positive effects on vole densities (Korpimaki et Norrdahl 1998, Klemola *et al.* 2000, Huitu *et al.* 2003). The density ratios of all lemmings between the experimental and control grids were higher in our study compared to what Salo *et al.* (2010) reported in their meta-analysis (1.9× vs. 1.7×). This is consistent with suggestions that in the High Arctic, predation may have a stronger impact on prey populations than in other areas (Gilg *et al.* 2003). The simple trophic system of the High Arctic tundra and the strong and immediate (i.e. non time-delayed) numerical response of several raptors during the summer may explain why predation had such a strong impact on lemming population growth (Gilg *et al.* 2006, Therrien *et al.* 2014). Predator reduction led to a large increase in lemming survival during the summer in our experiment. This shows that summer population growth is mainly limited by mortality caused by predators, a pattern already inferred in this system based on correlative evidence (Fauteux *et al.* 2015) and confirms that predation was sufficient to limit population size.

Habitat is unlikely to be a confounding factor in our experiment because trapping grids were both located in mesic tundra with similar plant communities and biomass. Furthermore, lemming demographic parameters did not differ between the control and experimental grids prior to the start of the experiment. Previous studies at our study site also found little impact of lemming grazing on plant biomass, even in peak years (Bilodeau *et al.* 2014).

The marginally higher body mass observed in the experimental grid compared to the control during the period of predator reduction may be related to the higher survival of lemmings observed in that grid as we hypothesized. Indeed, a higher proportion of lemmings may have reached older age classes and hence a higher body mass, thereby increasing average body mass in the population (Wilson *et al.* 1999). It is also possible that the absence of predators inside the experimental grid may have reduced the predation risk perceived by lemmings and thus increased the time spent feeding (Dupuch *et al.* 2014), thereby leading to higher body mass.

It is surprising that the difference in lemming density observed in August 2014 between the predator-reduction and control grids had vanished at snow-melt in 2015. At our study site, population declines usually occur in fall, likely due to high predation during this period (Fauteux *et al.* 2015). This is supported by the trend for a higher nest density inside the experimental grid compared to the control during winter 2014-2015. The breach of our exclosure by a fox during winter 2014-2015 may explain why the June 2015 density was not higher in the experimental grid compared to the control. We also note that the proportion of winter nests with signs of reproduction was unusually low on both grids that year (0.07, Fauteux *et al.* unpubl. data) compared to 2014 and previous winters of high abundance (0.20-0.34; Fauteux *et al.* 2015). Poorer snow conditions in 2015 compared to 2014 may have contributed to that (Domine *et al.* 2016).

Predator abundance at the study site was generally lower in 2015 compared to 2014 except for foxes which were more abundant. In 2015, snowy owls were absent, most long-tailed jaeger nests failed early and we did not observe any active ermine den in either years (Gauthier *et al.* 2015a). Considering that these predators can have a major impact in summer (they can eat up to 5 lemmings per day per individual depending on the species;

Gilg *et al.* 2003; Bilodeau 2013; Therrien *et al.* 2014), this may explain why lemming populations were able to grow during summer 2015 even though the population had declined by that spring. This is supported by a trend for higher survival of lemmings between July-August 2015 compared to the same period in 2014. Nonetheless, we note that population growth was much more pronounced in the experimental grid than in the control as a consequence of a higher survival rate in the former area. By the end of 2015, lemming populations had not yet crashed in our study area, possibly because ermines, a key predator (Gilg *et al.* 2003), were still low. Ermine populations often respond with a delay to lemming abundance, as we observed in 2012 (i.e. high ermine populations coincident with the crash of lemmings; Bilodeau 2013).

The proportion of juveniles was slightly higher in the experimental grid compared to the control during the predator-reduction period. This could be due to a higher fecundity of females or a better survival of juveniles after birth. However, female fecundity was apparently not affected by the reduction of predators and remained high on both grids (Fauteux *et al.* unpubl. data). Other predator removal experiments in lemmings and voles also reported no density-dependent effects on female reproductive activity (Reid *et al.* 1995, Wilson *et al.* 1999, Klemola *et al.* 2000). In contrast, juvenile density increased more inside the predator exclosure than on the control in 2015, which supports the hypothesis that the higher proportion of juveniles in the experimental grid was a consequence of higher juvenile survival in absence of predators.

### *3.6.2. Scope and caveats of the experiment*

The most serious problem encountered was the entry of foxes inside the predator exclosure between late summer 2014 and spring 2015. This is a common risk faced by large-scale predator manipulation experiments because fences are prone to damage (Reid *et al.* 1995, Wilson *et al.* 1999). Although we do not know the precise timing of this event, the high density of lemming nests inside our exclosure in winter 2014-15 suggests that it may have happened at snow melt and that it had a small impact overall (see above). Our predator observations and artificial nest depredations suggest that our exclosure

successfully excluded all predators at least during the summer, and that predator attraction was not a relevant confounding factor.

Our anti-predator fence was permeable to lemmings, which was confirmed by the observation of runways that had been carved in the vegetation under the fence. This prevented the so-called fence effect (Ostfeld 1994) by allowing natural movements and dispersal of individual lemmings. We found that adult males moved longer distances between trapping events than did females and juveniles. The search for females to mate may be responsible for these long movements but aggressiveness among males may also have led some to look for unoccupied areas (Krebs 1964, Predavec et Krebs 2000). Longer movements by males may drive them more often outside of the exclosure, exposing them to higher mortality risk (Reid *et al.* 1995, Wilson *et al.* 1999). This could also explain why we found a weak effect of our manipulation on male density. Dispersal of individuals and especially young outside our exclosure may also explain why total densities did not reach abnormally high levels compared to the pre-experimental period.

Other common criticisms of predator removal experiments are their small spatial scale and lack of replicates (Sundell 2006). We used an exclosure (9 ha) that was much larger than the average home range of lemmings (0.4-0.9 ha; Banks *et al.* 1975) in order to have a large enough population in our experimental grid. This, however, was done at the expense of experimental replication. Absence of spatial replicates in our study was partly compensated by the multiple years of measurement, including a 5-yr long pre-experiment survey (2008-2012). This allowed us to confirm that demographic parameters were similar between the two grids prior to our manipulation, a critical information in any before-after control-impact study (Smith 2013). We must also recognize that our study did not cover the full decline and low phases of the lemming cycle, although we believe that results presented herein provide compelling evidence in support of our hypotheses.

Lastly, we can compare our results to similar experiments that were conducted on a different lemming species (collared lemming) in the Canadian low Arctic (Table 3.3). Our study and those of Reid *et al.* (1995) and Wilson *et al.* (1999) all reported increases in density, survival, proportion of juveniles and body mass of lemmings when predators were excluded. The remarkable consistency in results obtained across experimental studies,

repeated in different environments provides robust empirical evidence in favor of the predation hypothesis and allows stronger inferences of general ecological patterns driving population dynamics (Salo *et al.* 2010, Prevedello *et al.* 2013).

### 3.7. Conclusion

Top-down control by predators has often been identified as one of the most plausible forces driving small mammal population cycles because of its potential to generate delayed density-dependent effects (Hanski *et al.* 1993, Korpimaki et Krebs 1996, Krebs 2013). In this study, we found that brown lemmings reached much higher densities in absence of predation due to a high survival rate. Therefore, our field experiment confirms that predation can limit their population size, as previously reported for another lemming species in the Canadian low Arctic (Reid *et al.* 1995, Wilson *et al.* 1999). It suggests that predation plays a key role in the population dynamics of lemmings, as previously found in boreal voles (Norrdahl et Korpimäki 1995, Huitu *et al.* 2003), and supports the hypothesis that small arctic herbivores are primarily controlled by top-down forces (Legagneux *et al.* 2012). Nonetheless, our predator-reduction experiment did not cover all phases of the lemming cycle and future work should examine how predation affects the demography during the low-phase of the cycle, which remains one of the most puzzling phases at the moment (Boonstra *et al.* 1998). We also do not know if predation can have carry-over effects over multiple seasons.

In contrast with the summer period, our understanding of small mammal population dynamics during winter is still limited (Krebs 2011). Recent work suggests that varying reproductive rate is the main driver of winter population growth rates of lemmings (Fauteux *et al.* 2015). In winter, poor snow conditions may interact with extrinsic biotic factors (e.g. reduced food availability when plants are encased in ice) or intrinsic factors (e.g. carry-over effects of stress caused by high predator density) and have a detrimental effect on reproduction. Therefore, the role of predation and its interactions with other factors in winter in affecting population cycles of arctic lemmings remain unclear. Camera traps have recently been proposed as a promising method to monitor lemming activity in winter

(Soininen *et al.* 2015) and such methodological innovations will be necessary to fully understand lemming cycles.

### 3.8. Acknowledgements

We thank David Gaspard and Gabriel Montpetit for their immense efforts when building the exclosure. We also thank Christine Lambert, Guillaume Slevan-Tremblay, Marie-Christine Cadieux, and all the Bylot team for their support. The research relied on the logistic assistance of the Polar Continental Shelf Program (Natural Resources Canada) and of Sirmilik National Park of Canada. The research was funded by the Natural Sciences and Engineering Research Council of Canada (Discovery Grants and Frontiers to Discovery programs), the Canadian International Polar Year Program and the Northern Student Training Program of Indian and Northern Affairs Canada, the Network of Centres of Excellence of Canada ArcticNet, the NSERC-CREATE Training Program Environord, the W. Garfield Weston Foundation, and the Fonds de recherche du Québec – Nature et technologies.

### 3.9. Data Accessibility

All data used in this manuscript are available at the NordicanaD website: http://www.cen.ulaval.ca/nordicanad/en_index.aspx (DOI: 10.5885/45400AW-9891BD76704C4CE2).

### 3.10. Suplementary material

Annexe S2.1. Sample size.

Annexe S2.2. Spatially-explicit capture-recapture models for densities.

Annexe S2.3. Methods and model selection for survival probabilities.

### 3.11. Tables

Table 3.1. Slope parameters ($\beta$) and their 95% confidence intervals (CI) for the effects of trapping grid (control vs experimental) and time period (before and after predator reduction) on lemming demographic parameters. We report both marginal $R_g^2$ (fixed-effects only) and conditional $R_c^2$ (with random effects). Year and months nested in year were used as the random factors for *J* and *M* while only year was used for $D^W$. Number of parameters (*K*) and observations (*n*) are also reported.

| Demographic parameter | Explanatory variables | $\beta$ | 95% CI (low) | (high) | *K* | *n* | $R_g^2$ | $R_c^2$ |
|---|---|---|---|---|---|---|---|---|
| *J* | grid | -0.05 | -0.44 | 0.33 | 6 | 1308 | 0.01 | 0.23 |
| | period | -0.47 | -1.64 | 0.72 | | | | |
| | **grid*period** | **0.63** | **0.07** | **1.20** | | | | |
| *M* | **grid** | **2.30** | **0.05** | **4.43** | 7 | 984 | 0.02 | 0.15 |
| | period | -2.17 | -8.27 | 4.02 | | | | |
| | grid*period | 3.12 | -0.05 | 6.39 | | | | |
| $D^W$ | grid | 0.35 | -0.07 | 0.78 | 6 | 16 | 0.04 | 0.97 |
| | period | -0.50 | -3.25 | 2.25 | | | | |
| | grid*period | -0.11 | -0.80 | 0.59 | | | | |

*J* = proportion of juveniles; *M* = body mass of adults; $D^W$ = density of winter nests.

Table 3.2. Number of individuals per 100 h of observation for each predator species moving, vocalising, or attacking prey near the experimental grid or near and in the control grid.

| | 2014 | | 2015 | |
|---|---|---|---|---|
| Species | Experimental grid ($n$ = 89 h) | Control grid ($n$ = 80 h) | Experimental grid ($n$ = 38 h) | Control grid ($n$ = 63 h) |
| Arctic fox | 0.0 | 6.3 | 2.6 | 4.8 |
| Snowy owl | 1.1 | 5.0 | 0.0 | 0.0 |
| Common raven | 3.4 | 12.5 | 0.0 | 21.0 |
| Glaucous gull | 2.2 | 6.3 | 5.3 | 7.9 |
| Long-tailed jaeger | 16.9 | 100.3 | 57.9 | 61.9 |
| Parasitic jaeger | 0.0 | 2.5 | 13.2 | 3.2 |
| Total | 23.6 | 132.9 | 79.0 | 98.8 |

Table 3.3. Comparison of results obtained by studies using large predator exclosures to study lemming demography in the Canadian Arctic. Empty cell indicates no information available. Reid *et al.* (1995) and Wilson *et al.* (1999): collared lemming. Our study: brown lemming.

| Parameter | Group | Reid et al. 1995 | Wilson et al. 1999 | This study |
|---|---|---|---|---|
| Density | Adult females | | | + + |
| | Adult males | ++ | ++ | 0 |
| | Juveniles | | | + + |
| Survival | Adult females | | + | + |
| | Adult males | ++ | | + |
| | Juveniles | | + | + |
| Prop. of juveniles/Recruitment | | + + | | ++ |
| Body mass | Adult females | | + + | + |
| | Adult males | | + + | |
| | Juveniles | | + | |
| Movements/ | Adult females | | 0 | 0 |
| Dispersal | Adult males | | 0 | 0 |
| | Juveniles | | 0 | 0 |

+ +, – – = statistical support for a positive (or negative) effect of predator exclusion

+, – = evidence suggests a weak positive (or negative) effect of predator exclusion

0 = no effect of predator exclusion

### 3.12. Figures

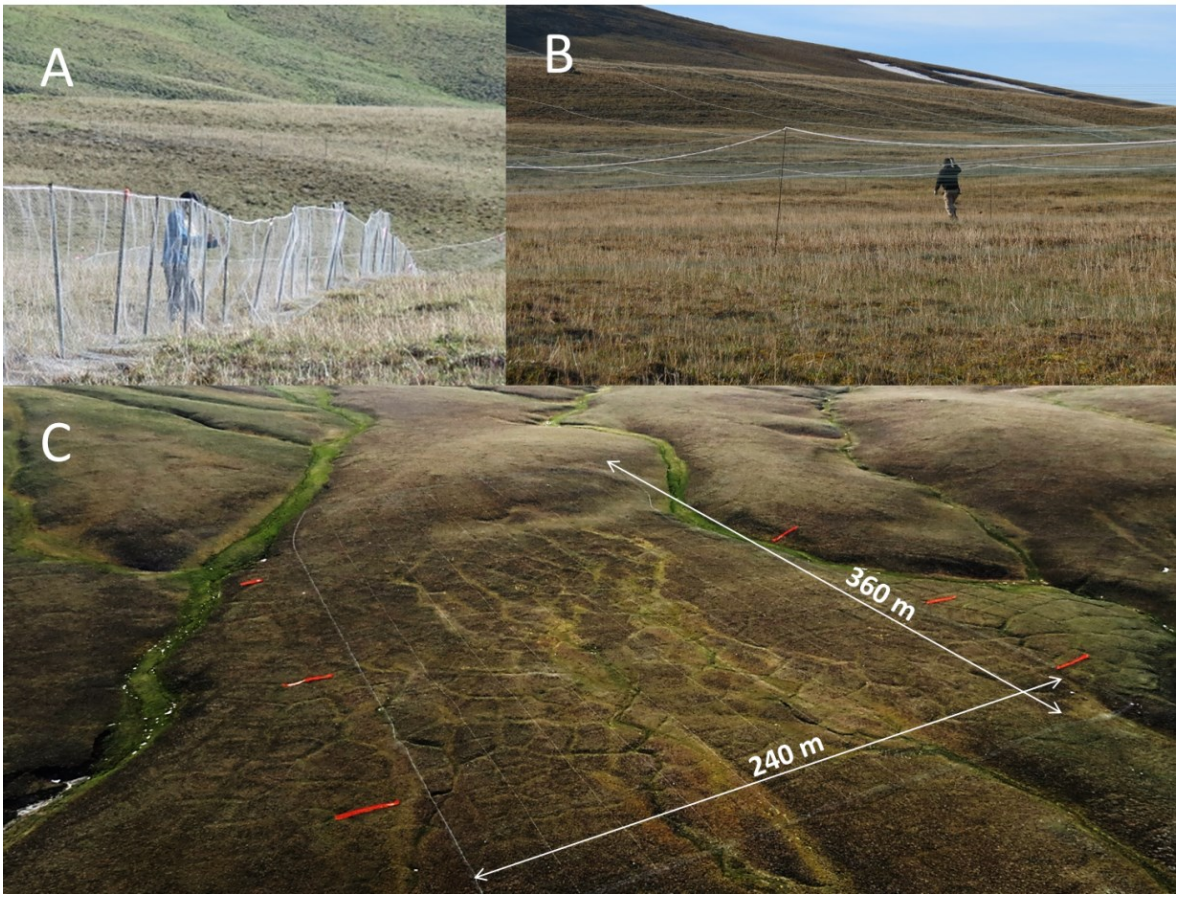


Fig. 3.1. Predator exclosure used to reduce predation pressure on brown lemmings. The fence around the perimeter was made of chicken wire (1-inch mesh) 1.4 m high (2.0 m high when crossing snow drift areas) attached to T-shaped steel bars in order to prevent foxes from entering the protected area (A). The fence had a 60-cm long outward extension on the ground to prevent foxes from digging under the fence. To exclude avian predators, we built a "roof" made of criss-crossing nylon fishing line 0.5 m apart in order to completely cover the 8.6 ha area (B). The roof was supported by steel rods and nylon cords spaced out every 20 m. The aerial photograph (C) shows the total area covered by the fence (8.6 ha).

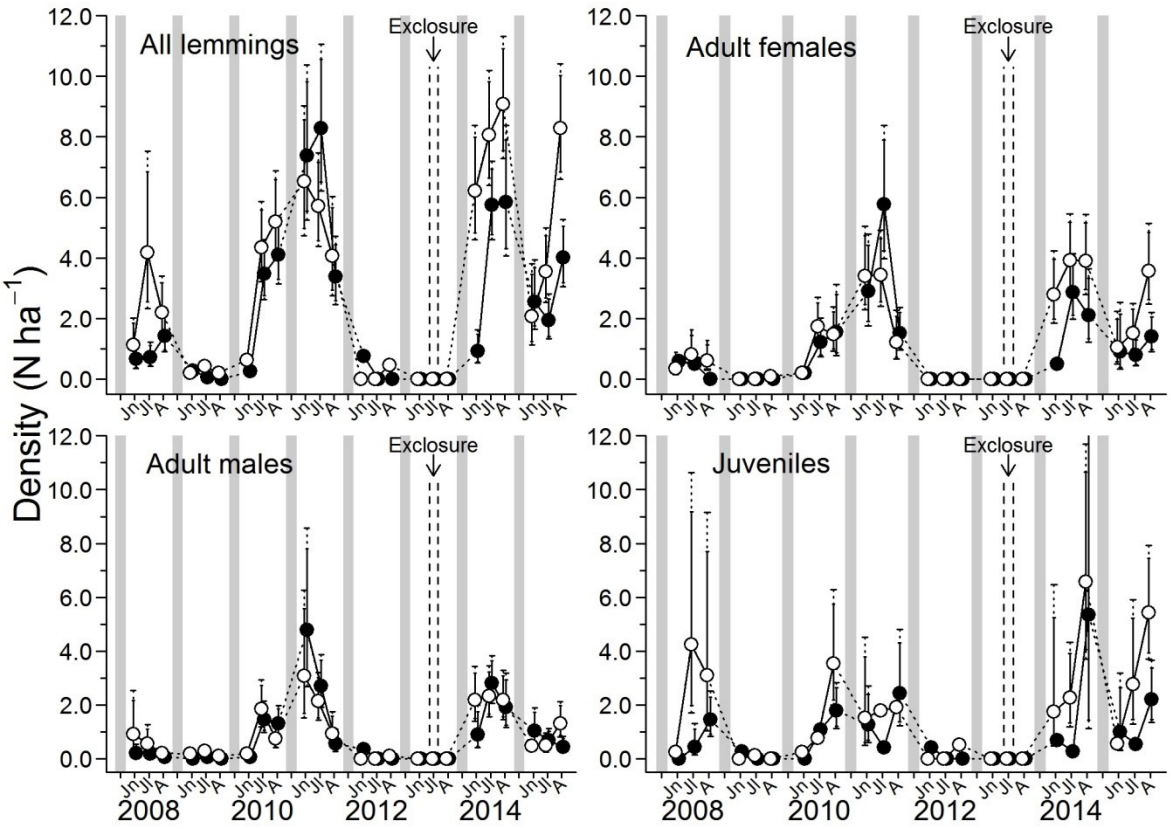


Figure 3.2. Temporal fluctuations of brown lemming densities (total and separated in adult males, adult females and juveniles) in the control (black circles) and experimental trapping grid (open circles) with their 90% (solid line) and 95% (dotted line) confidence intervals. Gray bars correspond to the winter period. The vertical dashed double-line separates the pre-treatment from the treatment (predator exclusion) period. Jn = June, Jl = July, A = August.

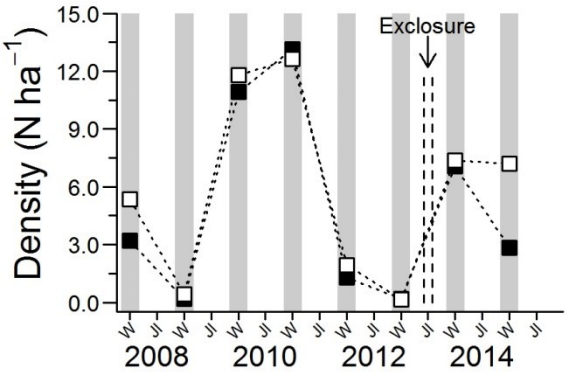


Figure 3.3. Temporal fluctuations of winter nest densities of brown lemmings for the control (black squares) and the experimental grid (open squares). The vertical dashed double-line separates the pre-treatment from the treatment (predator exclusion) period. Gray bars correspond to the winter period. Jl = July, W = winter.

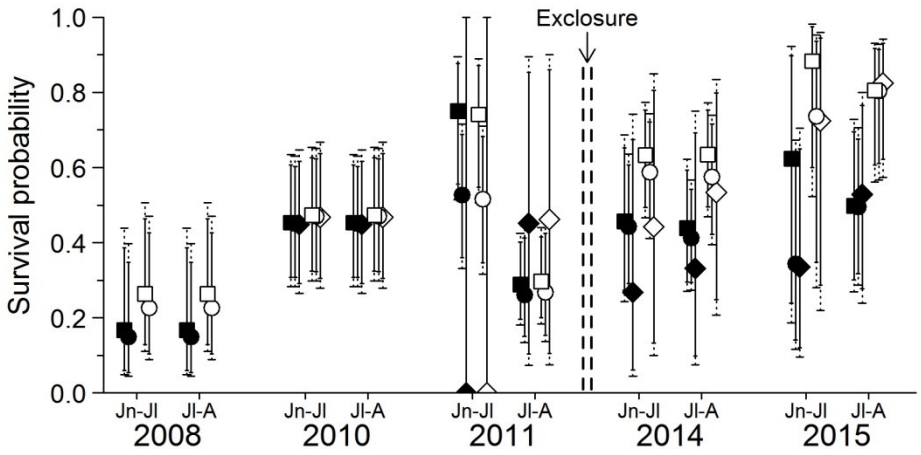


Figure 3.4. Monthly survival estimates of adult female (squares), adult male (circles), and juvenile (diamonds) brown lemmings with their 90% (solid line) and 95% (dotted line) confidence intervals. Black symbols = control grid; open symbols = experimental grid. The vertical dashed double-line separates the pre-treatment from the treatment (predator exclusion) period (≥2013). Jn = June, Jl = July, A = August.

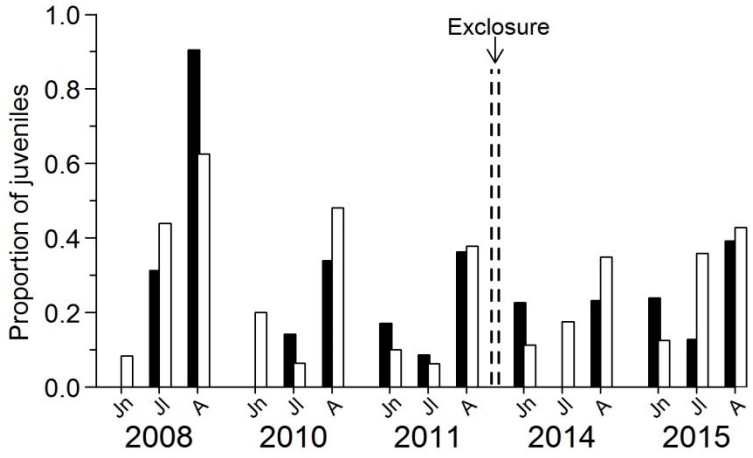


Figure 3.5. Proportion of juveniles among captured individuals on the control (black bars) and experimental (white bars) trapping grids. The vertical dashed double-line separates the pre-treatment from the treatment (predator exclusion) period (≥2013). Jn = June, Jl = July, A = August.

# CHAPITRE 4. Assessing stress in arctic lemmings: fecal metabolite levels reflect plasma free corticosterone levels

*Soumis :*

Fauteux, D., Gauthier, G., Berteaux, D., Bosson, C., Palme, R. et Boonstra, R. (2016). Assessing stress in arctic lemmings: fecal metabolite levels reflect plasma free corticosterone levels. *Journal of Comparative Physiology B.*

## 4.1. Résumé

L'étude du rôle écologique du stress chez les populations sauvages a déclenché le développement de techniques non-invasives pour mesurer les hormones de stress en utilisant des métabolites fécaux. Cependant, il reste incertain que les métabolites fécaux des corticostéroïdes (MFC) peuvent être un proxy fiable du corticostéroïde libre, soit celui qui est actif biologiquement. Nous avons examiné la validité de l'utilisation des concentrations de MFC comme proxy de la corticostérone libre avec un dosage immuno-enzymatique (DIE) à l'aide de lemmings bruns (*Lemmus trimucronatus*) capturés à la main et anesthésiés sur l'île Bylot, Nunavut, Canada, et ce, pendant l'été. Nous avons également examiné les facteurs endogènes qui pourraient expliquer la variabilité inter-individuelle. La corticostérone sanguine a été mesurée lors de la capture et 30 minutes plus tard. Les animaux ont ensuite été maintenus en captivité pendant 72 h pour obtenir des profils de changements dans les MFC au fil du temps. La corticostérone plasmatique libre a augmenté de 135 fois en moyenne 30 min après la capture, ce qui a confirmé que le traitement initial a été stressant. Nous avons constaté que les niveaux des MFC étaient fortement reliés avec la portion libre ($R^2$ = 0,53), mais très peu aux concentrations totales ($R^2$ = 0,02) de la corticostérone plasmatique, indépendamment de l'âge, du sexe et de l'état de la reproduction. Les concentrations maximales des MFC ont été atteintes 4 h après la capture, mais ils avaient déjà augmenté de façon importante après 2 h. Nous n'avons détecté aucun rythme circadien dans les MFC. Les concentrations totales de la corticostérone plasmatique étaient beaucoup plus élevées et celles de la corticostérone libre était légèrement plus élevée chez les femelles adultes comparativement aux mâles mais les concentrations les plus élevées de MFC ont été observées chez les mâles adultes. Cette différence confirme qu'il faut être prudent lors de l'évaluation des effets des facteurs externes sur les MFC et qu'il est impératif de considérer le sexe et l'état de la reproduction des individus.



*Mots clés : micromammifères, rongeurs, cycles, hypothèse de l'hormone libre, endocrinologie de la faune*

## 4.2. Summary

The study of the ecological role of stress in wild populations has triggered the development of non-invasive techniques to measure stress hormones using fecal metabolites. However, it is still unclear whether fecal corticosteroid metabolites (FCM) can be a reliable proxy of free, biologically active glucocorticoids. Here, we examined the validity of using FCM concentrations as a proxy for free corticosterone with an enzyme immunoassay (EIA) on brown lemmings (Lemmus trimucronatus) that were hand-captured and anesthetised on Bylot Island, Nunavut, Canada during the summer. We also examined endogenous factors that could explain inter-individual variability. Blood corticosterone was measured upon capture and 30 min later, and animals were kept in captivity for 72 h to obtain profiles of changes in FCM over time. Plasma free corticosterone increased 135 times on average 30 min after capture, which confirmed that initial handling was perceived as a stressor. We found that FCM levels were highly related with free ($R^2 = 0.53$) but very little with total ($R^2 = 0.02$) corticosterone levels, regardless of age, sex and reproductive condition. Maximum concentrations of FCM were reached 4 h after capture, but they had already increased after 2 h. We could not detect any circadian rhythm in FCM. Plasma total corticosterone levels were much higher and free corticosterone levels tended to be slightly higher in adult females than males but the highest FCM concentrations were found in reproductively active adult males. These differences confirm that one must be careful when assessing the effects of external factors on stress with FCM and should account for sex and reproductive condition.

*Key-words: small mammals, rodents, cycles, free hormone hypothesis, wildlife endocrinology.*

## 4.3. Introduction

New methods to measure endocrine responses of animals to stressful events have been increasingly developed over the past two decades to address both physiological and ecological questions (Boonstra 2013). The hypothalamic-pituitary-adrenocortical axis (HPA) is responsible for the secretion of glucocorticoids into the blood in response to a stressor. Glucocorticoids (cortisol or corticosterone, depending on the species) play key roles in the reproductive and immune systems of animals and influence their behavior (Sapolsky *et al.* 2000; Crespi *et al.* 2013; Creel *et al.* 2013). There is also an increasing interest in non-consumptive effects of predation or other factors on population dynamics and thus a thorough evaluation of methods to quantify stress under natural conditions are necessary (Sheriff *et al.* 2011a). Heterogeneity in stress responses within populations emphasizes the necessity to understand how the dynamics of glucocorticoids change among individuals as a function of age, sex, and reproductive state.

Non-invasive field methods to measure glucocorticoid metabolites in feces have proven useful to assess adrenocortical activity (Sheriff *et al.* 2011a). Enzyme immunoassays (EIA) are commonly used to quantify those metabolites (Palme 2005; Möstl et Palme 2002) and have been successfully developed for several small rodent species (voles, Ylönen *et al.* 2006; squirrels, Dantzer *et al.* 2010; ground squirrels, Bosson *et al.* 2009; chipmunks: Montiglio *et al.* 2012; Hammond *et al.* 2015). Measuring fecal corticosteroid metabolites (FCM) to quantify stress levels relies on a key assumption from the free hormone hypothesis: free glucocorticoids, which are biologically active, are mostly those metabolised in the liver, whereas glucocorticoids bound to corticosteroid binding globulin (CBG) are biologically inactive and are not metabolised (Sheriff *et al.* 2010; Perogamvros *et al.* 2012; Breuner *et al.* 2013). Recognizing this distinction is crucial because glucocorticoid metabolite concentrations will be strongly affected by metabolism. For instance, during a stressful event glucocorticoids are produced, but some of them are quickly bound by CBG and subsequently released during the progressive return to baseline concentrations. These slowly released glucocorticoids will then be metabolized, which should maintain elevated FCM concentrations compared to the baseline for some time (Schoech *et al.* 2013). However, evidence of the relationship between free glucocorticoids

and FCM is still scarce (i.e. Sheriff *et al.* 2010) despite the importance of this assumption when assessing the physiological impacts of stress (Breuner *et al.* 2013).

Numerous endogenous factors can affect glucocorticoid levels and hence the stress response of animals, including sex, age, reproductive state, and circadian rhythm (Boonstra et Boag 1992; Touma *et al.* 2003; Romero *et al.* 2008; Sheriff *et al.* 2009a). For example, Romero *et al.* (2008) reported that female brown lemmings (*Lemmus trimucronatus*) reached substantially higher levels of total corticosterone and CBG compared to males. Similar sex effects were found in other rodents (voles, Boonstra et Boag 1992; Fletcher et Boonstra 2006b; squirrels, Boonstra *et al.* 2001a; Bosson *et al.* 2012). Boonstra *et al.* (2001b) reported that reproductively active male ground squirrels (*Urocitellus parryii plesius*) had higher free cortisol concentrations than reproductively inactive males. Such differences have been related to the inhibitive effect of testosterone on the HPA axis or the stimulating effect of estrogen (Boonstra *et al.* 2007). Thus, even though fecal metabolites have the potential to be a good proxy of the physiological response of the HPA axis to a stressor, adequate validation accounting for potential confounding effects of sex, age and reproductive condition are required (Touma et Palme 2005). This is an essential prerequisite before examining the effects of external factors such as being exposed to low quality food or high predation risk on the stress response of individuals (McArthur *et al.* 2014).

We assessed the stress response of a cyclic brown lemming population in the high Arctic during the summer. Our main goal was to understand how lemmings respond to a standardized stressor and to determine whether FCM can be used as a good proxy for stress in this species, and under which conditions. In order to achieve this, we obtained blood samples at capture (i.e. baseline) and 30 min later (i.e. stressed) and a complete hormonal profile of the stress response using FCM over a period of 72 h. More specifically, our objectives were to determine: (1) if baseline, maximum, and relative change of plasma corticosterone and FCM levels vary as a function of age, sex, and reproductive condition; (2) the time required until maximum FCM levels are reached after capture stress; (3) if a circadian rhythm in FCM levels occurs even though lemmings live under 24-h daylight during the summer; and (4) if FCM levels are related to plasma free corticosterone and are

thus a good indicator of stress. Glucose concentrations were measured in parallel with plasma corticosterone because they have been found to change under acute and chronic stress conditions, and thus can provide complementary information on the state of animals (Boonstra *et al.* 1998; Breuner *et al.* 2013).

## 4.4. Methods

### *4.4.1. Study area*

Our study was conducted on Bylot Island in Sirmilik National Park, Nunavut, Canada (73°08'N; 80°00'W). The study site is in a large valley composed of two main habitat types, wet and mesic tundra (Duchesne *et al.* 2011b). Both habitats are used by brown lemmings with seasonal shifts towards wetter habitat in summer and more mesic habitat when snow settles in fall. The wet habitat consists mainly of tundra polygons with ponds and thaw lakes. The vegetation is composed of sedges (*Eriophorum* spp., *Carex aquatilis*), grasses (*Dupontia fisheri*) and brown mosses (such as *Limprichtia cossonii* and *Campylium stellatum*). The mesic tundra covers higher ground in the valley bottom and the surrounding hills and is dominated by prostrate shrubs (*Salix* spp., *Cassiope tetragona*), grasses (*Arctagrostis latifolia, Alopecurus alpinus*), and forbs (*Saxifraga* spp., *Ranunculus* spp.; Bilodeau *et al.* 2014). Snow typically covers the site for more than 8 months from early October until mid-June and the average annual temperature is -15°C (Cadieux *et al.* 2008). Animals are exposed to 24-h daylight from early May to early August and 24-h of darkness in winter. Collared lemmings (*Dicrostonyx groenlandicus*) are also present but at low density and the amplitude of their fluctuations is small compared with that of brown lemmings, which show 3-4 yr cycles at our study site (Gauthier *et al.* 2013). Brown lemmings can breed almost year-around, including under the snow in winter and throughout the summer (Gruyer *et al.* 2010; Fauteux *et al.* 2015).

### *4.4.2. Capture of animals*

In June and July from 2012 to 2014, we searched for brown lemmings and captured them by hand following the method of Romero *et al.* (2008) (none were captured in 2013

due to their very low numbers). Hand-capture was used to obtain baseline levels of corticosterone in the blood and in feces because the hormonal response to a stressor such as capture should appear in the blood within 3 minutes and FCM should increase a few hours after capture (Palme *et al.* 2005; Romero et Reed 2005; Delehanty et Boonstra 2012).

Lemmings were captured between 10:00-16:00 h by walking slowly through suitable habitat looking for movement on the ground. When a lemming was spotted, one or two observers walked slowly towards it until it ran back into a burrow. Observers waited immobile at a spot where they could monitor all potential burrow exits until the animal came out, typically a few seconds to 2-3 minutes later. One observer attempted to quickly grab the lemming by hand. If this failed, a second attempt was made within 2 minutes of the first attempt. A lemming that could not be captured within 2 minutes was abandoned.

Individuals were quickly sexed and their reproductive condition determined. In females, we noted if their pubic symphysis was open and if they were lactating or pregnant; in males, we noted if their scrotum was well-developed and testes prominent (Fauteux *et al.* 2015). Lemmings were immediately anesthetised by holding a delivery tube with a cotton ball soaked in 20% isoflurane over the nose and mouth following the method of Itah *et al.* (2004). A 75 µL blood sample was taken from the retro-orbital sinus of the anesthetised lemming with a heparinized Pasteur pipette tube. This method is a rapid and efficient way of obtaining blood samples in small mammals while minimising harm (Bradshaw 2003). Anesthesia of lemmings was generally fast (<60 s) as was blood sampling (<15 s) and thus all blood samples were obtained <3 min after capture. When the lemming had regained consciousness, we carried it to the field station in a small plastic box (<20 min walk). We collected fecal samples within 15 minutes of capture directly from the anus of the lemmings (if available) or from the transport box. We used flat-tipped forceps disinfected with benzalkonium chloride to collect fecal samples. Field manipulations and housing procedures were approved by the Animal Welfare Committee of Université Laval (2014-061) and Parks Canada (SIR-2013-13953).

*4.4.3. Blood and feces sampling after initial capture*

A second blood and fecal sample was taken at the field station 30 min post-capture. Glucose concentration (mg/dl) in blood samples (0 and 30 min post-capture) was obtained with a portable electronic reader on a 0.3 µL sub-sample (FreeStyle, Abbott Park, IL, USA). Blood samples were centrifuged at 13,000 g for 5 minutes in heparinized microhematocrit. The plasma fraction was transferred into 0.6-ml plastic tubes and stored at -20°C prior to shipping to the university for hormonal analyses.

Lemmings were held at the field station for 72 h in individual 40 x 28 x 24 cm hamster cages, fed *ad libitum* with fresh grasses, forbs, shrubs, pieces of apple, peanut butter and hamster chow and supplied with water. Lemmings were held in unheated rooms with windows to ensure natural fluctuations of light and temperature. We minimised potential contamination of feces by urine by adding double-bottoms made of steel wired mosquito nets.

Fecal samples of captive animals were collected at 2-h intervals for the first 8 h and at 4-h intervals afterwards (i.e. 8 h, 12 h, 16 h, etc.). Lemmings were kept in captivity for 72 h to assess the temporal variations of FCM and determine the presence or absence of a circadian rhythm. This also allowed them to return to baseline levels after habituation to captive conditions. At each sampling occasion, we randomly collected ~1 ml of dry feces (10-15 pellets) in 1.5-ml plastic tubes and removed all other feces from the cage. Fecal samples were stored in a -20°C freezer until shipping to the university. The time associated with each fecal sample corresponds to the end of the interval during which they were produced (e.g. feces collected at 12 h were excreted between 8 h and 12 h). Visibly wet feces were not collected to avoid urine-contaminated samples. At the end, all lemmings were released at their site of capture.

*4.4.4. Plasma corticosterone assay*

We measured total corticosterone in plasma in one run using a modified radioimmunoassay (Boonstra et Boag 1992). In order to extract steroids from plasma and saponify triglycerides, we vortexed 5 µl of plasma with 1 ml methylene chloride and 20 µl

ammonium hydroxide for 4 min, followed by centrifugation (225 g for 5 min). We subsampled duplicate 200 µl aliquots of the methylene chloride suspensions, dried them to completion under filtered air, and then reconstituted them in 300 µl phosphate buffered saline. For the assay procedure, we incubated the reconstituted aliquots overnight at 4°C with 100 µl CJM006 corticosterone antibody (1:20000; C. Munroe, UC Davis, CA) and 100 µl 1,2,6,7-[$^3$H] corticosterone (2 nM). We then separated free corticosterone with 200 µl dextran-coated charcoal (DCC) at 0°C, centrifuged them (1750 g for 15 min) at 0°C, and measured the radioactivity of the supernatant. Corticosterone values for unknowns were inferred from a standard curve of known corticosterone standards.

The cross reactivity for the CJM006 antibody is reported as, corticosterone 100%; desoxycorticosterone 14.25%; tetrahydrocorticosterone 0.9%; 11-desoxycortisol 0.03%; prednisone <0.01%; prednisolone 0.07%; cortisol 0.23%; cortisone <0.01%; progesterone 2.65%; testosterone 0.64%, and; estradiol 17b <0.01%. The average coefficient of variation for replicates was 16±5.5%

As recommended by Delehanty *et al.* (2015), we measured the maximum corticosterone binding capacity (MCBC) of each plasma sample. We used a slightly modified version of the dextran-coated charcoal (DCC) separation method of Hammond et Lähteenmäki (1983). In brief, plasma was stripped of endogenous steroids at room temperature in a DCC solution for 30 min. Stripped plasma (most at a final dilution of 1:30,000, but a few at 1:3,000 due to them having relatively low MCBC) were incubated with a 3.7 nM solution of 1,2,6,7-[$^3$H] corticosterone for 1 hour at 20°C. We ran two total binding replicates and one non-specific binding tube (to which we added additional 4000 nM corticosterone standard) for each sample. We separated bound and free 1,2,6,7-[$^3$H] corticosterone with an ice-cold DCC solution for 10 min, followed by centrifugation (1750 g for 15 min), and then measured the radioactivity (counts per minute, CPM) of the supernatant. MCBC was estimated by subtracting each sample's non-specific binding CPM from its total binding CPM, and then calculating the ratio of 1,2,6,7-[$^3$H] corticosterone in the supernatant to the amount of 1,2,6,7-[$^3$H] corticosterone added to each tube. The average specific binding was 10.7±1.9% of the total 1,2,6,7-[$^3$H] corticosterone added to each tube.

Free corticosterone concentrations were calculated using the equation of Barsano et Baumann (1989). We used the corticosterone binding globulin (CBG) affinity constant reported for brown lemmings ($K_d$ = 10.79; Romero *et al.* 2008).

### *4.4.5. Extraction and measurement of fecal corticosterone metabolites (FCM)*

We extracted fecal metabolites with a protocol developed for squirrels but modified for smaller samples (Touma *et al.* 2003; Bosson *et al.* 2009; Dantzer *et al.* 2010). Fecal samples were freeze-dried for ≥12 h and dried samples were refrozen with liquid nitrogen to facilitate crushing with a mortar and pestle. We subsampled 30 ± 5 mg of the resulting powder and recorded the mass precisely. Samples were extracted in 1 ml of an 80% methanol solution, vortexed (1500 rpm) for 30 min and centrifuged (2500 g) for 15 min. An aliquot (0.7 ml) of the supernatant was transferred into a 1.5-ml plastic tube and stored at -20°C until analysis by the enzyme immunoassay (EIA).

As a starting point, we first characterised FCM metabolites by reverse-phase high-performance chromatography (RP-HPLC; Touma *et al.* 2003) in two adult female lemmings (one pregnant, one non-reproductive) captured in 2012 and subsequently determined the immunoreactivity with two EIAs previously used in small rodents: namely a 5α-pregnane-3β,11β,21-triol-20-one EIA and an 11-oxoetiocholanolone EIA (Touma *et al.* 2003; Montiglio *et al.* 2012).

### *4.4.6. Statistical analyses*

Blood data were analysed using linear models with a Gaussian distribution as we had a single measurement per individual at each time period. One exception was when we used free corticosterone to test the stress response to capture: we used linear mixed effects models with "sample" (i.e. baseline at $t$ = 0 and stressed at $t$ = 30 min) as the fixed factor and individuals as the random factor.

We developed four candidate models to test the effects of various factors at $t$ = 0 and $t$ = 30 min on total corticosterone concentration ($total.c_0$ and $total.c_{30}$), maximum corticosterone binding capacity ($mcbc_0$ and $mcbc_{30}$), free corticosterone ($free.c_0$, $free.c_{30}$),

glucose concentration ($g_0$, $g_{30}$) and their relative change (i.e. ratio of values at $t$ = 30 and $t$ = 0; $r_{total.c}$, $r_{mcbc}$, $r_{free.c}$, and $r_g$). Model 1 tested for differences among adult females, adult males and juveniles (groups; based on body mass; adult females: ≥28g; adult males ≥30 g; juveniles: all others; Fauteux *et al.* 2015). Model 2 examined the effect of reproductive activity only, Model 3 tested for an interaction between sex and reproductive activity, and Model 4 was the null model. For the second and third models, juveniles were separated according to their sex and considered non-reproductive. Females were classified as reproductively active if they had a perforate vagina, were lactating, or were pregnant. Males were classified as reproductively active if they had a well-developed scrotum. We selected the most parsimonious model based on Akaike's second-order criterion (AICc) and report Akaike's weight of each model. When two models were equivalent (ΔAICc << 2), we based our interpretation on the model with the smallest number of parameters (Arnold 2010). Because juveniles were reproductively inactive and our global model included an interaction, we could not model-average estimates (Burnham *and* Anderson 2002). Tukey's multiple comparisons test from the "multcomp" package implemented in the R software (R Core Team 2014) were used to compare blood characteristics among lemming groups (Hothorn *et al.* 2008).

We determined the delay for FCM to appear in feces after capture using a linear model that compared FCM levels at $t$ = 0 to later samples (i.e. 0.5, 2, 4, 6, and 8 h after capture). We used the same four previously-described candidate models to test the effect of various factors on initial, maximal, and the relative change of FCM between the moment of capture and the maximal level attained. We conducted autocorrelation analyses on time series to determine if we could detect internal rhythm in ln-transformed FCM values at different time intervals: $t$ vs $t$+4 h, $t$+8 h, ..., $t$+24 h (Venables et Ripley 2002). Analyses started 12 h after capture (i.e. $t$ = 12 h) to exclude peak FCM concentrations induced by the capture.

Finally, we conducted an analysis to determine the relationship between total corticosterone, free corticosterone and FCM concentrations measured by the EIA. We paired blood samples at $t$ = 0 and $t$ = 30 min with the initial (i.e. $t$ = 0) and maximal FCM

concentrations, respectively. We used mixed-effects linear models with individual lemmings as the random factor.

Response variables were ln-transformed if it increased normality and homoscedasticity of residuals. Homoscedasticity was assessed visually for each model by plotting the residuals as a function of fitted values. When mixed effects models were used (i.e. when individual was included as a random effect), we estimated the coefficients of determination following Nakagawa et Schielzeth (2013). We report the marginal ($R^2_m$, related to fixed effect) unless mentioned otherwise. All means are presented with their respective standard errors (±S.E.) in the text and coefficient estimates from models are given with their respective 95% confidence intervals (CI).

## 4.5. Results

Twenty lemmings were captured and 18 were held in captivity: 9 adult females (6 reproductive and 3 non-reproductive), 5 adult females (3 reproductive and 2 non-reproductive) and 4 juveniles, 2 of each sex. Initial blood measurements were taken on two additional individuals (one reproductive male and one non-reproductive adult female) that had cardio-respiratory failures during anesthesia.

### *4.5.1. Plasma levels*

All lemming groups strongly responded to capture and anesthesia by showing much higher levels of free corticosterone 30 min later ($\beta$ = 4.05, CI = [3.28, 4.81], $R^2_m$ = 0.78; Figure 4.1). Initial total corticosterone concentrations and MCBC were on average 10-20 times higher in adult females ($\overline{total.c}_0$ = 3119 ± 614 ng/ml; $\overline{mcbc}_0$ = 6552 ± 1421 ng/ml) compared to adult males ($\overline{total.c}_0$ = 228 ± 83 ng/ml; $\overline{mcbc}_0$ = 471 ± 124 ng/ml) and juveniles ($\overline{total.c}_0$ = 153 ± 17 ng/ml; $\overline{mcbc}_0$ = 506 ± 40 ng/ml; Table 4.1). Similar results were found in samples taken 30 min after capture with higher concentrations in adult females ($\overline{total.c}_{30}$ = 7213 ± 1508 ng/ml; $\overline{mcbc}_{30}$ = 6726 ± 1333 ng/ml) compared to adult males ($\overline{total.c}_{30}$ = 676 ± 148 ng/ml; $\overline{mcbc}_{30}$ = 399 ± 95 ng/ml) and juveniles ($\overline{total.c}_{30}$ = 680 ± 59 ng/ml; $\overline{mcbc}_{30}$ = 499 ± 41 ng/ml; Table 4.1). Total corticosterone also increased

between $t$ = 0 and 30 min and this increase was higher in juveniles ($\bar{r}_{total.c}$ = 5.04 ± 0.84) than in adult females (1.99 ± 0.25), but slightly higher than in adult males (3.71 ± 0.67; Table 4.1), and there was no change in MCBC ($r_{mcbc}$) concentrations over time in any of the lemming categories (Figure 4.1). Free corticosterone concentrations ($free.c_0$, $free.c_{30}$) did not differ among any of the lemming categories for both samples taken at $t$ = 0 and 30 min later, probably owing to the high inter-individual variability (Figure 4.1; Annexe S3.1, Table S3.1).

Interestingly, models with an interaction between sex and reproductive activity had reasonable statistical support to explain variation in MCBC at $t$ = 0 (ΔAICc = 2.95) and 30 min (ΔAICc = 1.88; Annexe S3.1, Table S3.1). According to this model, reproductively active females ($\overline{mcbc}_0$ = 9129 ± 1639 ng/ml; $\overline{mcbc}_{30}$ = 8611 ± 1993 ng/ml) had higher MCBC concentrations at $t$ = 0 and 30 min than the non-reproductive females ($\overline{mcbc}_0$ = 1938 ± 521 ng/ml; $\overline{mcbc}_{30}$ = 2955 ± 845 ng/ml). In contrast, reproductively active males ($\overline{mcbc}_0$ = 347 ± 159 ng/ml; $\overline{mcbc}_{30}$ = 246 ± 186 ng/ml) had lower MCBC concentrations compared to their non-reproductive counterparts ($\overline{mcbc}_0$ = 800 ± 167 ng/ml; $\overline{mcbc}_{30}$ = 629 ± 79 ng/ml). To summarize, age and sex explained a large proportion of variation in total corticosterone and MCBC, though reproductive activity also influenced MCBC, but not in free corticosterone.

Initial levels of glucose varied with reproductive condition as reproductively active lemmings ($\bar{g}_0$ = 145 ± 10 mg/dl) had higher concentrations of glucose compared to inactive ones (116 ± 5 mg/dl; Table 4.1). The relative change of glucose levels between $t$ = 0 and 30 min later was also higher in juveniles compared to adults (Table 4.1; Figure 4.1; Annexe S3.1, Table S3.1).

### *4.5.2. Fecal corticosterone metabolite levels*

Generally, both antibodies picked up several FCM (Figure 4.2) and gave similar results for FCM concentrations (Pearson's $r$ = 0.58; Annexe S3.2, Figure S3.1). The 11-oxoetiocholanolone EIA detected one main metabolite eluting around HPLC fraction 70. In contrast, the 5α-pregnane-3β,11β,21-triol-20-one EIA detected several metabolites that

were more polar. Metabolites between fractions 32-41 were in higher concentrations in the reproductively active female compared with the inactive one, indicating slightly different patterns due to reproductive conditions. The 5α-pregnane-3β,11β,21-triol-20-one EIA reacted with more different metabolites (fractions 32-41 and 62-72) and thus may yield more stable measurements. We thus utilised the 5α-pregnane-3β,11β,21-triol-20-one EIA for all subsequent analyses. This antibody cross-reacts with metabolites having a 5α-3β,11β diol structure.

Adult males ($\overline{fcm}_0$ = 896 ± 217 ng/g) tended to have higher baseline FCM levels than juveniles (244 ± 31 ng/g), with adult females showing intermediate values (570 ± 155 ng/g), but the null model (i.e. no difference) was preferred based on parsimony (Annexe S3.1, Table S3.2). We found no difference in FCM concentrations between $t$ = 0 and 30 min ($\beta$ = 0.22, CI = [-0.30, 0.73]), but average FCM concentrations had increased by 521% 2 h after capture ($\beta$ = 1.83, CI = [1.32, 2.34]). FCM concentrations reached their highest levels 3.9 h (± 0.3) after capture across individuals (Figure 4.3) and samples taken 4 h after capture had on average the highest FCM concentration (1028% increase; $\beta$ = 2.30, CI = [1.791, 2.81]). Reproductively active lemmings ($\overline{fcm}_{\max}$ = 8117 ± 3003 ng/g) reached higher maximum FCM concentrations compared to reproductively inactive ones (2606 ± 390 ng/g; $\beta_{fcm}$ = 0.86, CI = [0.23, 1.50]). The relative change of FCM between initial and maximal concentrations was similar among lemming groups (Annexe S3.1, Table S3.2). The 72-h FCM concentration profile of each individual lemming is presented in the Annexe S3.3.

The autocorrelation analyses for circadian rhythm indicate that FCM levels measured at time $t$ and $t$+4 h were positively correlated (Table 4.2). The autocorrelation between FCM levels measured at time $t$ and $t$+24 h was weak though it approached the significance level.

When results of all lemmings were pooled, FCM were positively related to plasma free corticosterone concentrations ($\beta_{\text{free}.c}$ = 0.42 ± 0.07, CI = [0.28, 0.56], $R_m^2$ = 0.53; Figure 4.4), but not to total corticosterone concentrations ($\beta_{\text{total}.c}$ = 0.11± 0.14, CI = [-0.20, 0.42], $R_m^2$ = 0.02). Even after considering group, sex, and reproduction conditions in post-hoc

analyses, the strength of the relationship between FCM and total corticosterone remained much lower than the one between FCM and free corticosterone (Annexe S3.4).

## 4.6. Discussion

We assessed the stress response of brown lemmings in a highly cyclic population inhabiting the high Arctic. We showed that plasma corticosterone and FCM increased markedly after hand-capture, which confirms that both measures adequately detected the stress response of lemmings. Glucose concentrations also increased as expected under stressful conditions (Breuner *et al.* 2013). We found that FCM concentrations were highly related with plasma free corticosterone concentrations, but very little to total corticosterone concentrations even though they had also increased in response to the stressor; this is only the second time that such a relationship has been found (Sheriff *et al.* 2010). Lemmings reached maximal FCM levels on average 3.9 h after capture, suggesting rapid metabolism of corticosterone after being stressed. Sex, reproductive status, and age had relatively weak effects on plasma free corticosterone and FCM levels but strong effects on plasma total corticosterone levels. Our findings confirm the usefulness of FCM to measure stress levels as they reflect well the biologically active portion of corticosterone. Large inter-individual variability in blood parameters could be partly explained by age, sex or reproductive condition though less so for FCM, likely a consequence of our relatively small sample size. We found no evidence for a circadian rhythm in FCM at a site where sunlight in summer is present 24 h a day.

### *4.6.1. Measurement of FCM*

We found that the 5α-pregnane-3β,11β,21-triol-20-one EIA successfully detected an endocrine response in lemming feces to hand-capture and associated manipulations. Our results substantiates previous studies that show reliable detection of fecal glucocorticoid metabolites by this EIA in other rodent species (Touma *et al.* 2003; Bosson *et al.* 2009; Dantzer *et al.* 2010; Montiglio *et al.* 2012; Bosson *et al.* 2013; Hammond *et al.* 2015). The large increase in plasma total and free corticosterone and glucose 30 min after capture

coupled with the sharp increase in FCM concentrations 4 h after hand capture indicates that lemmings responded strongly to capture, anesthesia, and transport to the lab. Trapping has been shown to be stressful in several small mammals (Fletcher et Boonstra 2006b; Bosson *et al.* 2013). The combined effect of hand capture and anesthesia clearly elicited a strong stress response and thus can be an interesting alternative to hormonal challenges (e.g. with ACTH) when this test cannot be conducted due to logistical constraints (Touma et Palme 2005). The delay in the increase of FCM concentrations is similar to the 4-h delay found by Rogovin et Naidenko (2010) in bank voles (*Myodes glareolus*), which is half than in laboratory mice (*Mus musculus domesticus*, 8 h, Touma *et al.* 2003). This delay is also shorter than in larger rodents (7-8 h in Columbian ground squirrels, *U. columbianus*, North American red squirrels, *Tamiasciurus hudsonicus*, and eastern chipmunks, *Tamias striatus*, Bosson *et al.* 2009, Dantzer *et al.* 2010, Montiglio *et al.* 2012), which supports the hypothesis that the speed at which glucocorticoids are voided in feces may depend on gut passage time (Palme *et al.* 2005).

The objective in most field studies is to measure stress signatures in feces that are indicative of the "true" basal level and not affected by capture and handling. There is a lag between the moment of capture and the moment at which FCM concentrations start increasing substantially and this needs to be considered when sampling wild populations. Although it took about 4 h for lemmings to reach maximum FCM concentrations, lemmings generally reached half of their maxima only 2 h after capture. This speed of excretion is surprisingly fast when compared to other rodents (see above), which substantiates the necessity of validating FCM for new species under investigation. To our knowledge, this is the first time that such a rapid elevation of FCM in feces is observed in small mammals, which could be a consequence of the intensity of the stressor. Indeed, hand-capture followed by anesthetisation and transportation to the field station is likely to be more stressful than simply being captured in a live trap. Nonetheless, we recommend collecting lemming fecal samples in the field <2 h after a stressful event (such as closing of a trap) to avoid artificially created high stress levels. If the traps are visited at a frequency of >0.5 visit $h^{-1}$, variation in FCM concentrations due to individuals entering the traps at different moments within the interval should be minimal and FCM should provide a reliable measure of baseline stress level.

*4.6.2. Fecal corticosterone metabolites reflect plasma free corticosterone*

We found that variation in FCM concentrations were highly related ($R^2 = 0.53$) to that in free corticosterone recorded in the plasma following a stressful event. One potential source of variation in this relationship is that some lemmings may have already started to respond to our approach before capturing them and thus their plasma corticosterone level may not represent true basal level. However, our results show that free corticosterone was low for all lemmings at the moment of capture ($t = 0$), suggesting that any response to our presence at that time was weak. Interestingly, FCM concentrations were not related to total corticosterone, which substantiates the hypothesis that only free corticosterone (i.e. not bound to proteins) leaves blood circulation (reviewed in Perogamvros *et al.* 2012; Breuner *et al.* 2013) when metabolised by the liver as found in snowshoe hares (Sheriff *et al.* 2010). Our results do not address the possibility that bound glucocorticoids could play a role in this dynamics (Schoech *et al.* 2013), but are consistent with the idea that binding proteins prevent metabolism of corticosterone by the liver. Although plasma total corticosterone also increased after the stressor, the relatively small change compared to free corticosterone prevented a strong relationship with FCM even when accounting for sex differences in total corticosterone. In contrast, differences in free corticosterone and FCM between sexes and age were small, likely because they were buffered by the marked differences in plasma MCBC among sex and reproductive groups, which matched the differences observed in total corticosterone. Nonetheless, a considerable amount of the variation in FCM concentrations remained unexplained. Potential reasons for this may be that we did not sample the blood when the highest free corticosterone concentrations were reached in all individuals. Indeed, we limited blood sampling to two points in time and free corticosterone may have reached peak concentrations later than 30 min after capture (Romero *et al.* 2008). Other sources of variation may stem from the intra-population heterogeneity.

*4.6.3. Intra-population heterogeneity*

Age, sex and reproductive condition generally explained more variability in total (but not free) plasma corticosterone than in FCM. Our small sample size hampered our

ability to explain variations in FCM due to the large inter-individual variability recorded. For instance, two of the three reproductively active males reached very high levels ($fcm_{max}$ = 31 and 12 µg/g), whereas the two reproductively inactive males had much lower levels ($fcm_{max}$ = 3.6 and 3.3 µg/g; Online Resource C). This contrasts with plasma corticosterone levels, which was generally higher in females, probably because of the stimulatory effect of estrogen (reviewed in Boonstra *et al.* 2007). The large values observed in reproductively active males are interesting considering that several studies have shown that it is critical to consider reproductive condition when assessing stress levels in small mammals (Boonstra et Boag 1992; Kenagy *et al.* 1999; Boonstra *et al.* 2001a). High testosterone levels in reproductive males are often related to low MCBC levels resulting in high free glucocorticoids in the blood relative to non-reproductive males (e.g. *Antechinus swainsonii*, McDonald *et al.* 1986; arctic ground squirrels, Boonstra *et al.* 2001b).

Adult females had much higher total corticosterone and MCBC than adult males and juveniles in both baseline and stressed samples, but these differences were not marked in free corticosterone. Although adult female lemmings have some of the highest total corticosterone concentrations of all mammals, as first observed by Romero *et al.* (2008), they also have very high MCBC, which explains why their free corticosterone levels were only marginally higher than those of male or juvenile brown lemmings. This means that high MCBC compensated for high total corticosterone and could explain why little sex differences in FCM was found here or in other vole species (Bian *et al.* 2015). In contrast to what Charbonnel *et al.* (2008) reported in water voles (*Arvicola scherman*), we found no evidence of variation in baseline FCM concentrations with reproductive condition in females, possibly because variability in free corticosterone concentrations was relatively small. It is still unclear why reproductive female lemmings maintain such high total corticosterone and MCBC levels in the plasma compared to males and other species but this could be a useful reservoir for future highly energetic activities during more rigorous periods (i.e. reproduction in winter).

Juvenile lemmings showed a weaker stress response to capture compared to adult females, but similar to adult males, as was previously reported by Romero *et al.* (2008). This suggests that juveniles are either more resistant to stressors owing to a very efficient

negative feedback or their stress response was damped by an underdeveloped HPA axis. The second hypothesis may be more plausible as Seabloom *et al.* (1978) found that adrenals of juvenile meadow voles (*Microtus pennsylvanicus*) were less responsive to ACTH stimulation compared to adults. Interestingly, juveniles had the steepest increase in glucose concentrations once stressed, which indicates that they still efficiently mobilised energy in response to capture and anesthesia.

Metabolism of glucocorticoids can differ between sexes, thereby creating metabolites with different molecular structures (Touma *et al.* 2003; Lepschy *et al.* 2007). The proportion of metabolites excreted via the feces or the urine may also differ between sexes. For example, male mice excrete up to 75% of their glucocorticoid metabolites in feces whereas females excrete 50% (Touma *et al.* 2003, 2004). This difference in excretion routes, in combination with sex differences in excreted FCM and their immuno-reactivity in the EIA, could have contributed to the observed patterns in plasma free corticosterone and FCM in relation to sex. Although we cannot evaluate the variation in the percentage of corticosterone metabolites detected by our EIA between sexes, it successfully detected a response to the stressor in all groups. FCM measured by the 5α-pregnane-3β,11β,21-triol-20-one EIA thus appears adequate to detect a stress response in lemmings as revealed by free corticosterone, but comparisons of FCM levels between sexes and reproductive conditions cannot be extrapolated to plasma total corticosterone or MCBC (Touma *et al.* 2004).

### *4.6.4. Circadian rhythm*

Our autocorrelation analysis provided little evidence of a circadian rhythm in FCM concentrations in lemmings. This result contrasts with those of Andrews (1968) who found a circadian pattern in steroid secretion in captive brown lemmings of Alaska. A possible explanation for this difference may be the short period of habituation to captivity in our experiment coupled with the regular collection of fecal samples, which may have disrupted the normal daily activities of captive lemmings. This constant disturbance may also explain why a positive autocorrelation with a 4-h delay was present.

Diurnal rhythm in FCM has been observed in other small mammal species and it has been suggested that varying defecation rates according to the time of the day may play a role (Touma *et al.* 2003; Sheriff *et al.* 2009a). It is thus surprising that we found little evidence for such an endogenous cycle in lemmings. However, it is also possible that the 24-h daylight of the high arctic summer inhibits such cycles since we found that the probability of capturing lemmings during live-trapping sessions is unaffected by the time of day. It has also been suggested that reindeers (*Rangifer tarandus*) show weak or no circadian behavioural or hormonal patterns due to the shortness or the lack of photic variations during most of the year (van Oort *et al.* 2005; Lu *et al.* 2010). Thus, sampling fecal material at different time of the day may not represent a major source of bias during summer in the High Arctic.

### 4.7. Conclusion

We show that a 5α-pregnane-3β,11β,21-triol-20-one EIA is well suited for evaluating adrenocortical activity via FCM in arctic lemmings. We found that FCM is highly related with plasma free corticosterone ($R^2$ = 0.53) despite some differences related to sexes and age groups between plasma and fecal metabolites. Our study further supports the hypothesis that fecal metabolites reflect well the free, biologically active portion of plasma corticosterone. Recent studies have found that some small mammal populations showing large-amplitude fluctuations of abundance through time have phase-dependent stress responses (Charbonnel *et al.* 2008; Sheriff *et al.* 2009b; Bian *et al.* 2015), which has the potential to explain part of their population dynamics, as shown in snowshoe hare (Sheriff *et al.* 2009b). FCM may be a useful tool to study the stress response of lemmings to external factors such as predation, food depletion or competition (Sheriff *et al.* 2011b; Boonstra 2013). However, an important caveat when applying this technique is that fecal samples taken more than 2 h after a stressful event (e.g. live-trapping) may not be representative of baseline levels. Sex and reproductive condition of individuals should also be considered due to possible sex-specific differences in excreted glucocorticoid metabolites.

## 4.8. Acknowledgements

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## 4.9. Supplementary material

Annexe 3.1. Model selection for blood and FCM analyses.

Annexe 3.2. FCM concentrations measured by two different enzyme immunoassays cross-reacting with different metabolites.

Annexe 3.3. Temporal corticosterone metabolite profiles in faeces of individual lemmings in captivity

Annexe 3.4. Effects of age, sex, and reproductive condition on the relationship between FCM and plasma corticosterone

### 4.10. Tables

Table 4.1. Effects retained in the most parsimonious models testing for plasma differences in initial ($t$ = 0) samples, samples taken 30 min after capture, and relative change ($r$, ratio between values at $t$ = 30 and $t$ = 0). Variables include total corticosterone (*total.c*), maximum corticosterone binding capacity (*mcbc*) and glucose concentrations (*g*). Results from model selection are presented in Online resources A. The coefficients ($\beta$) with their 95% confidence intervals (CI) are presented (95% CI excludes 0 when in bold) along with the adjusted $R^2$ of each model.

| Response variable | Model | Comparisons | $R^2$ | $\beta$ | Low CI | High CI |
|---|---|---|---|---|---|---|
| ln(*total.c*$_0$) | 1 | **J - AF** | 0.82 | **-3.06** | **-4.15** | **-1.96** |
| | | **AM - AF** | | **-3.06** | **-4.08** | **-2.04** |
| | | AM - J | | -0.00 | -1.25 | 1.24 |
| ln(*total.c*$_{30}$) | 1 | **J - AF** | 0.73 | **-2.17** | **-3.26** | **-1.09** |
| | | **AM - AF** | | **-2.40** | **-3.42** | **-1.39** |
| | | AM - J | | -0.23 | -1.45 | 0.99 |
| $r_{total.c}$ | 1 | **J - AF** | 0.36 | **3.05** | **0.55** | **5.56** |
| | | AM - AF | | 1.72 | -0.78 | 4.23 |
| | | AM - J | | -1.33 | -4.28 | 1.62 |
| ln(*mcbc*$_0$) | 1 | **J - AF** | 0.74 | **-2.36** | **-3.72** | **-1.01** |
| | | **AM - AF** | | **-2.81** | **-3.94** | **-1.69** |
| | | AM - J | | -0.45 | -1.96 | 1.05 |
| ln(*mcbc*$_{30}$) | 1 | **J - AF** | 0.78 | **-2.43** | **-3.60** | **-1.27** |
| | | **AM - AF** | | **-2.98** | **-4.07** | **-1.90** |
| | | AM - J | | -0.55 | -1.85 | 0.76 |

| | | | | | | |
|---|---|---|---|---|---|---|
| $g_0$ | 2 | **repro** | 0.21 | 28.98 | 3.66 | 54.30 |
| $r_g$ | 1 | J - AF | 0.33 | 0.67 | -0.07 | 1.40 |
| | | AM - AF | | -0.35 | -1.09 | 0.39 |
| | | **AM - J** | | **-1.02** | **-1.88** | **-0.15** |

Note: J = juvenile (females < 28 g, males < 30 g); AF = adult females; AM = adult males; repro = reproductively active vs inactive (used as the reference group).

Table 4.2. Results from the autocorrelation analyses for potential circadian rhythm from FCM levels. Linear models with the individual as a fixed effect were used to consider high inter-individual heterogeneity in FCM levels. The coefficients ($\beta$) with their 95% confidence intervals (CI) are presented (95% CI excludes 0 when in bold) along with the marginal $R^2$. $t$ = 12 h after capture to exclude peak FCM levels.

| Model | $\beta$ | Low CI | High CI | $R^2$ |
|---|---|---|---|---|
| $t$, $t$+4 h | **0.22** | **0.07** | **0.37** | 0.63 |
| $t$, $t$+8 h | 0.03 | -0.15 | 0.20 | 0.53 |
| $t$, $t$+12 h | 0.01 | -0.15 | 0.17 | 0.57 |
| $t$, $t$+16 h | -0.06 | -0.23 | 0.12 | 0.55 |
| $t$, $t$+20 h | -0.00 | -0.21 | 0.21 | 0.47 |
| $t$, $t$+24 h | 0.16 | -0.06 | 0.38 | 0.48 |

## 4.11. Figures

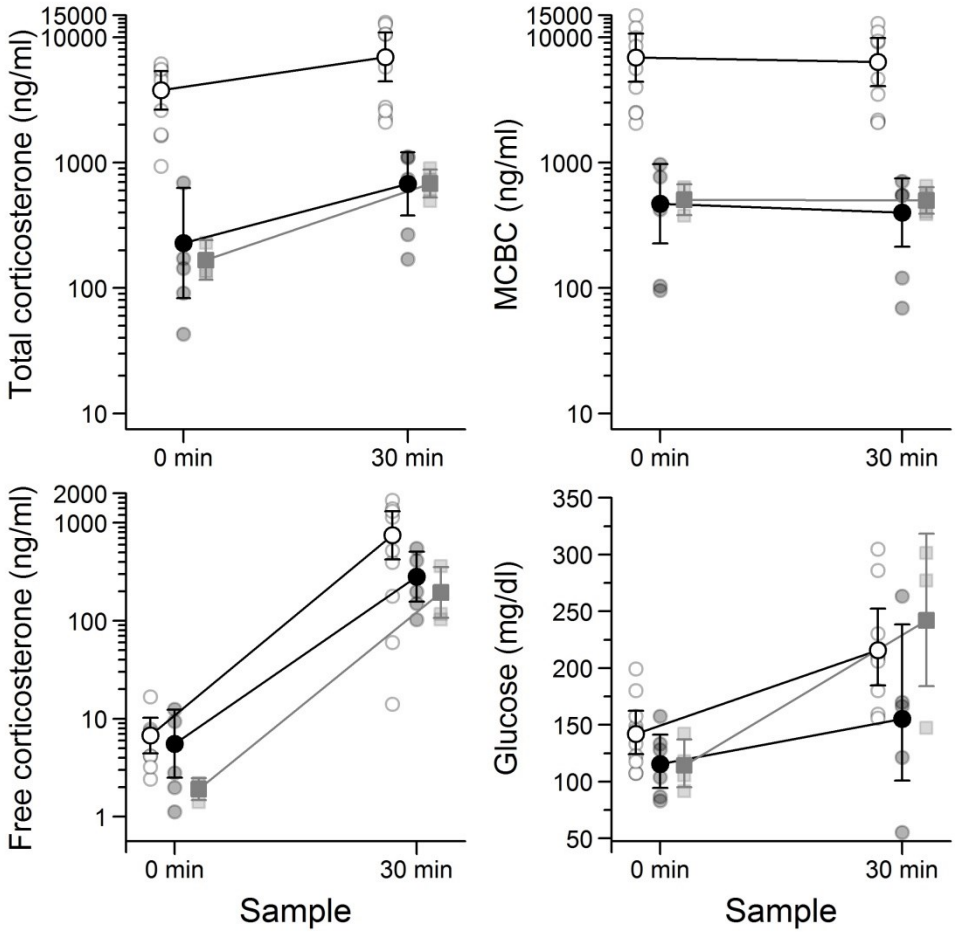


Figure 4.1. Average plasma concentrations of free and total corticosterone, maximum corticosterone binding capacity (MCBC), and glucose at time 0 (baseline) and 30 min after hand-capture in brown lemmings with their respective 95% confidence intervals. Animals were anesthetised prior to bleeds at both occasions. Mean concentrations for adult females ($n_0$ = 10; $n_{30}$ = 9; white circles), adult males ($n_0$ = 6; $n_{30}$ = 5; black circles), and juveniles ($n$ = 4; grey squares). Individual values are presented for each mean values.

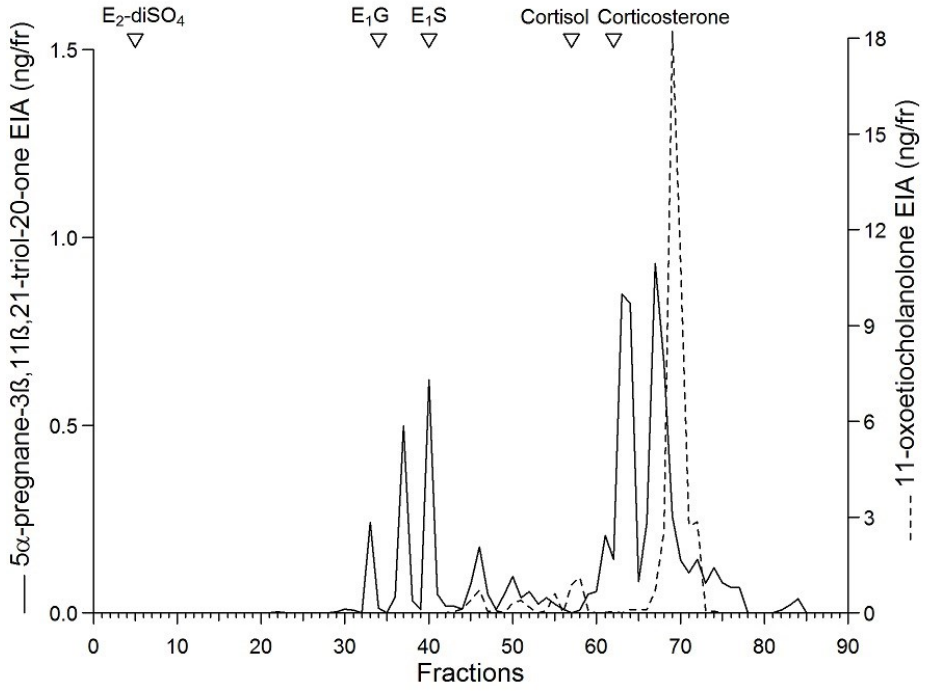


Figure 4.2. Reverse-phase high-performance liquid chromatography immunogram comparing cross-reactivity with lemming fecal glucocorticoid metabolites measured by two enzyme immunoassays (EIA). The mass of metabolites per fraction (ng/fr) measured on one reproductively inactive adult female are presented in the graph. Peak immunoreactivity occurred at fractions 62-72 with both antibodies, indicating cross-reactivity with metabolites of similar polarity. The elution times of the estradiol disulphate ($E_2$-di$SO_4$), estrone glucuronide ($E_1$G), estrone sulfate ($E_1$S), cortisol, and corticosterone standards are indicated by the open triangles.

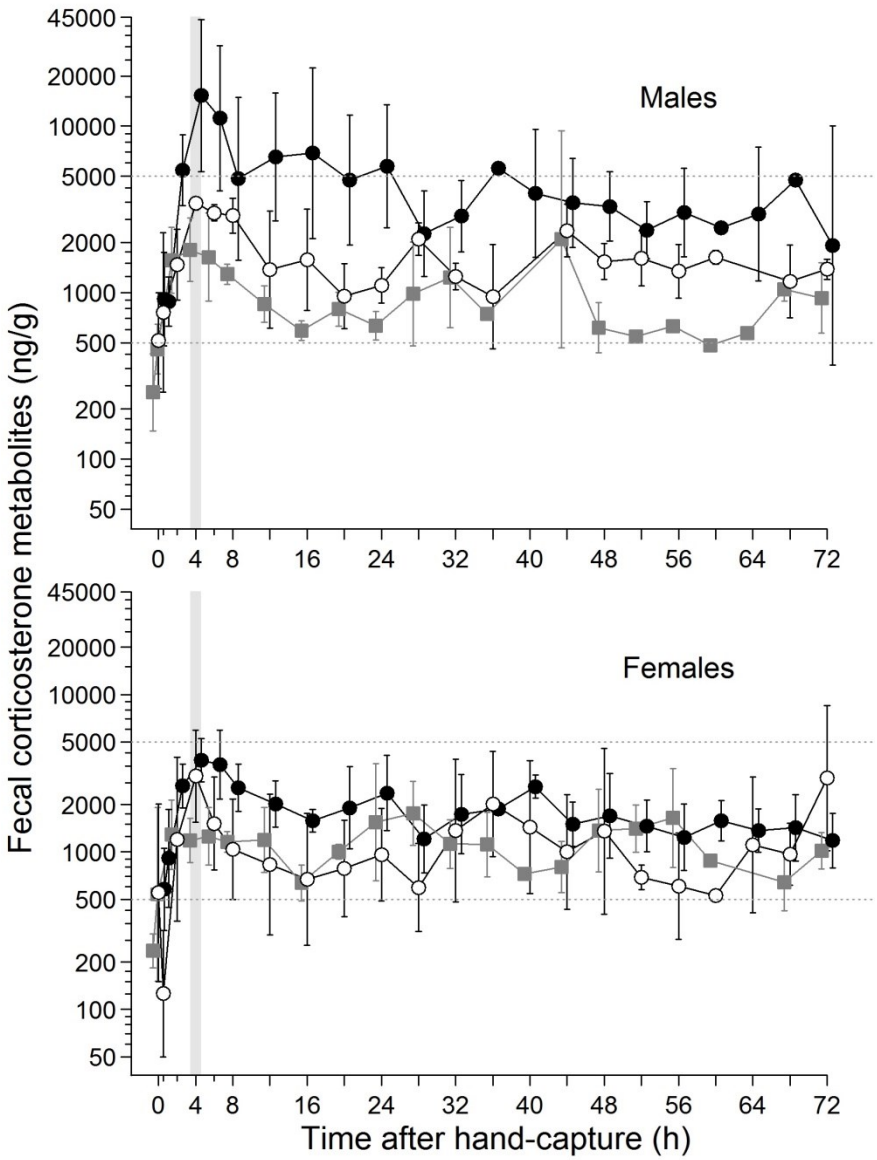


Figure 4.3. Time series of fecal corticosterone metabolites (FCM) concentrations (mean with 95% confidence intervals) in male and female lemmings measured by the enzyme immunoassay (see methods). Black circles represent reproductive adults ($n_{males}$ = 3; $n_{females}$ = 6), white circles non-reproductive adults ($n_{males}$ = 2; $n_{females}$ = 3), and grey squares juveniles ($n_{males}$ = 2; $n_{females}$ = 2). Lemmings were captured at time 0 and released 72 h later. The grey bar indicates the mean time when all lemmings reached their maximal FCM concentrations.

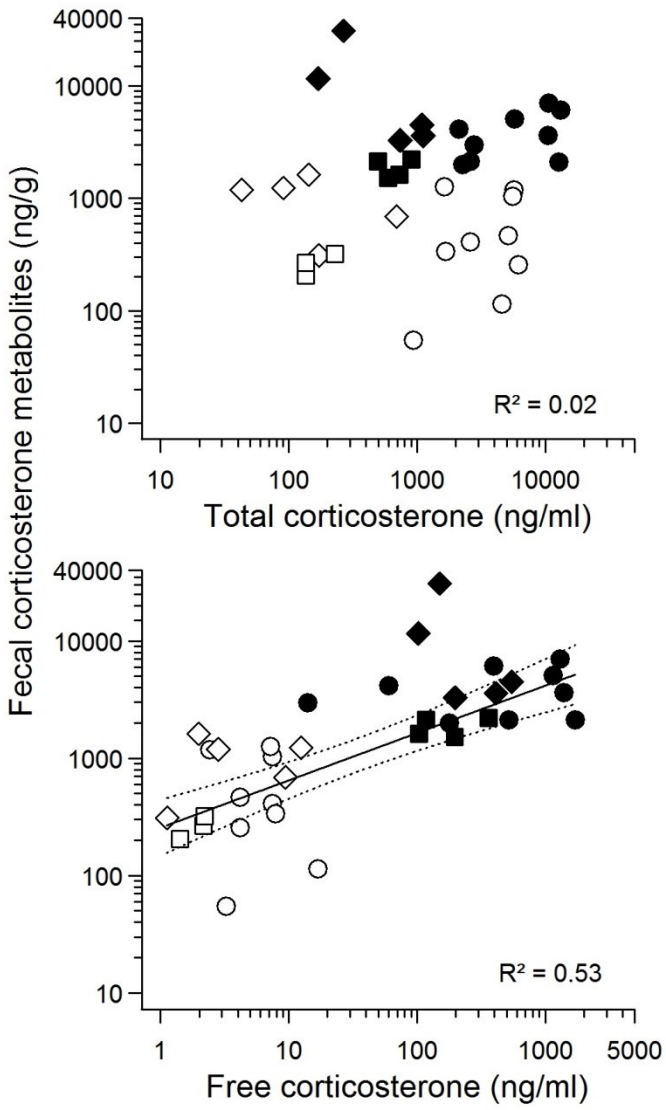


Figure 4.4. Relationships with their 95% confidence intervals (dotted lines) between plasma total or free corticosterone and fecal corticosterone metabolites (FCM) concentrations of lemmings. Samples collected at $t$ = 0 for plasma and FCM were paired (white points) whereas plasma samples collected at $t$ = 30 min were paired with maximal FCM concentrations recorded (i.e. between 2 to 6 h after capture depending on each individual; black points). Two observations (one for each paired samples) per lemming ($n$ = 18) were used to assess the relationship. Circles = adult females; diamonds = adult males; squares = juveniles.

# CHAPITRE 5. Predator-induced stress does not suppress reproduction in High Arctic lemmings

*Sera soumis prochainement à Ecology Letters*:

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## 5.1. Résumé

Les mortalités causées par la prédation peuvent fortement affecter les fluctuations de population, mais ses effets non-létaux ont peut-être été sous-estimés dans les études de dynamique des populations. La réduction de la reproduction causée par le stress chronique peut être un de ces effets qui pourrait avoir un impact majeur sur la croissance de la population de proies. Pour tester si la prédation peut réduire la reproduction dans les populations naturelles de proies régulièrement exposées à des risques élevés, nous avons étudié une population cyclique de lemmings bruns (cycles de 3-4 ans) sur l'Île Bylot, Canada, en 2014 et 2015. Nous avons construit un grand enclose pour exclure les prédateurs (9 ha) délimité par une clôture de 1,2 km couverte d'un grand filet. Nous avons évalué la condition reproductrice des lemmings en les piégeant à l'intérieur de l'exclos et dans un site témoin avec prédation naturelle et nous avons mesuré leur niveau de stress basaux en mesurant les métabolites de corticostérone dans leurs fèces. Les lemmings ont été stressés par les prédateurs car les concentrations de métabolites fécales de corticostérone étaient 1,7 fois plus élevées en dehors de l'exclos qu'à l'intérieur. Cependant, nous n'avons trouvé aucune preuve de réduction de la fécondité alors que les proportions de femelles gestantes/allaitantes étaient similaires entre les deux sites. De plus, les mâles ont montré une activité de reproduction plus élevée dans le site témoin par rapport au site de réduction des prédateurs. Ces résultats contrastent avec des études de laboratoire qui ont signalé une réduction de la reproduction chez les petits rongeurs lorsqu'ils sont exposés à des indices sensoriels des prédateurs (e.g. odeurs). Notre étude suggère que les lemmings maintiennent une reproduction élevée en situation de stress induit par la prédation, une situation qui pourrait être optimale lorsque les mortalités sont élevées.

*Mots clés: populations cycliques, contrôle par le haut, Cricetidae, glucocorticoïdes, hypothèse du stress adapté.*

## 5.2. Summary

Direct mortality induced by predation can strongly affect population fluctuations but its non-consumptive effects may have been underestimated in population dynamics studies. Fecundity reduction caused by chronic stress may be one of those effects and could have a major impact on the population growth of prey. To test whether predation can suppress reproduction in natural populations periodically exposed to high predation risk, we studied a cyclic population of brown lemmings (3-4 yr cycles) on Bylot Island, Canada, in 2014 and 2015. We constructed a large predator-reduction exclosure (9 ha) delimited by a 1.2 km fence and covered by a net. We assessed the reproductive condition of lemmings by trapping them inside the exclosure and in a control area and we measured their basal stress levels by sampling corticosterone metabolites in their faeces. Lemmings were stressed by predators as their fecal corticosterone metabolites were 1.7 times higher outside the predator exclosure than inside. However, we found no evidence of a reduction in fecundity because the proportion of pregnant/lactating females did not differ between the two areas. Moreover, males showed higher reproductive activity in the control area compared to the predator-reduced area. This result contrasts with laboratory studies that reported reproductive suppression in small rodents when exposed to predator cues (e.g. odors). Our study suggests that lemmings maintain high reproduction under predator-induced stress, a potentially optimal strategy when mortalities are high.

*Key-words: cyclic populations, top-down limitation, cricetidae, glucocorticoids, adaptive stress hypothesis.*

## 5.3. Introduction

Non-consumptive effects of stressful environmental factors on population dynamics have recently been the subject of a renewed interest since the pioneer works of Christian (1950). Individual responses to external stressors may scale up to the population level through their effects on reproduction or survival (McDonald *et al.* 1981; Sheriff *et al.* 2009) and could persist through maternal programming (Boonstra *et al.* 1998b; Inchausti et Ginzburg 2009; Sheriff et Love 2013). Predation and food limitation have often been identified as the most important factors affecting growth and declines in fluctuating populations of vertebrates (Sinclair et Krebs 2002). Although lethal effects can sometimes be sufficient to explain population fluctuations (Gilg *et al.* 2003), non-consumptive effects, mediated through physiology and behaviour, could also significantly impact reproduction (Boonstra *et al.* 1998a; Bian *et al.* 2015).

The interaction of glucocorticoids (i.e. stress hormones) with reproductive hormones and other biological processes (e.g. immune function and growth) has been shown in clinical studies and suggests potential trade-offs between reproduction and survival (Sapolsky *et al.* 2000; Whirledge et Cidlowski 2013). Repeated exposure to stressors may induce chronic stress which can disrupt homeostasis and suppress reproduction (Takahashi *et al.* 1990; Boonstra *et al.* 1998a; Herod *et al.* 2010). Such suppression may be adaptive in the short-term if it favours individual fitness through a reallocation of energy to survival (Lima 1986; Wingfield et Sapolsky 2003; Rogovin *et al.* 2008). In contrast, some studies found that chronically stressed rodents responded with increased reproductive activity or faster development of juveniles (Boonstra *et al.* 2001b; Dantzer *et al.* 2013). Long-term effects of stress may therefore vary according to the life-history of species, but whether stress increases of decreases the overall fitness of an individual remains unclear (Bonier *et al.* 2009).

A suppressive effect of stress on reproduction has a strong potential to affect the population dynamics of mammals in natural settings (Sheriff *et al.* 2009; Bian *et al.* 2015). Mechanisms of reproductive suppression can be behavioural (e.g. fear and avoidance of copulation) or physiological (e.g. inhibition of reproductive hormones, poor body condition) (Lima 1986; Wingfield et Sapolsky 2003). There is evidence that fecundity and

recruitment were reduced in snowshoe hares (*Lepus americanus*) and voles when females were exposed to stressful environments (Sheriff *et al.* 2009b; Bian *et al.* 2015). These studies further showed that stress experienced by females can have important consequences on subsequent generations through maternal effects, which could eventually prevent population growth. Reproductive suppression maintained through maternal effects could thus have a lasting impact on population fluctuations of cyclic species even when factors like predation or food are no longer limiting (Boonstra *et al.* 1998b; Inchausti et Ginzburg 2009). Although some field studies have reported reduced reproduction in small mammals when exposed to high predation (Korpimaki *et al.* 1994; Jochym et Halle 2012), evidence that this effect was induced by stress is still scant.

Small rodents are often considered keystone species in several food webs as they are prey to a vast spectrum of predators (Krebs 2011; Legagneux *et al.* 2012). They also typically have elevated stress responses in face of danger, which makes them ideal for studying non-consumptive effects of predation (Fletcher et Boonstra 2006b; Romero *et al.* 2008; Bosson *et al.* 2013). In the Arctic, cyclic lemming populations are exposed to highly fluctuating predation risk that reaches peak intensity during summer, every 3-5 yr (Gilg *et al.* 2006; Therrien *et al.* 2014). Brown lemming populations, for instance, can be decimated by predation within a few months during the peak summer phase (Fauteux *et al.* 2015b). Such highly stressful environment provides an ideal situation to determine whether predation induces elevated stress levels in lemmings and ultimately reduces fecundity. We experimentally addressed these questions with a large (9-ha) predator reduction exclosure, where lemmings were protected from both mammalian and avian predators. We collected fecal samples to measure stress levels non-invasively, and monitored reproductive activity for two years during which lemmings were at peak density and exposed to heavy predation. Based on the stress-induced reproduction suppression hypothesis, we predicted that: (1) lemmings in the predator-reduction area will have lower levels of stress than those in the control area exposed to natural density of predators, and (2) a higher level of fecundity will be found in the exclosure compared to the control. Since stress can have multiple physiological and behavioural effects on life-history traits (Crespi *et al.* 2013), we also predicted that (3) lowly stressed lemmings in the predator-reduction area will have higher

body mass and make longer movements because they should spend more time foraging and venture longer distances from their home range centroid due to low predation risk.

## 5.4. Methods

### *5.4.1. Study area*

Our study was conducted in the Qarlikturvik valley (50 km²) on Bylot Island, Nunavut, Canada (73°08'N; 80°00'W) where two rodent species can be found: brown and collared lemmings (*Dicrostonyx groenlandicus*). Both species fluctuate regularly in abundance but brown lemmings have much higher amplitude cycles, which can be up to 100-fold between low and high abundance years. Lemmings are also exposed to highly fluctuating predation pressure which is driven by their own abundance. During summer, the main predators of lemmings are the arctic fox (*Vulpes lagopus*), ermine (*Mustela erminea*), snowy owl (*Bubo scandiacus*), long-tailed jaeger (*Stercorarius longicaudus*), and rough-legged hawk (*Buteo lagopus*). In winter, only foxes and ermine reside on the island. We present more details on predation risk encountered by lemmings on our study site in Appendix S4.1.

Both lemmings can be found in the two main habitats of the valley (Duchesne *et al.* 2011b). The wet habitat is characterised by a mosaic of tundra polygons, ponds, and thaw lakes and is found mainly in the valley bottom. Sedges (*Eriophorum* spp., *Carex aquatilis*), grasses (*Dupontia fisheri*) and brown mosses (such as *Limprichtia cossonii* and *Campylium stellatum*) mainly compose the vegetation of the wet meadows in this habitat. Drier, mesic habitats cover higher grounds in the valley and the surrounding slopes and hills due to better drainage. The mesic habitat is the most abundant and is primarily composed of prostrate shrubs (*Salix* spp., *Cassiope tetagrona*), grasses (*Arctagrostis latifolia, Alopecurus alpinus*), forbs (*Saxifraga* spp., *Ranunculus* spp.) and some mosses (such a *Polytrichum swartzii*).

*5.4.2. Experimental design and lemming trapping*

We used two live-trapping grids for this study. Both had been monitored since 2008 and both were located in the mesic habitat. In 2012-2013, we built a predator-reduction fence around one grid (hereafter called exclosure) and left the other as a control. In 2012-2013, we built an 8.6-ha fence made of chicken wire (1-inch mesh) and 1.4 m high (2.0 m when crossing snow drift areas), which allowed movements of lemmings in and out of the grid. The wire attached to T-shaped steel bars around the experimental grid to exclude mammalian predators and covered it with a net made of criss-crossing fishing lines 0.5 m apart to exclude avian predators. Lemming abundance was monitored each month from June to August during capture occasions (referred to as primary occasions) spanning 3 consecutive days using capture-mark-recapture methods (Fauteux *et al.* 2015b). The control grid had 144 trapping stations (12 x 12 stations, 10.9 ha) and the exclosure had 96 stations (8 x 12, 6.9 ha). Each station was separated by 30 m and consisted of one Longworth trap. Independence of trapping grids was ensured by separating them by ~600 m, a distance much longer than typical lemming home range radii (Banks *et al.* 1975).

In 2014 and 2015, we used an additional trapping scheme to collect lemming faeces on each grid (fecal collection occasions), which differed from the standard one conducted at monthly intervals to assess density (primary occasions). Faecal pellets were collected between late June and early August during 3 trapping sessions in 2014 and 3 in 2015 in the exclosure and 6 in 2014 and 4 in 2015 on the control (more sessions were conducted on the control due to lower lemming abundance). A fecal collection occasion consisted of opening the traps in the morning (~10h) and visiting them every 2 h until their closure at 18h. Collecting faeces from animals that had stayed <2 h in traps was essential to ensure that FCM concentrations represented baseline levels (Chapitre 4). We chose a subset of 36 trapping stations used during the primary capture occasions. Trapping stations were selected based on the results from the previous trapping occasion to maximise the number of lemmings captured for feces collection. A minimum of three days separated feces collection occasions and the primary occasions to avoid potentially confounding effects of stress induced by previous captures. Each captured lemming was identified to species, sexed, weighed, and its reproductive condition noted. Only feces from adults (males: ≥30 g;

females: ≥28g; Fauteux et al. 2015) were kept for the analyses to eliminate potential confounding age effects. Males were classified as abdominal (i.e. testes retracted in the abdomen) or scrotal (i.e. testes in the scrotum). Females were classified as lactating or pregnant. Lemmings showing no signs of reproduction (i.e., males with an inconspicuous scrotum and females being neither pregnant nor lactating) were classified as non-reproductive. All captured lemmings were tagged, either with passive integrated transponders (PIT, AVID ®; Avid Identification Systems, Inc., Norco, CA, USA) or ear-tags (1005-1 Monel, National Band & Tag Company, Newport, KY, USA). All recaptures were eliminated from the analyses to avoid artificially elevated stress levels due to previous captures (Fauteux et al. submitted). Field manipulations were approved by the Animal Welfare Committee of Université Laval (2014-061) and Parks Canada (SIR-2013-13953).

*5.4.3. Sampling pellets and quantifying faecal corticosterone metabolites*

Faecal samples were collected directly at the anus of captured lemmings when possible or in the traps and placed in small plastic tubes (1.5 ml). Contamination by urine was prevented by placing a small elevated floor made of welded wire in the Longworth traps to retain pellets above the bottom of the trap. All wet pellets were discarded. We used surgical gloves and flat-tipped forceps that were pre-sterilised with benzalkonium chloride to collect pellets. Feces were placed in 1.5 ml plastic vials and stored at -20°C until analysis. In the laboratory, fecal corticosterone metabolites (FCM) were quantified with the 5α-pregnane-3β,11β,21-triol-20-one enzyme immunoassay (EIA) adapted for brown lemmings (Touma et al. 2003; Chapitre 4).

Briefly, fecal samples were freeze-dried ≥12 h prior to crushing with a mortar and pestle and liquid nitrogen. Each crushed sample was weighed up to 30 ± 5 mg and transferred in a separate 1.5-ml plastic tube in which we added 1 ml of an 80% methanol solution. The suspended samples were vortexed (1500 rpm) for 30 min and centrifuged (2500 g) for 15 min (Palme *et al.* 2013). Then, we transferred 0.7 ml of the supernatant into a new 1.5-ml plastic tube and stored at -20°C for later analysis with a 5α-pregnane-3β,11β,21-triol-20-one EIA (Touma *et al.* 2003).

*5.4.4. Statistical analyses*

We first aimed at determining the effect of predator reduction (i.e. control vs experimental trapping grid) on FCM levels of captured lemmings. Because reproductive condition can affect FCM levels (Fauteux et al. submitted), we developed seven candidate models to consider potential effects of: treatment (i.e. predator reduction), reproductive condition, sex, and additive or interactive effects of treatment and reproductive condition (2 models), and treatment and sex (2 models), on FCM concentrations. Reproductive condition and sex were placed in different models due to partial redundancy between these two variables (i.e. reproductive conditions differed between males and females). Linear mixed-effects models with a Gaussian distribution were used with year and month nested in year as random variables to control for potential seasonal or annual variability related to the phase of the population cycle (Boonstra *et al.* 2001a; Romero *et al.* 2008; Sheriff *et al.* 2009b).

We quantified the effects of the predator reduction on fecundity by comparing frequencies of each reproductive category between trapping grids. For this analysis, we used lemmings captured during the three primary occasions aimed at measuring density, to maximise our sample size (see above). For each sex, we modelled the frequencies of reproductive and non-reproductive individuals with a generalized linear mixed-effects model with a Poisson distribution. We modelled the interaction between trapping grids and reproductive conditions as fixed effects, and year as a random effect. We pooled lemmings captured at all occasions but eliminated recaptures within primary occasions.

To determine the effect of stress on body mass of lemmings captured during the fecal collection occasions, we developed 19 candidate models including additive and interactive effects of FCM concentrations, reproductive condition, sex, and trapping grid on body mass with linear mixed-effects models with Gaussian distributions. We used year and months nested within year as random effects. The same types of models were used to analyse movements but year was the only random effect. Movements of individuals were estimated by averaging the distance separating traps of each successive recaptures during primary capture occasions (at monthly intervals). Individuals that were recaptured in the same trap (distance of 0 m) were assigned an average distance of 5 m (i.e. the shortest

averaged distance observed after 0 m) for subsequent log-transformation. Lemmings used in this analysis were those captured during both fecal collection and on primary occasions but movements were estimated with captures within primary occasions only. For both body mass and movement analyses, model ranking was based on AICc and we model-averaged when more than one model had a reasonable statistical support ($\Delta$AICc <4) (Burnham et Anderson 2002).

All statistical analyses were run with the R software. We first calculated Cook's distance (Cook 1977) to measure the influence of extreme FCM values potentially caused by manipulations in the field (Chapitre 4). We used the package "nlme" to estimate coefficients in linear mixed-effects models (Bates *et al.* 2014). Model-averaging was conducted with the package "AICcmodavg" (Mazerolle 2015) and conditional $R^2$ adapted for mixed-effects models were estimated according to the methods of Nakagawa et Schielzeth (2013). All estimates reported in the results are given with their 95% confidence intervals (CI). Response variables were log-transformed to meet model assumptions when necessary (e.g. normality for Gaussian distributions).

### 5.5. Results

During the trapping sessions conducted to collect faecal samples, we captured 69 adult individuals in 2014 (control grid: 34; exclosure: 35) and 34 in 2015 (control grid: 18; exclosure: 16). During the monthly primary occasions used to determine density, we captured 215 adult individuals in 2014 (106 control grid, 109 experimental grid) and 98 in 2015 (49 control grid, 49 experimental grids). In 2014, lemming densities were, on average, 7.7 ind $ha^{-1}$ in the predator exclosure and 4.2 ind $ha^{-1}$ in the control. In 2015, densities were 4.6 ind $ha^{-1}$ in the exclosure and 2.8 ind $ha^{-1}$ in the control. Overall, the predator exclosure was successful and we found no indication of predators entering the experimental grid, except in one instance in spring 2015 when an arctic fox dug under the fence. The hole was quickly blocked and the fence reinforced (Chapitre 3).

*5.5.1. Effects of predator reduction on FCM*

Three individuals were identified as outliers with high influence (i.e. high Cook's distance) when verifying assumptions and they were excluded from the analyses. We found strong statistical support (Annexe S4.2, Table S4.2) for an additive effect of both predator reduction and reproductive condition on FCM concentrations (Table 5.1). In general, lemming FCM concentrations were 1.7 times lower in the predator reduction grid (697 ng/g, IC = [553, 878]) compared to the control (1193 ng/g, IC = [949, 1500]; Fig. 1A). Abdominal and scrotal males generally had the highest FCM concentrations whereas non-reproductive individuals had the lowest (Fig. 5.1B). Scrotal and abdominal males had similar FCM concentrations and lactating and pregnant females had similar FCM concentrations (Table 5.1). The model including an interaction between reproductive condition and trapping grid (ΔAICc = 2.69) suggests higher stress in the experimental grid for pregnant females (Table 5.1) but this is based on a very small sample size ($n$ = 2 during the fecal collection occasions in the control grid).

*5.5.2. Effects of predator reduction on fecundity*

Scrotal males were generally less frequently caught within the exclosure than on the control as revealed by the interaction between trapping grid and reproductive condition ($\beta$ = -0.84, CI = [-1.59, -0.10], $R_m^2$ = 0.42, $R_c^2$ = 0.72; Figure 5.2). In contrast, the proportion of abdominal males was similar between trapping grids ($\beta$ = -0.04, CI = [-0.81, 0.72]). The proportion of pregnant ($\beta$ = 0.15, CI = [-0.65, 0.94], $R_m^2$ = 0.43, $R_c^2$ = 0.83) and lactating females ($\beta$ = 0.08, CI = [-0.61, 0.76]) were similar between trapping grids. The proportion of non-reproductive males and females was not affected by trapping grid (Figure 5.2). Sample size used to calculate proportions in Figure 5.2 are reported in Annexe S4.3, Table S4.3.

*5.5.3. Effects of FCM on body mass and movements*

Body mass was not related to FCM (Table 5.2; Annexe S4.4, Table S4.4). Reproductive condition was the parameter explaining the most variation in body mass.

Scrotal males and pregnant females had the heaviest body mass, abdominal males and lactating females were intermediate, and non-reproductive individuals were the lightest lemmings. Predation reduction also had a positive but marginal effect on body mass (Table 5.2).

Movements were positively related to FCM concentrations ($\beta$ = 0.36, IC = [0.07, 0.64]; Figure 5.3, Annexe S4.5, Table S4.5) despite relatively low predictive value ($R^2_m$ = 0.10). Although they were included in the competing models, sex ($\beta$ = -0.18, IC = [-0.63, 0.27]), trapping grid ($\beta$ = -0.21, IC = [-0.65, 0.23]) and the interaction between FCM and grid ($\beta$ = 0.34, IC = [-0.23, 0.92]) had no effect on movements.

## 5.6. Discussion

Our results confirm that lemmings responded physiologically to predation risk by having elevated stress levels under natural predation pressure compared with individuals protected by a predator-reduction exclosure. Although lemmings had 42% lower stress levels in the exclosure than in the control, the proportion of reproductively active females was similar. Contrary to our initial predictions, adult males tended to be more reproductively active when exposed to high predation risk and distance moved tended to increase with stress level. Thus, our results suggest that even though lemmings were sensitive to high predation risk as indicated by their stress level, we found no evidence that this physiological effect reduced fecundity.

### *5.6.1. Effects of predation on fecundity*

Predator-reduction experiments generally have positive effects on northern small rodents by increasing population size and survival (Norrdahl et Korpimäki 1995b; Reid *et al.* 1995; Wilson *et al.* 1999). During our study, lemmings were on average 1.9 times (up to 6.7 times in June 2014) more abundant and survival of adults and juveniles were between 1.4 to 1.6 times higher in the exclosure compared to the control (2014-2015) (Chapter 3). In contrast, there are inconsistencies among studies that assessed the relationship between predation risk and reproduction on small rodents. Predator-reduction experiments showed

no effect on lemming fecundity in the Canadian low Arctic (Wilson *et al.* 1999) and on vole fecundity in Fennoscandia (Klemola *et al.* 2000; Huitu *et al.* 2003). These results contrast with other semi-natural experimental studies that reported lower reproduction levels in voles under high predation risk (Korpimaki *et al.* 1994; Jochym et Halle 2012). Charbonnel *et al.*(2008) speculated that high FCM levels could impair reproduction of voles during declines but our results show that small mammals can maintain high fecundity under elevated FCM levels. Therefore, the lower fecundity of lemmings observed during the peak and decline phases in some lemming and vole populations (Korpimäki *et al.* 1994; Erlinge *et al.* 2000) may have been caused by factors not related to stress. For example, Ylönen *et al.* (2006) found that voles exposed to olfactory cues of predation modified their foraging behaviour without showing stress-related responses.

### *5.6.2. Stress and reproduction*

Impairment of fecundity (e.g. interruption of ovulation, hormonal inhibition, disruptive behaviours) is one of the most commonly reported pathologies related to chronic stress in laboratory experiments (Bethea *et al.* 2008; Chrousos 2009), but recent studies have questioned the occurrence of this effect in wild populations because continued breeding under acute stress has now been reported in several species (Boonstra *et al.* 2001b; Dantzer *et al.* 2013). Evidence suggests that species with relatively short breeding seasons generally show no reproductive suppression when exposed to stressful events (McDonald *et al.* 1988; Boonstra et Boag 1992). In arctic ground squirrels, breeding males showed more signs of chronic stress compared to non-breeding males due to their high testosterone concentrations and low maximal cortisol binding capacity (Boonstra *et al.* 2001b). The trade-off faced by squirrels was a less efficient immune response, which could compromise their survival. Brown lemmings typically live less than 12 months (previous year-recaptures are extremely rare) and can reproduce during both the summer and winter periods with a possible interruption during the snow-melt period in early June (Gruyer *et al.* 2010; Fauteux *et al.* 2015b). Snow offers a protective cover from many predators (in particular birds of prey) but after snow melt, exposure to predation greatly increases. The high proportion of reproductively active males and females in the control grid during the

summer indicates that the elevated stress levels induced by predators were still insufficient to interrupt ovulation, foetal development or inhibit reproductive hormones. Moreover, the higher proportion of males in scrotal state in the control grid substantiates the hypothesis that the physiological trade-off forced by chronic stress may favor reproduction over survival through resistance of the gonadal axis in a short-lived species like lemmings (Wingfield et Sapolsky 2003).

The distance moved by lemmings among traps increased with FCM concentrations, but was not affected by predator-reduction itself. The association between stress level and movements is likely driven by reproductive males. Indeed, previous studies showed that male brown lemmings make longer movements compared to females probably due to mate searching (Banks et al. 1975, Chapter 3). A post-hoc examination of the effect of the reproductive variable revealed that scrotal males had the longest movements but that other males had similar movements compared to females. Thus, the positive relationship between FCM concentrations and movements may be a behavioural response to a stressor (e.g. predation), but it is also plausible that longer movements in unfamiliar environments require more vigilance and are more stressful (Trouilloud *et al.* 2004). In contrast with movements, stress apparently had no impact on foraging efficiency as the body mass of lemmings was not affected by FCM concentrations. This result substantiates the absence of effect of stress on body mass reported in cricetids (Boonstra et Boag 1992). Our results supports the hypothesis that high body mass found in lemming populations is mainly caused by high survival leading to the presence of older and larger individuals (Krebs 1964; Wilson *et al.* 1999; Chapter 3).

### *5.6.3. Limitations of the study and future investigations required*

As is often the case with large-scale experiments, we had no replication of the predator-reduction exclosure. Indeed, we favoured the construction of a single large exclosure over several smaller ones to increase the number of lemmings with their complete home range enclosed inside the protected area and minimize the risk that some would move out and become exposed to predation. Furthermore, a large exclosure also reduces the perimeter to area ratio and thus edge effects such as potential detection (e.g.

olfactory or visual) of terrestrial predators passing near the fence by lemmings. In addition to the difference in stress levels observed here, lemming abundance and survival was higher within the exclosure compared to the control during the experiment (2013-2015), a situation that did not prevail during a pre-experiment period (2008-2012) (Chapter 3). This increase in density occurred in spite of the fact that lemmings were free to move in or out of the exclosure. Two other large-scale predator-reduction experiments conducted built to protect collared lemmings in the Canadian low Arctic also reported no effect of predation on lemming fecundity (Reid *et al.* 1995; Wilson *et al.* 1999). Thus, we are confident that the predator-reduction experiment was successful and that our ability to reduce perceived predation risk was strong.

Our two-year study did not cover all phases of the lemming cycle. Indeed, brown lemmings can reach extremely low densities during low phases as indicated by a total absence of captures in 2013 despite 3500 trap-nights in our study area (Fauteux *et al.* 2015b). Moreover, we could not capture lemmings during winter due to the extreme temperatures, absence of daylight, and severe logistical constraints experienced in the High Arctic. In our study, we measured the impact of predation on lemming stress during peak years, which is the time when predator density is at its peak (Legagneux *et al.* 2012; Therrien *et al.* 2014). As a result, predation should have the highest direct and indirect effects on lemmings during the summer of peak abundance years. However, we acknowledge that predator-induced stress could have lasting effects over several generations due to maternal effects, and it remains unknown if there are carryover effects on lemming fecundity during winter (Boonstra *et al.* 1998b).

During this study (2014-2015), no ermine was detected in our study area during both summer and winter, as revealed by data collected from winter nests (Fauteux et al. submitted) and summer field observations. Predation of lemmings by ermines can easily be found in lemming nests when patches of skin and fur are left in them (Sittler 1995). Ermines can have a high impact on lemmings as a breeding female can capture up to 56 lemmings per day by travelling long distances to feed their family (Bilodeau 2013). The absence of ermine may have reduced the predation risks perceived by lemmings and this may have dampened their stress responses. Nonetheless, the summer lemming population

declined or remained stable in the control grid, which is indicative of intense predation, and lemmings had elevated stress levels despite the absence of mustelids. Would stress induced by ermines be more suppressive than the one induced by the other predators? Some studies found behavioural responses in voles when exposed to mustelid scents (Gorman 1984; Jochym et Halle 2012), but evidence of elevated glucocorticoid concentrations have yet to be demonstrated (Fletcher et Boonstra 2006a; Ylönen *et al.* 2006). Wilson et al. (1999) reported no difference in reproduction activity between collared lemmings captured in their predator-reduction exclosure compared to their controls in presence of ermines. Thus, even though ermines are likely a major source of stress for lemmings, there is no evidence yet that it could suppress reproduction.

This study was focused on effects of predator-induced stress on fecundity. In their meta-analysis of predator manipulation experiments, Salo *et al.* (2010) reported higher reproduction in populations protected from predators. However, their definition of reproduction was very general and included the proportion of juveniles in the population, which was also higher within our exclosure (Chapter 3). Because proportion of juveniles may be affected by early survival after birth and dispersal (Boonstra 1985; Reid *et al.* 1995), it may be a poor index of fecundity per se. We acknowledge that this study deals with one of the many aspects of reproduction that could be negatively affected by stress, such as litter size, body mass at birth, growth, or early juvenile survival (Sheriff *et al.* 2009; Bian *et al.* 2015). Thus, our study presents interesting venues for future investigations to better understand what physiological trade-offs are made by lemmings under elevated stress caused by predation.

## 5.7. Conclusion

Our study shows that high predator density induces stress responses in cyclic brown lemmings in the High Arctic but also that this response is insufficient to cause population-wide suppression of fecundity. Our results substantiate the hypothesis that stress responses in natural conditions may be adaptive and that the suppressive effects observed in laboratory conditions do not persist in nature unless the population can benefit from it (Boonstra 2013). We further hypothesize that highly vulnerable species with short lifespan

and relying on rapid population growth (*r*-selected species) such as cyclic lemmings and voles cannot afford reproductive suppression during high mortality episodes and that the physiological trade-offs favor the maintenance of high reproductive activity over survival mechanisms.

## 5.8. Acknowledgements

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## 5.9. Supplementary material

Annexe S4.1. Predation of lemmings on Bylot Island.

Annexe S4.2. Results of the model selection for faecal corticosterone metabolite concentration of lemmings.

Annexe S4.3. Sample size of lemmings used to estimate proportions in the population.

Annexe S4.4. Results of the model selection for body mass of lemmings.

Annexe S4.5. Results of the model selection for movements of lemmings.

## 5.10. Tables

Table 5.1. Model-averaged coefficient estimates of variables retained in top-models (ΔAICc<4) in relation to faecal corticosterone metabolite (FCM) concentration of adult lemmings. Year and months nested in year were used as random factors. Coefficients in bold indicate that the 95% confidence interval (CI) exclude 0. Model selection results are presented in Annexe S4.2, Table S4.2.

| Parameter | | Coefficient | Low 95% CI | High 95% CI |
|---|---|---|---|---|
| grid | | **-0.299** | **-0.553** | **-0.046** |
| repro | abdominal | **1.505** | **1.045** | **1.965** |
| | scrotal | **1.462** | **1.115** | **1.801** |
| | lactating | **0.670** | **0.195** | **1.145** |
| | pregnant | **0.551** | **0.167** | **0.935** |
| grid*repro | grid * abdominal | 0.363 | -0.550 | 1.276 |
| | grid * scrotal | -0.048 | -0.806 | 0.710 |
| | grid * pregnant | **1.247** | **0.186** | **2.307** |
| | grid * scrotal | 0.025 | -0.652 | 0.702 |

grid = grid effect (predator reduction vs control, which was the reference level); repro = reproductive condition (males: scrotal, abdominal; females: pregnant, lactating; both: non-reproductive, which was the reference condition).

Table 5.2. Model-averaged coefficient estimates of variables retained in top-models (ΔAICc<4) in relation to body mass of adult lemmings. Year and month nested in year was used as random factors. Coefficients in bold indicate that the 95% confidence interval (CI) exclude 0. Model selection results are presented in Annexe S4.4, Table S4.4.

| Parameter | | Coefficient | Low 95% CI | High 95% CI |
|---|---|---|---|---|
| FCM | | -0.06 | -3.41 | 3.29 |
| repro | abdominal | **18.04** | **9.32** | **26.75** |
| | scrotal | **24.45** | **17.71** | **31.19** |
| | lactating | **14.68** | **7.62** | **21.74** |
| | pregnant | **26.18** | **17.50** | **34.86** |
| grid | | 4.53 | -0.12 | 9.18 |
| FCM * grid | | 5.85 | -0.56 | 12.26 |
| FCM * repro | abdominal | -8.22 | -35.44 | 18.99 |
| | scrotal | -24.31 | -50.88 | 2.26 |
| | lactating | -30.10 | -61.11 | 0.90 |
| | pregnant | -21.64 | -46.79 | 3.50 |

FCM = faecal corticosterone metabolite concentration; grid = grid effect (predator reduction vs control, which was the reference level); repro = reproductive condition (males: scrotal, abdominal; females: pregnant, lactating; both: non-reproductive, which was the reference condition).

## 5.11. Figures

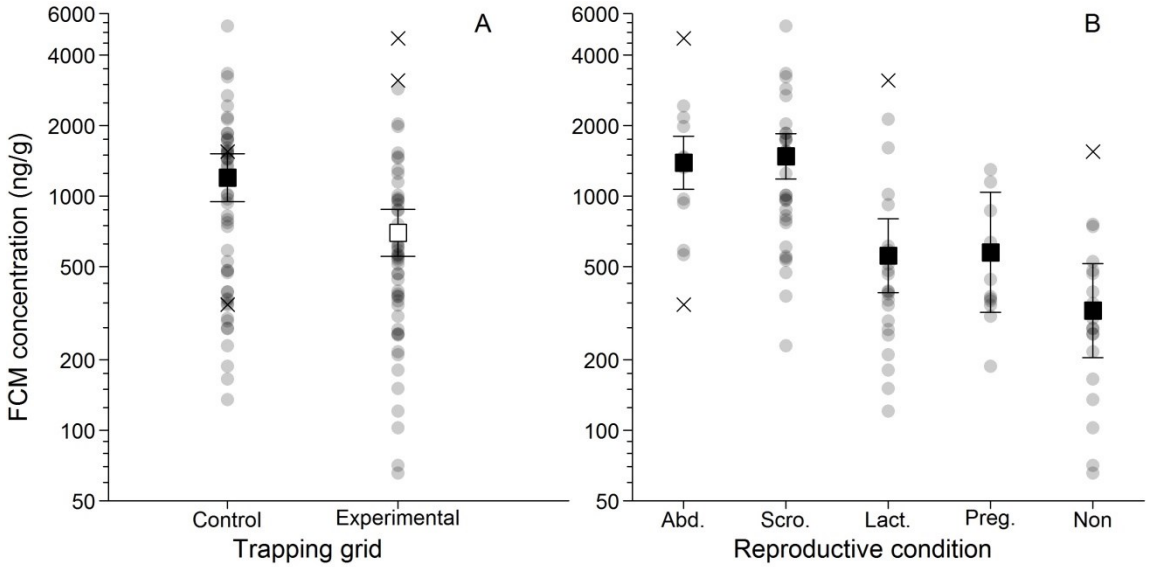


Figure 5.1. Average faecal corticosterone metabolite concentrations (FCM) of adult lemmings with 95% confidence intervals in the control (normal predation; black squares) and experimental grid (predator reduction; white squares, (A) and according to their reproductive condition (B). Individual data points are shown in gray and outliers are shown as crosses. Abd. = abdominal males; Scro. = scrotal males; Lact. = lactating females; Preg. = pregnant females; Non = non-reproductive males and females.

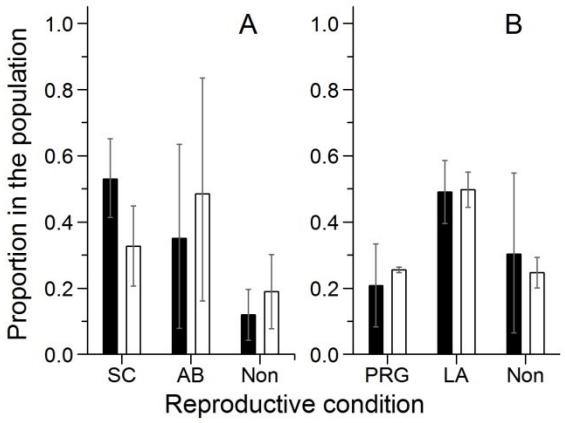


Figure 5.2. Average proportion of each reproductive categories among adult male (A) and female (B) lemmings captured in 2014 ($n$ = 215) and 2015 ($n$ = 98) in the control (black bars) and experimental (white bars) grids. Proportions of males and females were calculated separately. Estimates are presented with their 95% confidence intervals. SC = scrotal, AB = abdominal, Non = non-reproductive, PRG = pregnant, LA = lactating.

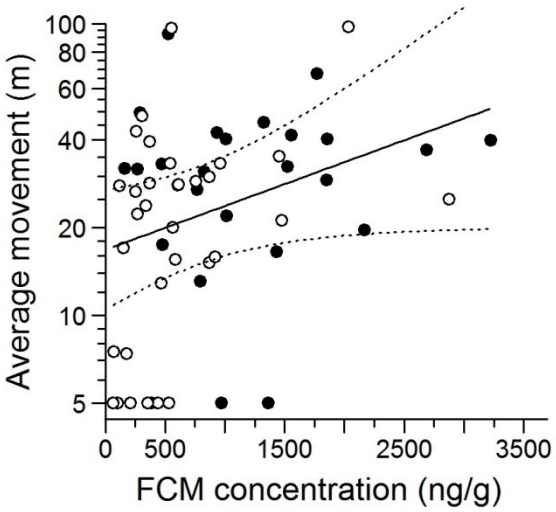


Figure 5.3. Average distance moved among traps by adult lemmings in 2014 ($n$ = 45) and 2015 ($n$ = 13) in the control (black points) and experimental grids (white points). Predicted relationship is presented with its 95% confidence intervals.

# CHAPITRE 6. Conclusion générale

### 6.1. La prédation : facteur limitant de la toundra Arctique

À la lumière de ma thèse, je peux conclure que la prédation est le facteur de régulation le plus important des petits herbivores dans le haut Arctique. Nous avons montré que les lemmings atteignent des densités plus élevées lorsqu'ils sont protégés de la prédation qu'en présence de celle-ci, ce qui indique que les ressources alimentaires n'étaient pas limitantes. Autrement dit, le taux de mortalité estival des lemmings en phase de pic d'abondance dépasse rapidement leur taux de croissance maximal et ce, avant qu'ils n'atteignent la capacité de charge du milieu. Cela expliquerait pourquoi d'autres études n'ont trouvé qu'un très faible impact des lemmings sur la végétation arctique (Legagneux *et al.* 2012; Bilodeau *et al.* 2014). Mes résultats tendent donc à rejeter la théorie d'exploitation des écosystèmes (EEH) dans sa forme actuelle (Oksanen et Oksanen 2000). Il semble que cette théorie ne peut prédire l'influence des interactions trophiques simplement en fonction de la productivité primaire. En effet, nous avons démontré que dans un milieu peu productif (haut Arctique), les prédateurs ont un rôle dominant qui régule les petits herbivores résidents (contrôle par le haut).

Les raisons pour lesquelles l'hypothèse d'Oksanen et Oksanen (2000) ne s'applique pas à notre système, et probablement pas de façon générale dans l'Arctique, sont multiples (Gauthier *et al.* 2009) mais deux facteurs essentiels que la théorie ignore sont les intrants allochtones et la mobilité des prédateurs. En effet, la migration des oiseaux connecte des écosystèmes ayant des productivités primaires très différentes. Par exemple, la grande oie des neiges se nourrit dans les terres agricoles très productives lorsqu'elle hiverne et les oiseaux limicoles se nourrissent d'invertébrés dans les milieux riverains qui ne gèlent pas en hiver. En migrant ensuite dans l'Arctique, ces oiseaux augmentent leur succès reproducteur (McKinnon *et al.* 2010) et contribuent, bien malgré eux, à enrichir les milieux. Les prédateurs profitent ainsi de l'apport énergétique offert par ces résidents temporaires. Par exemple, les renards arctiques persistent pendant les années de faible abondance de lemmings grâce aux proies alternatives (Bety *et al.* 2002; Gauthier *et al.* 2011). Le deuxième facteur ignoré par la théorie d'exploitation des écosystèmes, soit la mobilité des prédateurs, suggère également que l'Arctique est un amalgame de plusieurs systèmes trophiques interconnectés, ce qui nous force à revoir l'échelle à laquelle la productivité

primaire et l'efficacité écologique affectent les forces trophiques. Par exemple, le comportement de prospection des harfangs des neiges leur permettent de détecter les sites avec une grande quantité de lemmings où ils se reproduiront (Gilg *et al.* 2006; Therrien *et al.* 2014; Therrien *et al.* 2015). De récentes études ont montré une utilisation de sites marins en hiver par des prédateurs strictement terrestres en été (i.e. harfangs des neiges, renards arctiques; Therrien *et al.* 2011; Tarroux *et al.* 2012), indiquant ainsi que les milieux marins peuvent compenser partiellement ou totalement pour le très faible apport de proies provenant des milieux terrestres pendant l'hiver arctique. En considérant les relations trophiques statiques, la théorie EEH ignore le fait que ces relations sont grandement instables d'une saison à l'autre. En intégrant une telle dynamique à l'échelle de l'Arctique, sont celle de la mobilité des prédateurs (i.e. rapaces et renards), la théorie EEH pourrait être beaucoup plus inclusive et probablement montrer un rôle accru des prédateurs dans le réseau trophique arctique.

### 6.2. Effets directs et indirects de la prédation

Tout comme dans cette thèse, d'autres expériences de réduction de prédateurs, menées en Scandinavie et dans le bas Arctique canadien, n'ont trouvé aucun effet de la prédation sur la reproduction des lemmings et des campagnols (Wilson *et al.* 1999; Klemola *et al.* 2000; Huitu *et al.* 2003). Il semble donc que la réduction de la reproduction liée à une exposition élevée aux indices olfactifs de la présence de prédateurs n'est peut-être qu'un artefact lié aux manipulations en laboratoire, tel que suggéré par Norrdahl et Korpimäki (2000). Nous pouvons conclure que la mortalité causée par la prédation serait suffisante pour faire décliner les lemmings à des densités très faibles. Contrairement à ce qu'Inchausti et Ginzburg (2009) proposent, l'apparente impossibilité d'expliquer la totalité des fluctuations de populations durant un cycle complet par les mortalités liées à la prédation ne dépendrait pas du fait que les effets indirects ne sont pas considérés. Nos résultats suggèrent plutôt que l'instabilité saisonnière de cette force trophique (i.e. changements saisonniers) pourrait être un facteur important à considérer, tel que déjà suggéré par Barraquand *et al.* (2014). Nos résultats concordent donc avec ceux de Row *et al.* (2014) qui montrent que les effets de densité-dépendance pulsatiles plutôt que continus

et agissant sur la survie plutôt que la reproduction mènent plus facilement à des cycles de grande amplitude et de courte période.

Notre étude va à l'encontre du lien négatif trouvé entre le stress et la reproduction chez les lièvres (Sheriff *et al.* 2009b) et les campagnols (Bian *et al.* 2015). Dans le chapitre 5, nous montrons que malgré le niveau élevé de stress des lemmings induit par la prédation, ils n'ont pas réduit leur effort reproducteur, ce qui suggère une variabilité interspécifique dans les compromis lors de l'allocation énergétique. Boonstra (2013) propose que cette variabilité dépend des traits biodémographiques des espèces et que celles ayant une faible longévité ou une courte période de reproduction ne peuvent se permettre de réduire leur effort reproducteur même en présence de stress. Toutefois, il est important de mentionner que pendant ma thèse, nous n'avons étudié qu'un seul facteur lié à la reproduction soit la proportion d'individus en état reproducteur. D'autres composantes de la fécondité comme la taille des portées, la masse des juvéniles à la naissance ainsi que le nombre jeunes au sevrage sont d'autres paramètres importants qui peuvent aussi être affectés par le stress chronique (voir section 6.5; Sapolsky *et al.* 2000, Sheriff *et al.* 2009, Bian *et al.* 2015).

La phase de faible abondance qui peut durer pendant plusieurs années reste encore la période la plus nébuleuse des cycles de population (Boonstra *et al.* 1998b). Pendant l'été, nos résultats suggèrent que les lemmings maintiennent un taux de fécondité élevé malgré une mortalité élevée par la prédation. Quels sont les compromis? S'ils sont présents, quels sont les conséquences à plus long terme sur les juvéniles? Je propose quelques idées d'expériences pour répondre à ces questions dans la section 6.5.

### 6.3. La modernisation de l'étude de la dynamique des populations

À la lumière des analyses et des résultats de ce doctorat, on constate aisément que les méthodes d'analyse de la dynamique des populations ont grandement changé depuis les travaux pionniers de Charles Elton (1924). En effet, depuis les 50 dernières années ce domaine s'est modernisé à grande vitesse et les perspectives de recherche sont extrêmement intéressantes (Amstrup *et al.* 2005). Pendant longtemps, le nombre d'individus capturés par trappage mortel ou la chasse formait l'essentiel des données à long terme, mais il existe maintenant un nombre croissant d'études pour lesquelles les animaux sont marqués et

relâchés ce qui permet un suivi selon les méthodes de capture-marquage-recapture (CMR). Nous avons montré dans les chapitres 2 et 3 que les suivis à long terme de CMR offrent la possibilité de mener des analyses robustes de la démographie des individus et ainsi mieux identifier les mécanismes responsables des changements démographiques. Par exemple, grâce aux méthodes développées par Efford et Fewster (2013), nous pouvons obtenir la densité d'une population tout en considérant une probabilité de détection imparfaite, ce qui représente une avancée majeure en statistique écologique (voir aussi Efford 2004; Royle *et al.* 2014). Toutefois, ces méthodes ne sont pas parfaites et il était notamment difficile d'obtenir des estimés précis de la densité des juvéniles. En effet, ceux-ci sont rarement recapturés une fois marqués. Après avoir quitté le nid maternel, les jeunes tendent à se disperser et peuvent quitter la population susceptible d'être trappée (Reid *et al.* 1995). Pourtant, nos résultats montrent que les jeunes capturés bougeaient très peu (chapitre 3). Cela représente un défi statistique et laisse planer un doute sur la validité des estimations de densité de juvéniles estimées par les méthodes de capture-marquage-recapture spatialement explicite.

### 6.4. Limites de l'étude

La limite la plus importante de notre étude mais hors de notre contrôle est que la période active de l'exclos à prédateur n'a pas encore couvert un cycle de population complet. En effet, cette étude n'a couvert que les phases de croissance (2013-2014), du pic d'abondance (2014) et du déclin partiel de la population (2014-2015). Nous n'avons donc pas pu déterminer si la réduction de la prédation aura permis aux lemmings de rester abondants pendant la période complète de déclin et la phase de faible abondance. Ces résultats devraient être connus en maintenant l'exclos à prédateurs pendant les 2 ou 3 prochaines années. À la lumière des résultats de cette thèse, je prévois que la survie plus élevée à l'intérieur de l'exclos à prédateurs permettra aux densités de lemmings de rester plus élevées que dans le site témoin mais que la perméabilité de celui-ci amènera les lemmings à se disperser et éventuellement à décliner (Wilson *et al.* 1999). Il serait également possible qu'un maintien de la population de lemmings à une densité élevée réduise la biomasse de plante disponible pour la consommation et que celle-ci devienne limitante. Huitu et al (2003) ont montré qu'en réduisant l'abondance des prédateurs en forêt

boréale finnoise, la conséquence fut une augmentation de la densité des campagnols et une réduction considérable de la biomasse des plantes. Il sera intéressant de mesurer les taux de reproduction hivernaux afin de vérifier si le retrait de la prédation permet aux lemmings de rester abondants malgré de faibles taux de reproduction, possiblement causés par des conditions de neige difficiles, grâce à une survie élevée.

Basé sur les expériences vécues par d'autres chercheurs ayant fait une manipulation similaire à la nôtre (Reid *et al.* 1995; Wilson *et al.* 1999), nous avons fabriqué une clôture dont l'efficacité a été démontrée. En effet, nous n'avons aucune évidence de prédation par les prédateurs aviaires et nos résultats sont éloquents : la survie des lemmings était bel et bien plus élevée dans l'exclos. Toutefois, un renard arctique est entré à l'intérieur de l'exclos entre l'hiver et l'été 2015, ce qui a sans doute eu un impact important sur la densité des lemmings mesurée en juin dans l'exclos. Malgré que nous avons pu réagir rapidement une fois la brèche découverte, il sera important d'assurer un suivi rapide à chaque été afin d'empêcher ce genre d'événement de se reproduire.

Travailler avec les lemmings du haut Arctique nous force à travailler avec des tailles d'échantillons relativement petites car les densités dépassent rarement 10 individus $ha^{-1}$ pendant les pics d'abondance alors qu'ils peuvent atteindre 100 individus $ha^{-1}$ en Alaska et que les campagnols peuvent atteindre 300 individus $ha^{-1}$ (Boonstra et Boag 1992; Pitelka et Batzli 2007). Pour le chapitre 4, nous avons capturé et maintenu en captivité 18 lemmings bruns, ce qui était suffisant pour répondre à notre question (i.e. est-ce que les métabolites fécaux fournissent une bonne mesure du stress subi par les individus?). Toutefois, cela a été insuffisant pour évaluer simultanément l'effet du sexe et du statut reproducteur sur l'excrétion des métabolites fécaux de la corticostérone (MFC) des lemmings. En effet, il aurait été intéressant de comparer les niveaux de MFC de lemmings gestantes comparativement aux lemmings non-gestantes et de comparer les lemmings scrotaux versus les lemmings non-scrotaux. Les interactions entre les hormones de stress et les hormones de reproduction spécifiques à chaque sexe peuvent grandement affecter les concentrations de glucocorticoïdes libres en raison de leurs effets sur la transcortine (ou *corticosteroid binding globulin* en anglais; Boonstra *et al.* 2007). Brièvement, la testostérone réduit la concentration de la transcortine alors que l'estrogène l'augmente. Considérant que seuls les

glucocorticoïdes libres sont excrétés par les voies fécales, il aurait été intéressant de vérifier si les MFC sont robustes aux effets de ces hormones reproductrices. D'ici à ce que d'autres lemmings soient capturés et gardés en captivité, nous devrons considérer que l'état reproducteur peut être un effet confondant pouvant brouiller l'effet des facteurs externes. Il aurait également été intéressant d'échantillonner l'urine des lemmings afin de vérifier la proportion des métabolites excrétés par les deux voies métaboliques (i.e. urinaire et digestives). Touma *et al.* (2003) montrent que des différences dans les proportions excrétées entre ces 2 voies métaboliques pourraient expliquer les divergences sexuelles dans les MFC mesurées. Chez les souris mâles, 75% des MFC sont excrétées par les fèces alors que c'est plutôt 50% chez les femelles. Des adaptations locales en lien avec les besoins de thermorégulation pourraient aussi grandement affecter la quantité d'eau et de nourriture ingérées et excrétées et ainsi affecter la concentration de MFC (Hammond et Wunder 1995).

Enfin, il n'y a eu aucune hermine observée pendant toute la durée de l'expérience de réduction des prédateurs (2013 à 2015) ce qui présente à la fois un avantage et un désavantage. L'avantage est que nous avons effectivement exclu tous les prédateurs présents sur l'Île Bylot de la zone protégée, excepté le renard qui est entré à l'hiver 2014-2015. Le désavantage est que nous n'avons pas eu une situation où la prédation était maximale. Les hermines peuvent consommer jusqu'à 1,2% de la population des lemmings par jour (Bilodeau 2013), ce qui est une pression très importante. La prédation des hermines et des autres prédateurs étant additive, la présence du mustélidé aurait pu augmenter l'écart entre les densités de lemmings dans l'exclos et la grille témoin, renforçant ainsi l'effet limitant. De plus, la présence d'hermines auraient sans doute augmenté le stress vécu par les lemmings, notamment via les attaques ratées. Jedrzejewski *et al.* (1992) rapporte que les belettes ne réussissent que 23% de leurs attaques de prédation sur les campagnols, ce qui pourrait se produire également avec les lemmings. Il est à noter que l'exclos était partiellement perméable aux hermines pour éviter l'effet de clôture (ou fence effect; Ostfeld 1994), ce qui aurait pu avoir un effet non négligeable pour l'expérience si celles-ci avaient pu entrer et chasser les lemmings se trouvant dans l'exclos.

### 6.5. Nouvelles perspectives

Une des questions importantes découlant de cette thèse est : «Quels sont les facteurs pouvant affecter la reproduction hivernale des lemmings?». En effet, notre étude montre que l'hiver est une période extrêmement importante pour assurer un retour à une forte croissance des lemmings (Krebs 2011). La proportion de nids d'hiver avec signes de reproduction varie annuellement et nous avons démontré que la croissance hivernale de la population était fortement reliée à l'intensité de la reproduction en hiver et pouvait mener à une explosion de la population en début d'été. Il sera donc essentiel de déterminer le mécanisme expliquant les variations annuelles dans l'intensité de la reproduction hivernale. Pendant l'hiver 2015, le taux de reproduction a été anormalement faible dans les deux grilles de trappage (i.e. expérimentale et témoin), ce qui suggère que le retrait de la prédation n'a eu aucun effet sur la fécondité hivernale. Malgré que cette observation soit ponctuelle ($n$ = 1), l'absence d'effet de la prédation estivale sur la reproduction des lemmings laisse présager que la prédation n'a pas d'effet non plus sur la reproduction hivernale. La dégradation des conditions de neige par des événements de fonte en début d'hiver (e.g. création de croûte glacée près du sol) a déjà été proposée comme pouvant être responsable de la disparition des cycles des lemmings et campagnols en Scandinavie (Kausrud *et al.* 2008). La fécondité plus faible de l'hiver 2015 comparativement à 2014 pourrait être expliquée par une épaisseur de neige plus faible (Domine *et al.* 2016). L'effet des variations annuelles dans la qualité de la neige est une hypothèse qui devra être étudiée sérieusement en identifiant les propriétés mécaniques (e.g. résistance au cisaillement par des griffes des lemmings; F. Domine, comm. pers.) de la couche basale de la neige. La dureté de la neige pourrait en effet entraver les lemmings dans leurs déplacements et augmenter leurs dépenses énergétiques pour se déplacer et trouver suffisamment de nourriture, réduisant d'autant leur allocation possible d'énergie à la reproduction. L'interaction entre les conditions de neige et les facteurs biotiques (e.g. accès à la nourriture) est donc un suspect important pour expliquer une chute de la reproduction en hiver.

Notre étude est la première à analyser un lien entre la démographie des lemmings et le stress. Il reste donc encore beaucoup de travail à faire et beaucoup d'idées à explorer. Au

chapitre 4, nous avons développé une méthode pour mesurer le stress des lemmings de façon non-invasive et permettant la récolte d'une grande quantité d'échantillons. Une approche serait d'étudier d'autres formes de paramètres démographiques pouvant être affectés par le stress que ceux étudiés ici. Nous nous sommes en effet concentrés sur la probabilité pour les individus d'être en état reproducteur et avons confirmé que les mâles sont capables de copuler et que les femelles sont capables de porter des fœtus même en présence de stress pendant l'été. Une limite de notre étude est toutefois que nous n'avons pas pu mesurer d'autres aspects importants de la fécondité, c'est-à-dire la taille des portées, la masse des nouveau-nés et leur survie initiale. En effet, de récentes études semblent montrer un effet du stress véhiculé par les effets maternels sur le recrutement (Dantzer *et al.* 2013; Bian *et al.* 2015). Ces études ont montré des résultats contradictoires où de jeunes écureuils roux (*Tamiasciurus hudsonicus*) grandissent rapidement dans un environnement stressant alors que les jeunes campagnols nordiques (*Microtus oeconomus*) stressés atteignent la maturité à un poids plus faible que ceux non-stressés. Il serait très intéressant de capturer des lemmings gestantes provenant de chaque phase du cycle et les maintenir en captivité pour étudier ces paramètres dans un environnement contrôlé. Ce type d'expérience requérait peu de matériel, les manipulations seraient simples et peu invasives (e.g. observations visuelles, pesées d'individus). Cela aiderait à mieux analyser les effets maternels qui pourraient avoir un impact à long terme pendant la phase de faible abondance et ainsi affecter la démographie hivernale des lemmings (Boonstra *et al.* 1998b). Cela nous permettrait également de vérifier comment les lemmings maximisent leur aptitude phénotypique (ou fitness) lorsqu'ils sont stressés.

Nos résultats suggèrent que la reproduction est maintenue coûte que coûte. Quels sont les systèmes ou processus (e.g. digestif, immunitaire ou la croissance) qui écopent de la réallocation de l'énergie? Les compromis physiologiques faits par les lemmings restent donc à être démontrés. Les populations cycliques des lemmings représentent des sujets très intéressants pour déterminer les stratégies évolutives des espèces ayant une courte longévité et une croissance de population rapide (espèces *r*) et établir des comparaisons avec d'autres espèces ayant une plus grande longévité et une croissance de population plus lente (espèces K; Boonstra 2013).

### 6.6. Du haut Arctique au reste du monde

L'étude des cycles de populations de lemmings représente une des plus vieilles questions en écologie des populations et les difficultés à identifier les facteurs de régulation sont une formidable leçon d'humilité scientifique (Chitty 1996; Stenseth 1999; Krebs 2013). Dennis Chitty fut l'un des plus importants contributeurs à la littérature des cycles des petits rongeurs mais ses expériences ont plutôt résulté en un rejet dramatique de son hypothèse qui l'intéressait beaucoup : que les effets intrinsèques (i.e. affaiblissement génétique) sont responsables des cycles. Malgré ce qu'il considérait parfois comme des échecs (Chitty 1996), ses réfutations d'hypothèses ont alimenté de nombreux débats (Heikki Hentonen, comm. pers) et ont incité plusieurs autres chercheurs à explorer les cycles. Grâce aux nombreuses études faites sur les cycles des lemmings et campagnols nordiques par les Elton, Chitty, Christian, Krebs, Stenseth et Björnstadt, les mécanismes régulant les cycles des rongeurs se précisent de plus en plus tant dans les milieux nordiques qu'en Australie, au Japon, en Espagne ou en Allemagne (Stenseth 1999; Singleton *et al.* 2010; Luque-Larena *et al.* 2013). En plus de contribuer aux concepts fondamentaux de l'écologie, l'étude des cycles des populations permet de mieux prédire les éclosions de maladies tant chez les humains que les animaux (e.g. zoonoses; Tärnvik *et al.* 2004) et de prévoir et gérer les irruptions de rongeurs dans les milieux agricoles et forestiers (Stenseth *et al.* 2003; Sullivan et Sullivan 2010; Coeurdassier *et al.* 2012). Cet impact tant écologique qu'économique témoigne de l'importance de poursuivre les recherches et étudier la dynamique des populations dans l'Arctique malgré la simplicité du système trophique. Cette simplicité nous permet d'identifier les mécanismes de régulation qui peuvent ensuite être transposés dans des systèmes plus complexes et ainsi contribuer aux recherches faites partout dans le monde. Considérant que cette thèse supporte l'hypothèse de la prédation comme étant une force trophique dominante en milieu peu productif, il se pourrait que la prédation et son impact sur la dynamique des populations de proies ait été un facteur clé contribuant à la diversification des espèces de l'Arctique comme ce fut le cas dans les récifs coralliens, les lacs et les forêts tropicales (Terborgh 2015).

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# Annexe S1: supplementary material for Chapter 2

**Annexe S1.1. Sample size**

Table S1.1. Number of individual lemmings captured during each primary trapping period and used for the analyses, excluding recaptures. Unknown adults were used in analyses that did not require the knowledge of sex (e.g. proportion of juveniles analyses, M5 and M8, Table 1). The age of individual was determined at their first capture.

| Year | Month | Adult males | Adult females | Unknown adults | Juveniles† |
|---|---|---|---|---|---|
| 2004 | June‡ | - | - | - | - |
| | July | 45 | 19 | 4 | 28 |
| | August | 5 | 3 | 2 | 47 |
| 2005 | June | 5 | 6 | 0 | 0 |
| | July | 4 | 8 | 0 | 1 |
| | August | 1 | 0 | 1 | 4 |
| 2006 | June | 2 | 1 | 0 | 3 |
| | July | 4 | 1 | 0 | 1 |
| | August | 0 | 3 | 0 | 11 |
| 2007 | June | 0 | 1 | 0 | 1 |
| | July | 7 | 2 | 0 | 1 |
| | August | 4 | 1 | 0 | 8 |
| 2008 | June | 20 | 24 | 1 | 17 |
| | July | 40 | 34 | 1 | 23 |
| | August | 12 | 13 | 0 | 55 |
| 2009 | June | 2 | 0 | 0 | 2 |
| | July | 5 | 0 | 0 | 1 |
| | August | 4 | 4 | 0 | 2 |
| 2010 | June | 6 | 8 | 0 | 5 |
| | July | 81 | 60 | 0 | 14 |
| | August | 52 | 42 | 0 | 52 |
| 2011 | June | 57 | 75 | 1 | 34 |
| | July | 98 | 123 | 8 | 19 |
| | August | 28 | 40 | 2 | 49 |
| 2012 | June | 5 | 0 | 0 | 2 |
| | July | 2 | 1 | 0 | 2 |
| | August | 1 | 0 | 0 | 2 |
| 2013 | June | 0 | 0 | 0 | 0 |
| | July | 0 | 0 | 0 | 0 |
| | August | 0 | 0 | 0 | 0 |

†In the fecundity and adult body mass analyses, juveniles that eventually reached the minimum body mass for maturity at recaptures (see Annexe S3) were noted as being adult and included in the analyses.

‡No trapping survey was conducted in June 2004

## Annexe S1.2. Methods and model selection for the estimation of survival probabilities

### *S1.2.1. Estimation of survival probabilities*

To estimate survival, we used Pollock's robust design with the Huggins parameterisation in order to reduce the number of variables included in the models (Williams *et al.* 2002). We developed 16 models (Table S1.2) for which we verified the strength of evidence for constant survival compared to varying survival between primary periods (i.e. June, July, and August) and trapping grids. We also considered whether migration was absent or random (Markovian parameterisation) and whether capture probability varied according to time between primary and/or secondary occasions. Because traps remained on site between primary occasions without new baits, we assumed that all lemmings developed habituation evenly to the traps between these periods. Thus, probabilities of recapture were considered equal to the probabilities of capture (i.e. no trap happiness). We used Akaike's second order criterion (AICc) for model selection. All real estimates of survival were model-averaged if the Akaike's weight ($w_i$) of the top model was <0.90 (Burnham et Anderson 2002). We ran a separate analysis for each year because inter-annual recaptures were virtually absent (a single case in 10 years of trapping) and we never detected movements between grids. Estimations of coefficients and their respective unconditional 95% confidence intervals were calculated with the package "RMark" (Laake *et al.* 2013) and the R software. Because primary occasions in 2004-2007 were separated by shorter intervals than in 2008-2013 (average of 20 days instead of 30), we adjusted real estimates of survival probabilities to $S^{3/2}$ for those years. We used the delta method to calculate the new variance (Powell 2007).

### *S1.2.2. Summary of model selection*

In 2004, models where survival was constant over time and equal between grids had the highest support (sum of Akaike's weight of all models with constant survival, $\Sigma w_i = 0.58$) compared to models where survival differed between trapping grids ($\Sigma w_i = 0.22$) or between primary periods ($\Sigma w_i = 0.22$; Table S1.3). Models with no migration were the most parsimonious ($\Sigma w_i = 0.76$) and there was considerable evidence that capture probabilities varied over time among the secondary periods ($\Sigma w_i = 0.99$).

In 2008, models with a constant survival over time and equal between grids had again the highest support ($\Sigma w_i = 0.61$) compared to those where survival varied between primary periods ($\Sigma w_i = 0.27$) or trapping grids ($\Sigma w_i = 0.15$, Table S1.3). Models without migration also received the most support ($\Sigma w_i = 0.74$). The most parsimonious models indicated that capture probabilities varied only between primary periods ($\Sigma w_i = 0.99$).

In 2010, models where survival probabilities varied between trapping grids received the most support ($\Sigma w_i = 0.61$) compared to models where survival varied among primary periods ($\Sigma w_i = 0.40$) or with a constant survival ($\Sigma w_i = 0.20$, Table S1.3). Models with an absence of migration had the highest support ($\Sigma w_i = 0.76$). Models where capture probabilities varied among secondary periods received the highest support ($\Sigma w_i = 0.99$).

In 2011, models where survival probabilities varied according to primary periods ($\Sigma w_i = 0.99$) and trapping grids ($\Sigma w_i = 0.86$) received the highest support. In contrast with the other years, models with random migration received the highest support ($\Sigma w_i = 0.70$).

Models where capture probabilities varied through time during the secondary periods were preferred ($\Sigma w_i = 0.99$).

Table S1.2. Description of the robust design models used to estimate survival probabilities every year while controlling for probabilities of capture and migration (γ). In all models, probability of capture was equal to probability of recapture. Factors including in the model for each parameter is shown. The number of parameters (*K*) differs for some models in 2008 (in parentheses) because the number of secondary occasions was higher compared to other years (see methods).

| Model ID | *K* | Survival | Migration | Probability of capture |
|---|---|---|---|---|
| m1 | 4 | Constant | No | Primary period only |
| m2 | 19 (31) | Constant | No | Primary*secondary period |
| m3 | 5 | Constant | Random | Primary period only |
| m4 | 20 (32) | Constant | Random | Primary*secondary period |
| m5 | 6 | Trapping grid | No | Primary period only |
| m6 | 21 (32) | Trapping grid | No | Primary*secondary period |
| m7 | 7 | Trapping grid | Random | Primary period only |
| m8 | 22 (33) | Trapping grid | Random | Primary*secondary period |
| m9 | 9 | Trapping grid*Primary period | No | Primary period only |
| m10 | 24 (34) | Trapping grid*Primary period | No | Primary*secondary period |
| m11 | 10 | Trapping grid*Primary period | Random | Primary period only |
| m12 | 25 (35) | Trapping grid*Primary period | Random | Primary*secondary period |
| m13 | 5 | Primary period | No | Primary period only |
| m14 | 20 (32) | Primary period | No | Primary*secondary period |
| m15 | 6 | Primary period | Random | Primary period only |
| m16 | 21 (33) | Primary period | Random | Primary*secondary period |

According to the standard notation of the robust design model (Williams *et al.* 2002), no migration: $\gamma'' = 0$ and $\gamma' = 1$; random migration: $\gamma'' = \gamma'$ (and both are constant). * = interaction

Table S1.3. Ranking of models estimating survival probabilities of brown lemmings based on the difference in AICc with respect to the preferred model and its relative support (AICc weight, $w_i$). Model descriptions are presented in Table B1.

| Year | Model ID | ΔAICc | $w_i$ |
|---|---|---|---|
| 2004 | m2 | 0.00 | 0.44 |
| | m6 | 2.10 | 0.15 |
| | m14 | 2.11 | 0.15 |
| | m4 | 2.33 | 0.14 |
| | m8 | 4.43 | 0.05 |
| | m16 | 4.45 | 0.05 |
| | m10 | 6.63 | 0.02 |
| | m12 | 8.99 | 0.00 |
| | m1 | 144.78 | 0.00 |
| | m5 | 146.59 | 0.00 |
| | m13 | 146.60 | 0.00 |
| | m3 | 146.83 | 0.00 |
| | m7 | 148.65 | 0.00 |
| | m15 | 148.66 | 0.00 |
| | m9 | 150.55 | 0.00 |
| | m11 | 152.63 | 0.00 |
| 2008 | m1 | 0.00 | 0.45 |
| | m13 | 1.91 | 0.17 |
| | m3 | 2.05 | 0.16 |
| | m5 | 3.58 | 0.08 |
| | m15 | 3.97 | 0.06 |
| | m7 | 5.65 | 0.03 |
| | m9 | 5.68 | 0.03 |
| | m11 | 7.78 | 0.01 |
| | m2 | 8.02 | 0.00 |
| | m14 | 10.09 | 0.00 |
| | m4 | 10.22 | 0.00 |
| | m6 | 11.90 | 0.00 |
| | m16 | 12.30 | 0.00 |
| | m8 | 14.12 | 0.00 |
| | m10 | 14.48 | 0.00 |
| | m12 | 16.74 | 0.00 |
| 2010 | m6 | 0.00 | 0.29 |
| | m10 | 1.50 | 0.14 |
| | m14 | 1.51 | 0.14 |
| | m2 | 1.53 | 0.14 |
| | m8 | 2.16 | 0.10 |
| | m16 | 3.66 | 0.05 |
| | m4 | 3.67 | 0.05 |
| | m12 | 3.68 | 0.05 |
| | m5 | 5.53 | 0.02 |

| | | | |
|---|---|---|---|
| | m9 | 6.67 | 0.01 |
| | m13 | 7.12 | 0.01 |
| | m1 | 7.27 | 0.01 |
| | m7 | 7.58 | 0.01 |
| | m11 | 8.74 | 0.00 |
| | m15 | 9.16 | 0.00 |
| | m3 | 9.30 | 0.00 |
| 2011 | m12 | 0.00 | 0.60 |
| | m10 | 1.65 | 0.26 |
| | m16 | 3.62 | 0.10 |
| | m14 | 5.71 | 0.03 |
| | m8 | 17.89 | 0.00 |
| | m6 | 20.58 | 0.00 |
| | m4 | 24.47 | 0.00 |
| | m2 | 27.58 | 0.00 |
| | m11 | 51.93 | 0.00 |
| | m9 | 53.59 | 0.00 |
| | m15 | 55.83 | 0.00 |
| | m13 | 57.93 | 0.00 |
| | m7 | 69.77 | 0.00 |
| | m5 | 72.44 | 0.00 |
| | m3 | 76.49 | 0.00 |
| | m1 | 79.58 | 0.00 |

**Annexe S1.3. Body mass criteria used to determine maturity**

We used information on reproductive conditions collected over many years to determine the minimum body mass at which a lemming could be considered a mature adult. Females were considered as reproductive if their mammary glands were visible, their hymen was perforated or foetuses were palpable. Males were considered to be in reproductive conditions if their testicles were scrotal. Females were systematically examined for reproductive conditions every year of the study (2004-2013) but reproductive condition of males were examined only from 2010 to 2013. Based on these criteria, 335 females and 166 males were classified as reproductive individuals.

To determine the minimum body mass, we plotted the frequency distribution of body mass of reproductive individuals and generated a normal distribution curve based on the average and standard deviations for males and females separately (Figure S1.1). We then cumulated the area under the curve (AUC) until reaching 1% (or first percentile) of the total area starting with the lowest values. We assumed that the body mass corresponding to this probability density was the age at which individuals became reproductively mature. This allowed us to exclude individuals that had showed signs of reproduction at very low body mass (i.e. <1% of the AUC), which could represent exceptions or measurement errors. Using this criteria, the minimum body mass for brown lemmings to be considered adults were 28 g for females and 30 g for males.

We acknowledge that body mass may not be an absolute measure of sexual maturity and that this value may vary to some extent between years of high and low population density. Indeed, several studies (including this one) have shown that lemmings are smaller during years of low abundance (Krebs 1964; Gilg 2002). Nonetheless, all females that we caught with signs of reproduction had a body mass ≥28 g ($n = 22$) during years of low abundance whereas in years of high abundance, this proportion reached 0.99 ($n = 313$). During 2012, a low abundance year, the proportion of reproductive males ≥30 g was 0.83 ($n = 6$) while this value reached 0.99 ($n = 160$) during high abundance years (2010 and 2011). The small difference in the proportion of reproductive males between low and high abundance years may be an artifact due to the very small number of observations in the low abundance year.

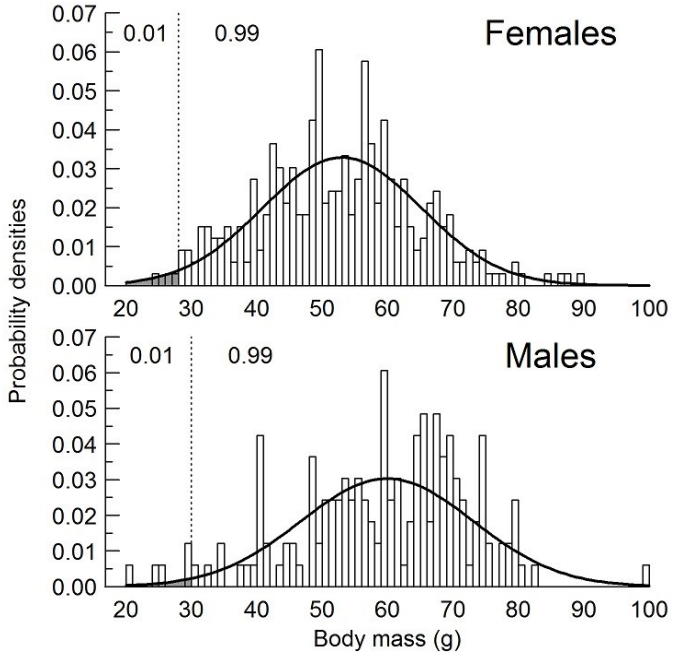


Fig. S1.1. Body mass distribution of brown lemmings showing signs of reproduction split according to sex ($n$ = 335 females and 166 males). The thick lines show a normal distribution based on the mean and standard deviation of the data. The first percentile of the area under the curve (dotted line) determines the body mass threshold used for adults.

# Annexe S2: supplementary material for Chapter 3

**Annexe S2.1. Sample size.**

Table S2.1. Number of individual lemmings captured at each time period on each grid annually (recaptures are ignored).

| Year | Month | Experimental grid | | | Control grid | | |
|---|---|---|---|---|---|---|---|
| | | Adult males | Adult females | Juveniles | Adult males | Adult females | Juveniles |
| 2008 | June | 7 | 4 | 1 | 4 | 6 | 0 |
| | July | 6 | 8 | 11 | 5 | 5 | 2 |
| | August | 2 | 7 | 15 | 1 | 0 | 19 |
| 2009 | June | 2 | 0 | 0 | 0 | 0 | 2 |
| | July | 3 | 0 | 1 | 1 | 0 | 0 |
| | August | 1 | 1 | 0 | 0 | 0 | 0 |
| 2010 | June | 2 | 2 | 1 | 1 | 2 | 0 |
| | July | 23 | 20 | 3 | 31 | 17 | 8 |
| | August | 12 | 16 | 26 | 24 | 15 | 20 |
| 2011 | June | 15 | 27 | 12 | 28 | 24 | 7 |
| | July | 23 | 33 | 7 | 38 | 52 | 3 |
| | August | 10 | 12 | 17 | 7 | 18 | 12 |
| 2012 | June | 0 | 0 | 0 | 6 | 0 | 3 |
| | July | 0 | 0 | 0 | 0 | 0 | 0 |
| | August | 1 | 0 | 2 | 0 | 0 | 0 |
| 2013 | June | 0 | 0 | 0 | 0 | 0 | 0 |
| | July | 0 | 0 | 0 | 0 | 0 | 0 |
| | August | 0 | 0 | 0 | 0 | 0 | 0 |
| 2014 | June | 22 | 25 | 6 | 12 | 5 | 5 |
| | July | 27 | 35 | 13 | 46 | 34 | 2 |
| | August | 22 | 32 | 30 | 22 | 21 | 15 |
| 2015 | June | 6 | 9 | 3 | 13 | 7 | 7 |
| | July | 9 | 16 | 14 | 16 | 11 | 4 |
| | August | 17 | 32 | 39 | 10 | 20 | 22 |

**Annexe S2.2. Spatially-explicit capture-recapture models for densities.**

To facilitate statistical convergence of SECR models with multiple primary occasions and lemming groups (adult females, adult males or juveniles), the 3 groups were considered as if they were 3 separate sessions (only groups with ≥5 individuals captured during each primary occasion were included). This approach allows complex parameterisation of the detection probabilities and movements and the use of a conditional likelihood where lemming densities and their respective 95% confidence intervals are derived *a posteriori* from the models (Borchers and Efford 2008). This also reduces the number of parameters to estimate in each model and speeds up greatly computing time. In addition to group effects, we also examined for possible trap-dependence on detection probabilities (i.e. trap happiness/shyness; Table S2.2). These same effects were applied to capture data from both grids in the same analysis but separate estimates were obtained for each grid. We used the halfnormal distribution for the detection function and a buffer width of 100 m, as suggested by Krebs et al. (2011) for tundra rodents. The most parsimonious models were selected based on the second-order Akaike's criterion (AICc; Williams *et al.* 2002).

During years of very low abundance (<5 individuals) and/or when recaptures were too low (<2), we used the minimum number alive divided by the average effective sampling area (ESA) estimated by the SECR models (control grid 2008-2015: $ESA_{adult\ males}$ = 16.89 ha, $ESA_{adult\ females}$ = 10.00 ha, $ESA_{juveniles}$ = 7.35 ha; experimental grid 2008-2011: $ESA_{adult\ males}$ = 10.22 ha, $ESA_{adult\ females}$ = 10.48 ha, $ESA_{juveniles}$ = 3.92 ha; experimental grid 2012-2015: $ESA_{adult\ males}$ = 12.59 ha, $ESA_{adult\ females}$ = 9.28 ha, $ESA_{juveniles}$ = 5.37 ha).

Model selection issued from the SECR analysis is presented in Table S2.3. Trap-happiness was detected in 2008, 2010, 2014, and 2015 while no trap-dependence was found in 2011. Movements were generally lower for recaptured individuals in 2008, 2010 and 2014, but not in 2011 and 2015. Variations in distances moved by lemmings between trapping grids were inconsistent but adult males generally showed longer movements compared to adult females and juveniles (Fig. S2.1). During the predator exclusion period, males had shorter movements (no overlap of 95% CI) in the experimental grid than in the control in June and July 2014 and females in August 2014 but the opposite effect occurred in August 2014 for males.

Table S2.2. Spatially-explicit capture-recapture candidate models used for estimating brown lemming densities and movements based on the conditional likelihood (see text).

| Model | Detection | Movements |
|---|---|---|
| M1 | primary*group | primary*group |
| M2 | primary*group+*b* | primary*group |
| M3 | primary*group+*b* | primary*group+*b* |

group = adult males, adult females and juveniles (both sexes pooled); primary = primary occasions (months); *b* = trap-dependence; * = interaction; + = additive.

Table S2.3. Top models ranked according to AICc used to evaluate lemming densities during high abundance years. Densities were estimated with the top-ranked model. We used the halfnormal distribution and a buffer width of 100 m for all five models. The number of parameters (*K*) varied between years because some could not be estimated due to low sample size (≤5 individuals).

| Year | Rank | Detection | Movements | *K* | ΔAICc | $w_i$ |
|---|---|---|---|---|---|---|
| 2008 | 1 | primary*group+*b* | primary*group+*b* | 28 | 0.00 | 1.00 |
| | 2 | primary*group+*b* | primary*group | 27 | 21.83 | 0.00 |
| | 3 | primary*group | primary*group | 26 | 21.95 | 0.00 |
| 2010 | 1 | primary*group+*b* | primary*group+*b* | 26 | 0.00 | 1.00 |
| | 2 | primary*group+*b* | primary*group | 25 | 10.84 | 0.00 |
| | 3 | primary*group | primary*group | 24 | 15.53 | 0.00 |
| 2011 | 1 | primary*group+*b* | primary*group | 37 | 0.00 | 0.49 |
| | 2 | primary*group | primary*group | 36 | 0.40 | 0.40 |
| | 3 | primary*group+*b* | primary*group+*b* | 38 | 3.04 | 0.11 |
| 2014 | 1 | primary*group+*b* | primary*group+*b* | 32 | 0.00 | 0.84 |
| | 2 | primary*group+*b* | primary*group | 31 | 3.26 | 0.16 |
| | 3 | primary*group | primary*group | 30 | 11.32 | 0.00 |
| 2015 | 1 | primary*group+*b* | primary*group+*b* | 38 | 0.00 | 0.64 |
| | 2 | primary*group+*b* | primary*group | 37 | 0.77 | 0.30 |
| | 3 | primary*group | primary*group | 36 | 1.17 | 0.25 |

group = adult males, adult females and juveniles (both sexes pooled); primary = primary occasions (months); *b* = trap-dependence; * = interaction; + = additive.

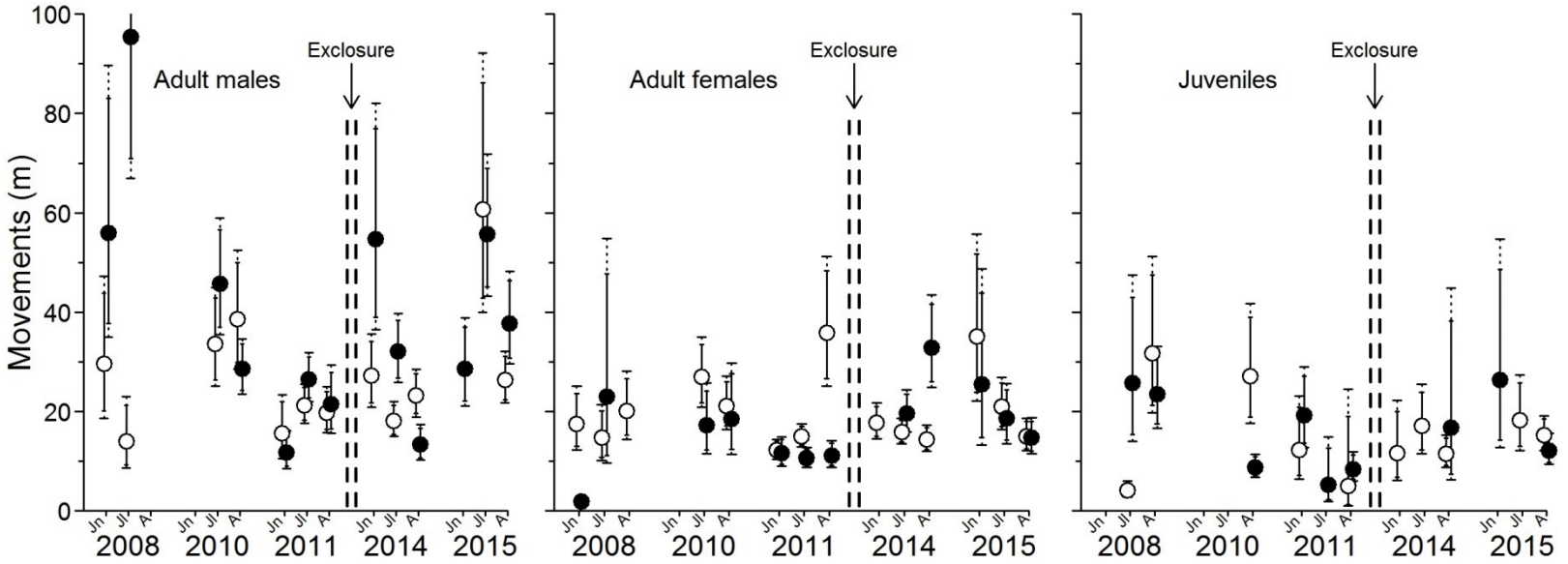


Figure S2.1. Mean distance moved between capture sites and their 90% (solid line) and 95% (dotted line) confidence intervals for brown lemmings inside the control (black circles) and experimental grid (open circles). Movements were estimated from the distance separating traps in which individuals were recaptured within primary occasions. Absence of data points at some occasions is due to low sample size or absence of captures. The vertical dashed double-line separates the pre-treatment from the treatment (predator exclusion) period (≥2013). Jn = June, Jl = July, A = August.

**Annexe S2.3. Methods and model selection for survival probabilities.**

*S2.4.1. Methods*

We developed up to 112 candidate models to test whether survival was related to predation reduction (grid effect), age, sex, and time (Table S2.4). We tested statistical interactions between grids and some other parameters because we thought that the effect of predator reduction could vary over the summer or among age/sex groups. We also tested for the presence/absence of random migration. Several candidate models were created to determine whether detection probabilities varied according to primary occasions, age/sex or were influenced by a trap-response (i.e. trap-shyness/happiness). A high number of candidate models were used to consider that complex models could perform well for years with large sample sizes while simpler models could perform better for years with low sample sizes. The statistical support of each model was assessed with AICc. We used model-averaged parameter values across models with $\Delta$AICc < 4.

*S2.4.2. Model selection*

Ranking of models are presented in Table S2.5. Survival probabilities were affected by different factors among years according to the top models ($\Delta$AICc < 4). In 2008, models with a trapping grid effect on survival had slightly less statistical support ($\Sigma w_i = 0.44$) than those without this effect ($\Sigma w_i = 0.53$) and there was little support for a group effect ($\Sigma w_i = 0.23$). Migration was absent ($\Sigma w_i = 0.81$). Probabilities of detection primarily varied among lemming groups ($\Sigma w_i = 0.59$) but also among capture occasions ($\Sigma w_i = 0.53$). Lemmings showed a negative trap-dependence ($\Sigma w_i = 1.00$) indicating lower capture probability after the first capture.

In 2010, models where survival was the same on both grids received the most support ($\Sigma w_i = 0.74$) compared to those where it differed ($\Sigma w_i = 0.26$), and there was little evidence of a group effect ($\Sigma w_i = 0.06$). Similar to 2008, absence of migration received the highest support ($\Sigma w_i = 0.78$). Detection probabilities varied among groups ($\Sigma w_i = 1.00$), often in interaction with primary periods ($\Sigma w_i = 0.91$), and was affected by trap-shyness ($\Sigma w_i = 1.00$).

The 2011, survival probabilities did not vary between grids ($\Sigma w_i = 0.86$) but varied among lemming groups in interaction with time ($\Sigma w_i = 1.00$). The most parsimonious models indicate that there was no migration ($\Sigma w_i = 0.59$). Detection probabilities varied between primary occasions ($\Sigma w_i = 1.00$) but, in contrast with the two previous years, no trap-dependence effect was found ($\Sigma w_i = 0.70$).

In 2014, the most parsimonious models provide a high support for variation in survival probabilities among trapping grids ($\Sigma w_i = 0.88$). Migration was absent ($\Sigma w_i = 0.88$). Probabilities of detection varied primarily among lemmings groups ($\Sigma w_i = 1.0$) and was also affected by a trap-dependence effect ($\Sigma w_i = 1.0$) but this time trap happiness was detected.

In 2015, there was again strong support for a grid effect on survival probabilities ($\Sigma w_i = 0.96$). High statistical support was found for an absence of migration ($\Sigma w_i = 0.79$).

Probabilities of detection varied according to both groups and primary occasions in interaction with each other ($\Sigma w_i = 1.00$) and trap-dependence was absent ($\Sigma w_i = 0.77$).

Table S2.4. List of variables used to build candidate models for estimating survival probabilities of brown lemmings. All possible combinations were made between the variables to obtain the most parsimonious model. We used Pollock's robust design and the Huggins parameterisation.

| Model | Survival | Migration | Detection |
|---|---|---|---|
| [M1, M112] | constant;<br>grid;<br>group;<br>group*grid;<br>grid*$t$;<br>group*$t$;<br>grid*$t$+group*$t$ | absent;<br>random | constant;<br>constant+$b$;<br>group;<br>group+$b$;<br>primary;<br>primary+$b$;<br>primary*group;<br>primary*group+$b$ |

grid = experimental vs. control grid; group = adult males, adult females and juveniles (both sexes pooled); $t$ = time period (June-July and July-August); $b$ = trap-dependence; primary = primary occasions; * = interaction; + = additive.

Table S2.5. Top models ranked according to AICc used to evaluate survival probabilities of lemmings during high abundance years prior (2008, 2010 and 2011) and after (2014 and 2015) the predator exclosure experiment. Models with ΔAICc < 4 were used for model-averaged estimates of survival (presented in Fig. 3.4).

| Year | Rank | Survival | Migration | Detection<br>First capture | *K* | ΔAICc | $w_i$ |
|---|---|---|---|---|---|---|---|
| 2008 | 1 | grid | absent | primary*group+*b* | 9 | 0.00 | 0.15 |
| | 2 | constant | absent | primary*group+*b* | 8 | 0.05 | 0.14 |
| | 3 | grid | absent | constant+*b* | 4 | 0.70 | 0.10 |
| | 4 | constant | absent | constant+*b* | 3 | 0.93 | 0.09 |
| | 5 | group | absent | primary*group+*b* | 9 | 1.61 | 0.07 |
| | 6 | group | absent | constant+*b* | 4 | 1.98 | 0.06 |
| | 7 | grid | random | primary*group+*b* | 10 | 2.42 | 0.04 |
| | 8 | constant | random | primary*group+*b* | 9 | 2.42 | 0.04 |
| | 9 | grid | absent | group+*b* | 5 | 2.62 | 0.04 |
| | 10 | constant | absent | group+*b* | 4 | 2.81 | 0.04 |
| | 11 | grid | random | constant+*b* | 5 | 2.90 | 0.03 |
| | 12 | group*grid | absent | constant+*b* | 6 | 2.93 | 0.03 |
| | 13 | group*grid | absent | primary*group+*b* | 11 | 3.06 | 0.03 |
| | 14 | constant | random | constant+*b* | 4 | 3.08 | 0.03 |
| | 15 | grid | absent | primary+*b* | 6 | 3.57 | 0.02 |
| | 16 | constant | absent | primary+*b* | 5 | 3.71 | 0.02 |
| | 17 | group | absent | group+*b* | 5 | 3.92 | 0.02 |
| | 18 | group | random | primary*group+*b* | 10 | 4.04 | 0.02 |
| 2010 | 1 | constant | absent | primary*group+*b* | 11 | 0.00 | 0.44 |
| | 2 | grid | absent | primary*group+*b* | 12 | 1.66 | 0.19 |
| | 3 | constant | random | primary*group+*b* | 12 | 2.14 | 0.15 |
| | 4 | constant | absent | group+*b* | 5 | 3.31 | 0.09 |
| | 5 | grid | random | primary*group+*b* | 13 | 3.81 | 0.07 |
| | 6 | group | absent | primary*group+*b* | 13 | 4.07 | 0.06 |
| 2011 | 1 | group**t* | absent | primary*group | 15 | 0.00 | 0.33 |
| | 2 | group**t* | random | primary*group | 16 | 0.42 | 0.26 |
| | 3 | group**t* | absent | primary*group+*b* | 16 | 1.28 | 0.17 |
| | 4 | group**t* | random | primary*group+*b* | 17 | 2.32 | 0.10 |
| | 5 | grid**t*+group**t* | absent | primary*group | 17 | 3.45 | 0.06 |
| | 6 | grid**t*+group**t* | random | primary*group | 18 | 3.87 | 0.05 |
| | 7 | grid**t*+group**t* | absent | primary*group+*b* | 18 | 4.73 | 0.03 |
| 2014 | 1 | grid | absent | primary*group+*b* | 12 | 0.00 | 0.20 |
| | 2 | grid | absent | group+*b* | 6 | 0.11 | 0.19 |
| | 3 | group*grid | absent | primary*group+*b* | 16 | 1.24 | 0.11 |
| | 4 | grid | random | primary*group+*b* | 13 | 2.07 | 0.07 |
| | 5 | grid | absent | group+*b* | 7 | 2.14 | 0.07 |
| | 6 | grid**t*+group**t* | absent | primary*group+*b* | 18 | 2.49 | 0.06 |
| | 7 | grid**t*+group**t* | absent | group+*b* | 12 | 2.95 | 0.05 |
| | 8 | group*grid | random | primary*group+*b* | 17 | 3.33 | 0.04 |

| | | | | | | | |
|---|---|---|---|---|---|---|---|
| | 9 | group*$t$ | absent | primary*group+$b$ | 16 | 3.51 | 0.03 |
| | 10 | group | absent | primary*group+$b$ | 13 | 3.61 | 0.03 |
| | 11 | group*grid | random | group+$b$ | 11 | 3.68 | 0.03 |
| | 12 | grid*$t$ | absent | primary*group+$b$ | 14 | 3.89 | 0.03 |
| | 13 | grid*$t$ | absent | group+$b$ | 8 | 3.90 | 0.03 |
| | 14 | group | absent | group+$b$ | 7 | 3.98 | 0.03 |
| | 15 | group*$t$ | absent | group+$b$ | 10 | 3.99 | 0.03 |
| | 16 | constant | absent | primary*group+$b$ | 11 | 4.35 | 0.02 |
| 2015 | 1 | grid | absent | primary*group | 11 | 0.00 | 0.28 |
| | 2 | grid*$t$+group*$t$ | absent | primary*group | 17 | 0.48 | 0.22 |
| | 3 | grid | absent | primary*group+$b$ | 12 | 1.83 | 0.11 |
| | 4 | grid | random | primary*group | 12 | 2.10 | 0.10 |
| | 5 | grid*$t$+group*$t$ | absent | primary*group+$b$ | 18 | 2.40 | 0.08 |
| | 6 | grid*$t$+group*$t$ | random | primary*group | 18 | 2.63 | 0.07 |
| | 7 | grid*$t$ | absent | primary*group | 13 | 2.94 | 0.06 |
| | 8 | grid | random | primary*group+$b$ | 13 | 3.94 | 0.04 |
| | 9 | group*$t$ | absent | primary*group | 15 | 4.10 | 0.04 |

grid = experimental vs. control grid; groups = adult males, adult females and juveniles (both sexes pooled); $t$ = time period (June-July and July-August); $b$ = trap-dependence; primary = primary occasions; * = interaction; + = additive.

# Annexe S3: supplementary material for Chapter 4

**Annexe S3.1. Model selection for blood and FCM analyses.**

Table S3.1. Ranking of models testing for the effect of various factors on initial ($t$ = 0) samples, samples taken 30 min after capture, and relative change ($r$, ratio between values at $t$ = 30 and $t$ = 0). Variables include total and free corticosterone (*total.c* and *free.c*), maximum corticosterone binding capacity (*mcbc*), and glucose concentrations (*g*). Model selection is based on the Akaike's second-order criterion (AICc). The number of parameter (*K*), the degrees of freedom (*df*), ΔAICc and adjusted $R^2$ are reported for each model.

| Response variable | Model | Comparison | *K* | *df* | ΔAICc | $R^2$ |
|---|---|---|---|---|---|---|
| total.$c_0$ | 1 | group | 4 | 16 | 0.00 | 0.82 |
| | 3 | sex+repro+sex*repro | 5 | 15 | 11.24 | 0.72 |
| | 4 | intercept (null) | 2 | 18 | 28.97 | – |
| | 2 | repro | 3 | 17 | 31.00 | 0.00 |
| total.$c_{30}$ | 1 | group | 4 | 15 | 0.00 | 0.73 |
| | 3 | sex+repro+sex*repro | 5 | 14 | 5.30 | 0.69 |
| | 4 | intercept (null) | 2 | 17 | 19.87 | – |
| | 2 | repro | 3 | 16 | 20.80 | 0.05 |
| $r_{total.c}$ | 1 | group | 4 | 14 | 0.00 | 0.36 |
| | 4 | intercept (null) | 2 | 16 | 3.30 | – |
| | 2 | repro | 3 | 15 | 5.04 | 0.01 |
| | 3 | sex+repro+sex*repro | 5 | 13 | 7.70 | 0.15 |
| *mcbc*$_0$ | 1 | group | 4 | 15 | 0.00 | 0.74 |
| | 3 | sex+repro+sex*repro | 5 | 14 | 2.95 | 0.73 |
| | 4 | intercept (null) | 2 | 17 | 20.02 | – |
| | 2 | repro | 3 | 16 | 22.47 | 0.00 |
| *mcbc*$_{30}$ | 1 | group | 4 | 15 | 0.00 | 0.78 |
| | 3 | sex+repro+sex*repro | 5 | 14 | 1.88 | 0.79 |
| | 4 | intercept (null) | 2 | 17 | 22.97 | – |
| | 2 | repro | 3 | 16 | 24.41 | 0.02 |
| $r_{mcbc}$ | 4 | intercept (null) | 2 | 15 | 0.00 | 0.00 |
| | 2 | repro | 3 | 13 | 2.15 | 0.00 |
| | 3 | sex+repro+sex*repro | 5 | 12 | 3.21 | 0.24 |
| | 1 | group | 4 | 14 | 5.05 | 0.00 |
| free.$c_0$ | 1 | group | 4 | 15 | 0.00 | 0.22 |
| | 4 | intercept (null) | 2 | 17 | 0.56 | – |
| | 2 | repro | 3 | 16 | 3.47 | 0.00 |
| | 3 | sex+repro+sex*repro | 5 | 14 | 8.97 | 0.00 |
| free.$c_{30}$ | 4 | intercept (null) | 2 | 17 | 0.00 | – |
| | 2 | repro | 3 | 16 | 2.86 | 0.00 |
| | 1 | group | 4 | 15 | 5.71 | 0.00 |
| | 3 | sex+repro+sex*repro | 5 | 14 | 10.06 | 0.00 |

| | | | | | | |
|---|---|---|---|---|---|---|
| $r_{free.c}$ | 4 | intercept (null) | 2 | 15 | 0.00 | – |
| | 2 | repro | 3 | 14 | 2.87 | 0.00 |
| | 1 | group | 4 | 13 | 6.65 | 0.00 |
| | 3 | sex+repro+sex*repro | 5 | 12 | 10.65 | 0.00 |
| $g_0$ | 3 | sex+repro+sex*repro | 5 | 15 | 0.00 | 0.41 |
| | 2 | repro | 3 | 17 | 0.84 | 0.21 |
| | 4 | intercept (null) | 2 | 18 | 3.60 | – |
| | 1 | group | 4 | 16 | 6.03 | 0.08 |
| $g_{30}$ | 4 | intercept (null) | 2 | 17 | 0.00 | |
| | 1 | group | 4 | 15 | 1.19 | 0.15 |
| | 2 | repro | 3 | 16 | 2.82 | 0.00 |
| | 3 | sex+repro+sex*repro | 5 | 14 | 7.04 | 0.00 |
| $r_g$ | 1 | group | 4 | 14 | 0.00 | 0.33 |
| | 4 | intercept (null) | 2 | 16 | 2.59 | – |
| | 2 | repro | 3 | 15 | 2.87 | 0.09 |
| | 3 | sex+repro+sex*repro | 5 | 13 | 9.51 | 0.01 |
| $p_0$ | 4 | intercept (null) | 2 | 17 | 0.00 | – |
| | 2 | repro | 3 | 16 | 2.90 | 0.00 |
| | 1 | group | 4 | 15 | 3.84 | 0.01 |
| | 3 | sex+repro+sex*repro | 5 | 14 | 6.71 | 0.00 |
| $p_{30}$ | 4 | intercept (null) | 2 | 15 | 0.00 | – |
| | 2 | repro | 3 | 14 | 2.58 | 0.00 |
| | 1 | group | 4 | 13 | 4.28 | 0.01 |
| | 3 | sex+repro+sex*repro | 5 | 12 | 8.57 | 0.00 |
| $r_p$ | 4 | intercept (null) | 2 | 14 | 0.00 | – |
| | 2 | repro | 3 | 13 | 3.14 | 0.00 |
| | 1 | group | 4 | 12 | 3.29 | 0.09 |
| | 3 | sex+repro+sex*repro | 5 | 11 | 9.54 | 0.00 |

Note: group = juvenile (females < 28 g, males < 30 g), adult females and adult males; repro = reproductively active vs inactive (used as the reference group).

Table S3.2. Ranking of models quantifying the effects of individual covariates on fecal corticosterone metabolites concentrations (*fcm*). Model ranking is based on the Akaike's second-order criterion (AICc). The number of parameter (*K*), the degrees of freedom (*df*), ΔAICc and adjusted $R^2$ are reported for each model.

| Response variable | Model | Comparison | *K* | *df* | ΔAICc | $R^2$ |
|---|---|---|---|---|---|---|
| $fcm_0$ | 1 | group | 4 | 16 | 0.00 | 0.12 |
| | 2 | repro | 3 | 17 | 0.48 | 0.00 |
| | 4 | intercept (null) | 2 | 19 | 0.77 | – |
| | 3 | sex+repro+sex*repro | 5 | 15 | 5.46 | 0.00 |
| $fcm_{max}$ | 3 | sex+repro+sex*repro | 5 | 14 | 0.00 | 0.50 |
| | 2 | repro | 3 | 16 | 1.17 | 0.30 |
| | 1 | group | 4 | 15 | 2.22 | 0.34 |
| | 4 | intercept (null) | 2 | 17 | 5.79 | – |
| $r_{fcm}$ | 4 | intercept (null) | 2 | 17 | 0.00 | – |
| | 2 | repro | 3 | 16 | 0.83 | 0.05 |
| | 1 | group | 4 | 15 | 4.39 | 0.00 |
| | 3 | sex+repro+sex*repro | 5 | 14 | 5.64 | 0.06 |

Note: group = juvenile (females < 28 g, males < 30 g), adult females and adult males; repro = reproductively active vs inactive (used as the reference group).

**Annexe S3.2. FCM concentrations measured by two different enzyme immunoassays cross-reacting with different metabolites.**

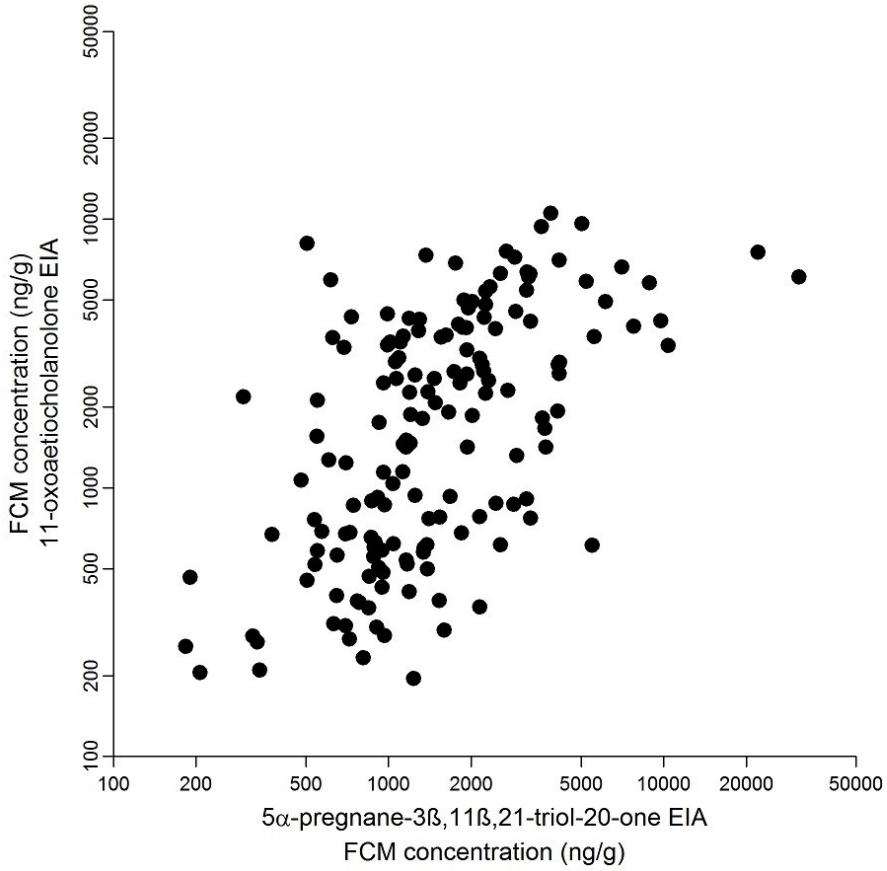


Figure S3.1. Correlation between concentrations of fecal corticosterone metabolites (FCM) measured by enzyme immunoassays using two different antibodies. Concentrations were correlated on the ln-scale (Pearson $r = 0.58$, $p < 0.001$). Measurements of FCM concentrations with both assays were performed on 9 different lemmings with 10 to 21 samples each (total $n = 308$).

**Annexe S3.3. Temporal corticosterone metabolite profiles in feces of individual lemmings in captivity.**

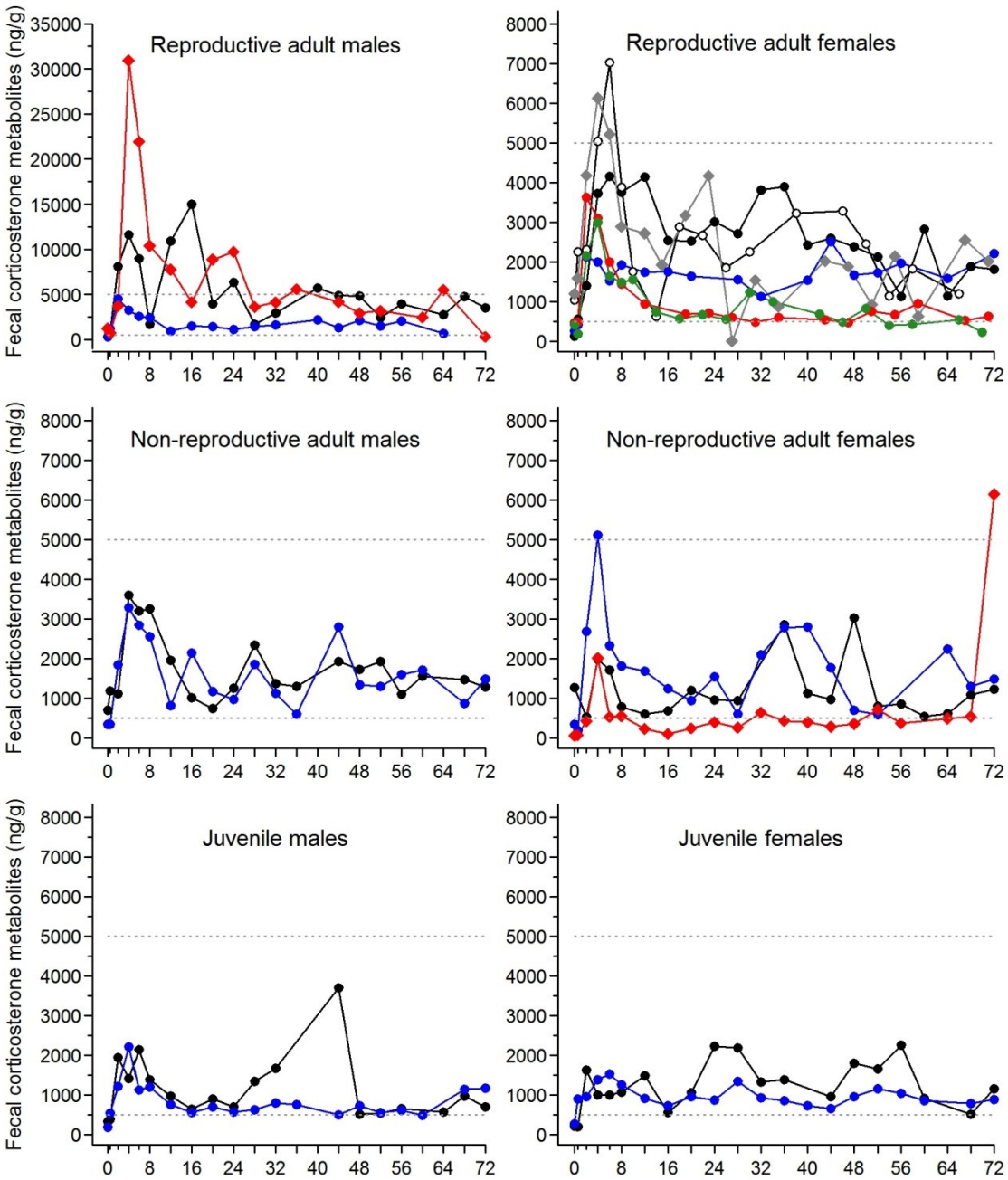


Figure S3.2. Time series of fecal corticosterone metabolites concentrations of lemmings (each line represent one individual) measured by enzyme immunoassay (see methods). Each panel represent a category of lemming based on age, sex, and reproductive condition. Lemmings were captured at time 0 and released 72 h later.

**Annexe S3.4. Effects of age, sex, and reproductive condition on the relationship between FCM and plasma corticosterone.**

Analyses of the relationship between fecal corticosterone metabolites (FCM) and plasma total or free corticosterone revealed that the former was weak ($R^2$ = 0.02) while the latter was fairly strong ($R^2$ = 0.53). Higher variability among sexes or reproductive conditions in total corticosterone compared to free corticosterone could be responsible for this difference. In order to examine this question, we built a set of 6 candidate models that included the additive effects of either group (adult males, females and juveniles) or sex and reproductive condition in combination with plasma corticosterone concentration (Tables S3.3 and S3.4). We calculated the total $R^2$ of each model ($R_f^2$) as well as the partial $R^2$ ($R_p^2$) associated with either total or free corticosterone, our variables of primary interest. Partial $R^2$ were calculated by the difference between the $R^2$ of the full model (estimated by the method of Nakagawa et Schielzeth (2013) for mixed models) and the $R^2$ of a simplified model without the total or free corticosterone covariate.

Including a group effect in the model allowed us to uncover a significant relationship between FCM and total corticosterone but the latter variable explained a fairly small proportion of the variance ($R_p^2$ = 0.18; Tables S3.3 and S3.5, Fig. S3.3). For free corticosterone, the preferred model included additive effects of sex and reproductive condition and this model again revealed a strong relationship between FCM and free corticosterone concentrations, with the latter variable still explaining a very high proportion of the variability in FCM ($R_p^2$ = 0.55; Tables S3.4 and S3.6; Figure S3.3). Therefore, even when controlling for differences among sexes or reproductive condition, free corticosterone explained a much higher proportion of variance in FCM than total corticosterone.

Table S3.3. Ranking of models quantifying the relationship between FCM and total corticosterone (*total.c*) with individual covariates. Mixed-effects models were used with individual lemmings as the random variable. The partial marginal coefficients of determinations for the total corticosterone covariate ($R_p^2$) and the coefficient for the full model ($R_f^2$) are presented.

| Model | *K* | ΔAICc | $R_p^2$ | $R_f^2$ |
|---|---|---|---|---|
| *total.c* + group | 6 | 0.00 | 0.18 | 0.28 |
| *total.c* + sex | 5 | 0.14 | 0.15 | 0.22 |
| *total.c* + sex*repro | 7 | 1.27 | 0.21 | 0.32 |
| *total.c* + sex + repro | 6 | 2.54 | 0.12 | 0.23 |
| null | 3 | 3.16 | - | - |
| *total.c* | 4 | 5.19 | - | 0.02 |
| *total.c* + repro | 5 | 6.67 | 0.01 | 0.05 |

Note: group = juvenile, adult females and adult males; repro = reproductively active vs inactive (used as the reference group).

Table S3.4. Ranking of models quantifying the relationship between FCM and free corticosterone (*free.c*) with individual covariates. Mixed-effects models were used with individual lemmings as the random variable. The partial marginal coefficients of determination for the free corticosterone covariate ($R_p^2$), and the coefficient for the full model ($R_f^2$) are presented.

| Model | *K* | ΔAICc | $R_p^2$ | $R_f^2$ |
|---|---|---|---|---|
| *free.c* + sex + repro | 6 | 0.00 | 0.55 | 0.66 |
| *free.c* + sex + repro + sex*repro | 7 | 1.41 | 0.57 | 0.68 |
| *free.c* + group | 6 | 2.95 | 0.53 | 0.63 |
| *free.c* + sex | 5 | 3.11 | 0.53 | 0.60 |
| *free.c* + repro | 5 | 4.14 | 0.54 | 0.59 |
| *free.c* | 4 | 5.98 | - | 0.53 |
| null | 3 | 29.01 | - | - |

Note: group = juvenile, adult females and adult males; repro = reproductively active vs inactive (used as the reference group).

Table S3.5. Effects retained in the most parsimonious model (Table S3.3) testing the relationship between FCM and total corticosterone (*total.c*) while considering individual covariates.

| Parameter | $\beta$ | Low CI | High CI |
|---|---|---|---|
| *total.c* | **0.67** | **0.19** | **1.15** |
| group (J – AF) | 1.25 | -0.34 | 2.84 |
| group (AM – AF) | **2.57** | **0.97** | **4.18** |

Note: J = juvenile; AF = adult females; AM = adult males.

Table S3.6. Effects retained in the most parsimonious model (Table S3.4) testing the relationship between FCM and free corticosterone (*free.c*) while considering individual covariates.

| Parameter | $\beta$ | Low CI | High CI |
|---|---|---|---|
| *free.c* | **0.43** | **0.31** | **0.55** |
| sex | **0.77** | **0.19** | **1.36** |
| repro | **0.69** | **0.12** | **1.26** |

Note: sex = males and females (used as the reference group); repro = reproductively active vs inactive (used as the reference group).

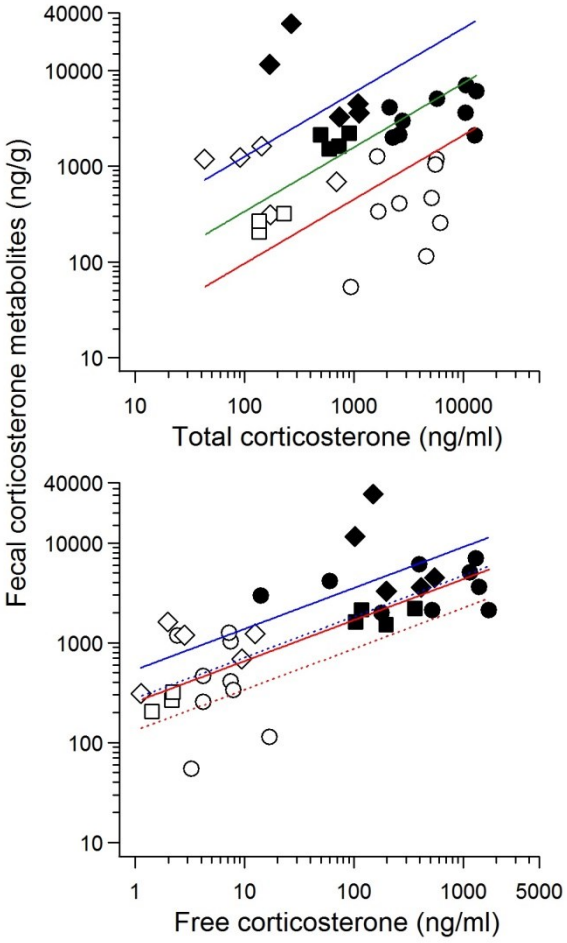


Figure S3.3. Relationships between plasma total or free corticosterone and FCM concentrations in lemmings when considering individual covariates. Estimates are based on models presented in Tables S3.5 and S3.6. Samples collected at $t = 0$ for plasma and FCM were paired (white points) whereas plasma samples collected at $t = 30$ min were paired with maximal FCM concentrations recorded (i.e. between 2 to 6 h after capture depending on each individual; black points). Two observations (one for each paired samples) per lemming ($n = 18$) were used to assess the relationship. Circles = adult females; diamonds = adult males; squares = juveniles. Top figure: blue line = adult males; green line = juveniles; red line = adult females. Bottom figure: blue solid line = reproductive males; blue dotted line = non-reproductive male; red solid line = reproductive females; red dotted line = non-reproductive females.

# Annexe S4: supplementary material for Chapter 5

**Annexe S4.1. Abundance of predators on Bylot Island.**

A large guild of predators feed upon lemmings in the Canadian Arctic tundra (Gauthier *et al.* 2011; Krebs 2011). During summers of high lemming abundance, the estimated total consumption of lemmings by avian predators on Bylot Island can reach up to ~3% $day^{-1}$ of the population (Therrien *et al.* 2014), a value high enough to overcome the maximum estimated population growth (2.4% $day^{-1}$) of lemmings. Bilodeau (2013) also estimated that in a year of high ermine abundance on Bylot Island, they can consume up to 1.2% $day^{-1}$ of the lemming population. In Greenland, Gilg (2002) indicated that predators were consuming up to 3.4% $day^{-1}$ of the lemming population, which was also high enough to exceed lemming population growth.

In the Arctic, the abundance of nesting snowy owls, long-tailed jaegers, rough-legged hawks and ermines are highly and positively related to lemming abundance (Gilg *et al.* 2006; Therrien *et al.* 2014). In contrast, the abundance of arctic fox, glaucous gulls, parasitic jaegers, and peregrine falcons are relatively stable throughout the phases of the lemming cycle, probably owing to their more generalist diet (Legagneux *et al.* 2012). In Table S4.1, we present predator densities on Bylot Island reported in other studies. In 2014, snowy owl ($n$ = 98), long-tailed jaeger ($n$ = 77), and rough legged hawk nests ($n$ = 31) were highly abundant and the raptors had high nesting success (96%, 52%, and 87%, respectively; Beardsell 2016, Gauthier *et al.* 2015, 2016). Despite the high lemming abundance in 2015, snowy owls were virtually absent from the study area but long-tailed jaeger ($n$ = 38) and rough-legged hawk nests ($n$ = 21) were present in relatively large number although jaegers had very low nesting success (6%; Gauthier *et al.* 2016). In 2014 and 2015, there were 44 and 45 active arctic fox dens and the foxes showed high breeding activity (64% and 69%, respectively), as was expected for high lemming abundance years (Gauthier *et al.* 2015, 2016). Ermines were absent in both years. Experiments conducted with artificial bird nests in our study area revealed a high predator activity in both years as most eggs disappeared within 2 days (J. Bêty, pers. comm; Fauteux et al. submitted). These observations suggest that the abundance and activity of lemming predators in our study area were high during both study years, with the exception of the ermine and snowy owls in 2015.

Table S4.1. Mammalian predator densities (individuals $km^{-2}$) and raptor nest densities (nests $km^{-2}$) observed on Bylot Island. For species with relatively stable densities, we give average value across years and for those with highly variable densities we give the typical vlues for years of lemming abundance (Legagneux *et al.* 2012; Therrien *et al.* 2014).

| Species | | Densities (N $km^{-2}$) |
|---|---|---|
| with stable densities | Arctic fox | 0.08 |
| | Glaucous gull | 0.16 |
| | Parasitic jaeger | 0.02 |
| | Peregrine falcons | 0.01 |
| with variable densities | Snowy owl | 0.11 |
| | Long-tailed jaeger | 0.92 |
| | Rough-legged hawk | 0.15 |
| | Ermine | 0.40 |

**Annexe S4.2. Results of the model selection for faecal corticosterone metabolite concentration of lemmings.**

Table S4.2. Ranking of candidate models testing the effects of predator reduction (grid), reproductive condition (repro) and sex on faecal corticosterone metabolite concentration of adult lemmings. Year and months nested in year were used as random factors. *K* = number of parameters; ΔAICc = delta of Akaike's criterion; $w_i$ = Akaike's weight; $R_m^2$ = marginal $R^2$ (fixed-effects only); $R_g^2$ = condition $R^2$ (both fixed and random effects).

| Model | *K* | ΔAICc | $w_i$ | $R_m^2$ | $R_g^2$ |
|---|---|---|---|---|---|
| grid + repro | 9 | 0.00 | 0.69 | 0.49 | 0.54 |
| repro | 8 | 2.68 | 0.18 | 0.45 | 0.53 |
| grid * repro | 13 | 3.25 | 0.14 | 0.52 | 0.57 |
| grid * sex | 7 | 35.03 | 0.00 | 0.22 | 0.35 |
| grid + sex | 6 | 37.70 | 0.00 | 0.19 | 0.31 |
| sex | 5 | 40.02 | 0.00 | 0.15 | 0.31 |
| grid | 5 | 52.50 | 0.00 | 0.05 | 0.20 |
| null | 4 | 56.32 | 0.00 | - | - |

* = interactive effects; + = additive effects.
grid = grid effect (predator reduction vs control); repro = reproductive condition (males: scrotal, abdominal; females: pregnant, lactating; both: non-reproductive).

**Annexe S4.3. Sample size of lemmings used to estimate proportions in the population.**

Table S4.3. Sample sizes of adult lemmings captured during monthly capture occasions (primary) used to assess densities at our study site. These sample sizes include monthly recaptures but not within primary occasion recaptures (only one capture per month).

| | | 2014 | | 2015 | |
|---|---|---|---|---|---|
| | | Control | Experimental | Control | Experimental |
| Males | Abdominal | 16 | 23 | 19 | 20 |
| | Scrotal | 47 | 28 | 18 | 8 |
| | Non-reproductive | 17 | 20 | 1 | 3 |
| Females | Pregnant | 17 | 23 | 3 | 9 |
| | Lactating | 30 | 46 | 12 | 17 |
| | Non-reproductive | 9 | 19 | 12 | 10 |

**Annexe S4.4. Results of the model selection for body mass of lemmings.**

Table S4.4. Ranking of candidate models testing the effects of faecal corticosterone metabolites (FCM), predator reduction (grid) and reproductive condition (repro) on body mass of adult lemmings. Year and months nested in year was used as random factors. ΔAICc = delta of Akaike's criterion; $w_i$ = Akaike's weight; $R^2_m$ = marginal $R^2$ (fixed-effects only); $R^2_g$ = condition $R^2$ (both fixed and random effects).

| Model | *K* | ΔAICc | $w_i$ | $R^2_m$ | $R^2_g$ |
|---|---|---|---|---|---|
| repro + grid | 9 | 0.00 | 0.37 | 0.43 | 0.43 |
| repro | 8 | 1.14 | 0.21 | 0.40 | 0.40 |
| FCM * grid + repro | 11 | 1.86 | 0.15 | 0.44 | 0.44 |
| FCM + repro + grid | 10 | 2.47 | 0.11 | 0.43 | 0.43 |
| FCM + repro | 9 | 3.47 | 0.07 | 0.40 | 0.40 |
| FCM * repro + grid | 14 | 3.57 | 0.06 | 0.48 | 0.48 |
| FCM * repro | 13 | 4.64 | 0.04 | 0.46 | 0.46 |
| FCM * grid | 7 | 33.38 | 0.00 | 0.15 | 0.15 |
| FCM + grid | 6 | 34.86 | 0.00 | 0.12 | 0.12 |
| FCM * grid + sex | 8 | 35.67 | 0.00 | 0.15 | 0.15 |
| FCM + sex + grid | 7 | 37.01 | 0.00 | 0.12 | 0.12 |
| FCM * sex + grid | 8 | 38.41 | 0.00 | 0.13 | 0.13 |
| FCM | 5 | 38.91 | 0.00 | 0.06 | 0.06 |
| sex + grid | 6 | 41.06 | 0.00 | 0.06 | 0.06 |
| FCM + sex | 6 | 41.49 | 0.00 | 0.05 | 0.05 |
| grid | 5 | 41.81 | 0.00 | 0.03 | 0.03 |
| null | 4 | 42.23 | 0.00 | - | - |
| FCM * sex | 7 | 42.62 | 0.00 | 0.06 | 0.06 |
| sex | 5 | 42.67 | 0.00 | 0.02 | 0.02 |

FCM = faecal corticosterone metabolite concentrations; grid = effects of predator reduction; repro = reproductive condition (males: scrotal, abdominal; females: pregnant, lactating; both: non-reproductive).

**Annexe S4.5. Results of the model selection for movements of lemmings.**

Table S4.5. Ranking of candidate models testing the effects of faecal corticosterone metabolites (FCM), predator reduction (grid), and reproductive condition on average distance moved by adult lemmings among traps. Year was used as the random factor. ΔAICc = delta of Akaike's criterion; $w_i$ = Akaike's weight; $R^2_m$ = marginal $R^2$ (fixed-effects only); $R^2_g$ = condition $R^2$ (both fixed and random effects).

| Model | *K* | ΔAICc | $w_i$ | $R^2_m$ | $R^2_g$ |
|---|---|---|---|---|---|
| FCM | 4 | 0.00 | 0.33 | 0.10 | 0.16 |
| FCM + grid | 5 | 1.83 | 0.13 | 0.11 | 0.17 |
| FCM + sex | 5 | 1.86 | 0.13 | 0.11 | 0.17 |
| FCM * grid | 6 | 3.01 | 0.07 | 0.13 | 0.17 |
| FCM + sex + grid | 6 | 3.48 | 0.06 | 0.12 | 0.18 |
| Grid | 4 | 3.74 | 0.05 | 0.04 | 0.10 |
| null | 3 | 4.06 | 0.04 | - | - |
| FCM * sex | 6 | 4.21 | 0.04 | 0.11 | 0.17 |
| FCM * grid + sex | 7 | 4.61 | 0.03 | 0.14 | 0.19 |
| repro | 7 | 4.75 | 0.03 | 0.14 | 0.17 |
| FCM + repro | 8 | 5.52 | 0.02 | 0.17 | 0.21 |
| FCM * sex + grid | 7 | 5.91 | 0.02 | 0.12 | 0.18 |
| sex | 4 | 6.05 | 0.02 | 0.05 | 0.05 |
| sex + grid | 5 | 6.14 | 0.02 | 0.04 | 0.10 |
| repro + grid | 8 | 6.46 | 0.01 | 0.16 | 0.20 |
| FCM + grid + repro | 9 | 7.77 | 0.01 | 0.17 | 0.23 |
| FCM * grid + repro | 10 | 8.97 | 0.00 | 0.20 | 0.24 |
| FCM * repro | 12 | 13.74 | 0.00 | 0.22 | 0.26 |
| FCM * repro + grid | 13 | 16.65 | 0.00 | 0.22 | 0.27 |

FCM = faecal corticosterone metabolite concentrations; grid = effects of predator reduction; repro = reproductive condition (males: scrotal, abdominal; females: pregnant, lactating; both: non-reproductive).