# Mouvements et utilisation de l’habitat en hiver chez un prédateur nomade: le harfang des neiges

**Thèse**

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**Doctorat en biologie**
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Sous la direction de :

Gilles Gauthier, directeur de recherche
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# Résumé de la thèse

La migration est un processus écologique permettant aux individus d'exploiter des habitats où les ressources alimentaires et les conditions environnementales fluctuent de façon saisonnière. Certaines espèces présentent une étonnante variabilité et imprévisibilité dans leurs comportements migratoires, notamment les migrateurs facultatifs. L'objectif général de cette thèse est de mieux comprendre l'écologie des espèces migratrices dont les déplacements sont imprévisibles durant la période hivernale et peuvent influencer la reproduction subséquente. Mon projet s'est penché sur le harfang des neiges, un prédateur aviaire considéré comme un migrateur nomade et irruptif (i.e. effectuant des migrations massives périodiquement). Les objectifs spécifiques étaient de déterminer la variabilité interindividuelle dans les mouvements, l'utilisation de l'habitat, la fidélité au site d'hivernage et la contribution de proies provenant de différents habitats au régime alimentaire du harfang en hiver par une approche intégrant plusieurs méthodes d'analyses. Pour ce faire, 31 femelles adultes ont été suivies par télémétrie satellitaire entre 2007-2016 afin de caractériser l'utilisation de l'espace et de l'habitat, et d'évaluer l'impact de différents facteurs environnementaux sur ceux-ci. L'analyse d'isotopes stables ($^{13}$C et $^{15}$N) dans les plumes récoltées sur des individus pendant l'été a été utilisée pour mesurer la contribution des habitats terrestres et marins au régime alimentaire hivernal. Finalement, des données citoyennes sur l'abondance hivernale des harfangs issues du *Christmas Bird Count*, combinées à des mesures sur l'abondance des proies en été dans l'Arctique, ont permis d'apporter un éclairage nouveau sur les causes des irruptions hivernales de harfangs aux latitudes tempérées. Les suivis satellitaires ont confirmé la forte utilisation de l'Arctique et des milieux marins par le harfang en hiver. La couverture de neige et l'abondance des lemmings ont permis d'expliquer une partie de la variabilité interindividuelle dans l'utilisation de l'espace. Nous montrons aussi que les harfangs sont généralement constants d'une année à l'autre dans leur utilisation de zone latitudinale (Arctique vs milieux tempérés) et d'habitat (terrestre vs marin) durant l'hiver et qu'ils présentent une fidélité plus forte à leur site d'hivernage qu'à leur site de reproduction. Nos analyses démontrent que les irruptions hivernales périodiques dans les latitudes tempérées seraient en partie dues à un succès reproducteur élevé l’été précédent dans l’Arctique grâce à une forte abondance de nourriture. Ceci permet de déboulonner un mythe bien ancré selon lequel les espèces nordiques comme les harfangs migrent au sud en masse pendant l’hiver par manque de nourriture dans le Nord. L’analyse isotopique des plumes a confirmé que le milieu marin pouvait contribuer de façon importante au régime alimentaire du harfang en hiver. Une partie de la variabilité interindividuelle dans la contribution marine au régime alimentaire a pu être expliquée par leur utilisation de l’habitat tel que mesuré par les suivis satellitaires. Dans un contexte de changements globaux, le harfang, comme d’autres prédateurs arctiques mobiles qui connectent des écosystèmes distants, à la fois terrestres et marins, pourrait être affecté de plusieurs façons durant son cycle annuel. Les travaux de cette thèse contribuent à améliorer nos connaissances sur l’écologie des migrateurs facultatifs, en particulier chez les espèces aux mouvements imprévisibles. L’étude contribue également à améliorer notre compréhension des interactions entre les différentes périodes du cycle annuel des espèces migratrices et des liens entre écosystèmes qui sont générés par le mouvement des prédateurs.

# Abstract

Migration is an ecological process allowing individuals to exploit habitats where food resources and environmental conditions fluctuate seasonally. Some species have highly variable and unpredictable migratory behaviours, and especially facultative migrants. The general aim of this thesis is to better understand the wintering ecology of migratory species with unpredictable movement patterns during winter, which may affect their subsequent breeding. My project focused on the snowy owl, an avian predator considered both a nomadic and irruptive migrant. The specific objectives consisted in determining the interindividual variability in movements, habitat use, wintering site fidelity and contribution of prey from different habitats to their diet in winter through an approach integrating multiple analytical methods. To achieve this, 31 adult females were tracked by satellite telemetry between 2007-2016 to characterise space and habitat use and evaluate the impact of some environmental factors on them. Stable isotope analyses ($^{13}$C et $^{15}$N) of feathers sampled on snowy owls in summer were used to estimate the contribution of marine and terrestrial habitats to their winter diet. Finally, citizen-based data on winter abundance of snowy owls from *Christmas Bird Count* coupled with estimates of summer prey abundance in the Arctic allowed to shed new lights on the causes of snowy owls' winter irruptions at temperate latitudes. Satellite tracking confirmed the extensive use of the Arctic and marine environments by wintering snowy owls. Snow cover and lemming abundance could explain part of the interindividual variability in space use. We also show that snowy owls were generally consistent from one year to the next in their use of latitudinal zones (Arctic vs temperate areas) and habitats (terrestrial vs marine) in winter and that they showed a greater fidelity to wintering than to breeding sites. Our analyses show that periodic winter irruptions at temperate latitudes are at least in part attributable to high reproductive success during the preceding summer because of an abundance of food. These results allowed us to debunk a long-standing myth about irruptive snowy owls, stating that they migrate south massively because of a lack of food in the North. Feather isotopic analyses also confirmed that the marine environment could contribute significantly to the diet of snowy owls in winter. Part of the interindividual variability in the marine contribution to the diet could be explained by the habitat use of snowy tracked by satellite telemetry. In a context of global changes, the snowy owl, as other

mobile arctic predators connecting distant ecosystems, both terrestrial and marine, could be affected in multiple ways during its annual cycle. The work presented in this thesis contributes to further our knowledge of the ecology of facultative migrants, particularly in species with unpredictable movement patterns. This study also contributes to further our understanding of the interactions among different parts of the annual cycle of migrating species and the links between ecosystems generated by the movements of predators.

# Table des matières

# Liste des tableaux

CHAPITRE 2

CHAPITRE 3

CHAPITRE 4

CHAPITRE 5

# Liste des figures

CHAPITRE 1

CHAPITRE 2

CHAPITRE 3

CHAPITRE 4

CHAPITRE 5

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# Avant-propos

Ma thèse comporte 6 chapitres incluant les chapitres d'introduction et de conclusion qui sont rédigés en français ainsi que 4 chapitres centraux présentés sous forme d'articles scientifiques rédigés en anglais. Je suis l'auteure principale de chacun de ces 6 chapitres et ainsi, la principale responsable de la planification, la récolte de données sur le terrain, les revues de littérature, la récolte et la mise en forme des bases de données, les analyses, l'interprétation des résultats et la rédaction des articles scientifiques. Pour les chapitres 2, 3, 4 et 5, j'ai étroitement collaboré avec mon directeur de recherche, Gilles Gauthier de l'Université Laval, ainsi que mon co-directeur Joël Bêty de l'UQAR, et Jean-François Therrien, chercheur sénior au *Hawk Mountain Sanctuary*, en Pennsylvanie. D'autres co-auteurs ont aussi contribué dans une moindre mesure à certains chapitres. Les chapitres 3 et 4 sont présentement publiés, et les chapitres 2 et 5 seront soumis prochainement.

Le chapitre 1 est une introduction générale des thèmes abordés à travers les différents chapitres de ma thèse, soit la migration, l'écologie hivernale à travers l'utilisation de l'espace, de l'habitat, la fidélité aux sites et les liens entre les différentes parties du cycle annuel, en plus d'explorer les techniques pour étudier le régime alimentaire hivernal. J'y présente aussi les objectifs, hypothèses et prédictions de ma thèse.

Le chapitre 2, « **Wintering space use and site fidelity in a nomadic species, the snow owl»,** présente les mouvements migratoires, l'utilisation de l'habitat hivernal et la fidélité au site de harfangs des neiges suivis par télémétrie satellite. Ce chapitre est en préparation et sera le prochain manuscrit soumis pour publication. Les coauteurs sont Gilles Gauthier, Jean-François Therrien et Joël Bêty.

Le chapitre 3, « **Pulsed resources at tundra breeding sites affect winter irruptions at temperate latitude of a top predator: the snowy owl »** évalue le lien entre l'abondance de proies sur le site de reproduction et les irruptions hivernales de harfangs des neiges à nos latitudes en mettant en compétition deux hypothèses contrastantes de la littérature. Ce chapitre a été publié dans la revue *Oecologia* en février 2016 et les coauteurs sont Gilles Gauthier, Jean-François Therrien, Karen M. Clark (Gouvernement des Territoires du Nord-Ouest) et Joël Bêty.

Le chapitre 4, « **Variability in stable isotopes of snowy owl feathers and contribution of marine resources to their winter diet** » étudie les variations intra- et inter-individuelles d'isotopes stables dans les plumes prélevées en été et évalue le potentiel de cette technique pour déterminer la contribution de l'environnement marin dans le régime alimentaire hivernal des harfangs. Ce chapitre a été publié dans la revue *Journal of Avian Biology* en Mai 2017 et les coauteurs sont Gilles Gauthier, Jean-François Therrien, Guy Fitzgerald (Faculté de Médecine vétérinaire, Université de Montréal), Jennifer Provencher (Acadia University) et Joël Bêty.

Le chapitre 5, « **Combining satellite tracking and stable isotope analyses of feathers to link winter habitat use, diet and reproduction of snowy owls** », suit et complémente le chapitre 4. Ce chapitre examine si la variabilité interindividuelle dans les contributions marines au régime alimentaire mesurée par les plumes peut être reliée à l'utilisation hivernale de l'habitat par les harfangs et peut influencer les performances reproductives et la condition corporelle des harfangs par effets reportés. Ce chapitre est en préparation et sera soumis prochainement pour publication. Les coauteurs sont Gilles Gauthier, Jean-François Therrien et Joël Bêty.

J'ai aussi publié des ouvrages non-révisées par les pairs issus de mes travaux de doctorat, notamment un rapport d'activités présenté au service Environnement Mine Glencore Xstrata Nickel, Raglan intitulé « **Étude des mouvements et de la nidification du Harfang des neiges au Nunavik** » en février 2013, et un article traduit en danois « **Sneugler jager havfugle i polarisen om vinteren** » pour la *Danish Ornithological Society/Birdlife Denmark*, en 2015.

# CHAPITRE 1 : Introduction générale

Déjà en 343 avant J-C, Aristote dissertait sur la migration animale : « Tous les animaux sont naturellement sensibles aux variations du chaud et du froid; ceux d'entre eux qui ont la faculté de se déplacer font comme les hommes, dont les uns se retirent seulement dans leurs maisons pendant l'hiver, tandis que d'autres, maîtres d'une grande étendue de pays, vont passer l'été dans les lieux frais, et l'hiver dans les lieux tempérés » (Liv. VIII, Chap. 12. Trad. Camus,1783). En reconnaissant ainsi l'existence des migrations animales, il pavait la voie aux naturalistes qui s'y intéresseraient dès lors et jusqu'à aujourd'hui encore.

Les espèces migratrices sont présentes dans une grande diversité de taxons du règne animal, des insectes (e.g. libellule, Wikelski et al. 2006; Dingle 1972) aux grands mammifères (e.g. éléphant de savane d'Afrique, *Loxodonta Africana*, Thouless 1995) et ce autant en milieu terrestre (e.g. paruline rayée, *Setophaga striata,* DeLuca et al. 2013; caribous, *Rangifer tarandus,* Le Corre et al. 2014) qu'aquatique (e.g. anguille: Beguer-Pon et al. 2015; baleine à bosse, *Megaptera novaeangliae*, Zerbini et al. 2006). Si la migration en général soulève depuis longtemps un intérêt scientifique certain, la migration aviaire suscite en plus, un intérêt populaire phénoménal. C'est que les oiseaux ont une capacité fascinante, celle de voler, qui fait rêver la plupart des bipèdes terrestres que nous sommes. On estime à près de 20% les espèces d'oiseaux considérées comme migratrices (Kirby et al. 2008). Les migrations de longue distance comme celle de la sterne arctique *Sterna paradisaea* (Egevang et al. 2010) qui migre d'un pôle à l'autre, ou les migrations de longue haleine telle que celle de la barge rousse *Limosa lapponica* (Gill et al. 2005) sont des prouesses physiologiques particulièrement fascinantes.

## 1.1. La migration aviaire

En écologie, la migration se définie généralement comme un mouvement régulier entre deux sites fixes, ou plus précisément entre un site de reproduction et une autre localisation où les migrateurs pourront survivre le reste de l'année (Dingle 1996, Greenberg and Marra 2005, Rappole 2013). La migration implique donc un mouvement typiquement directionnel, récurrent et saisonnier, et se doit d'être de plus longue distance que les mouvements journaliers (Dingle and Drake 2007). La migration est une adaptation aux ressources fluctuant spatialement et temporellement, et permet ainsi aux migrateurs d'exploiter les endroits où les ressources saisonnières sont abondantes et d'éviter les zones où elles ne le sont pas (Newton and Dale 1996, Alerstam et al. 2003, H-Acevedo and Currie 2003, Dean 2004, Dingle and Drake 2007, Dalby et al. 2014). Les sites exploités à chaque saison peuvent ainsi être géographiquement et temporellement éloignés, faisant de la migration un élément important dans la dynamique et la répartition spatiale des populations. Outre l'abondance et la disponibilité saisonnière des ressources, il a aussi été montré que l'évitement de la prédation peut être un autre facteur important permettant d'expliquer les migrations aviaires (Hebblewhite and Merrill 2009, McKinnon et al. 2010). Au cours de leur cycle annuel, les oiseaux migrateurs viseront donc à exploiter les milieux qui leur permettront de maximiser leur aptitude phénotypique (Alerstam et al. 2003, Rappole et al. 2003, Rappole and Schuchmann 2003). Grâce à leur mobilité et à la vitesse de leurs déplacements, les oiseaux ont développé des systèmes de migration variés, leur permettant d'exploiter efficacement ces différents environnements saisonniers.

### *1.1.1. Les types de migration*

Les patrons migratoires sont complexes, peuvent prendre différentes formes et sont souvent considérés comme des continuums qui varient en termes de distance (migrations de courte à longue distance), d'intensité (migrations partielles à complètes) ou de degré d'obligation des mouvements (migration facultative à obligatoire; Newton 2006a, 2008). Évidemment, ces patrons migratoires ne sont pas mutuellement exclusifs et peuvent varier de façon saisonnière, annuelle, individuelle ou entre les espèces. Malgré la diversité de ces stratégies, les patrons migratoires chez les animaux sont souvent caractérisés par une régularité. Cependant, cette régularité migratoire est seulement avantageuse dans des environnements relativement prévisibles, où les conditions rencontrées par les migrateurs seront similaires d'années en années (Newton 2012). Chez les espèces qui exploitent des ressources alimentaires ou des habitats moins prévisibles, la flexibilité migratoire peut donc être plus profitable (Andersson 1980, Terrill and Ohmart 1984, Dean 2004).

Sur le spectre des comportements migratoires, on retrouve, à une extrémité, les migrations dites obligatoires. Celles-ci sont généralement régulières dans le temps et dans l'espace et sont souvent contrôlées par des processus endogènes tels que les rythmes circadiens ou circannuels (Gwinner 1996, Newton 2012). À l'autre extrémité de ce spectre, on y place les migrations facultatives qui sont, comme leur nom l'indique, optionnelles, mais aussi variables sous plusieurs aspects (e.g. phénologie, régularité et distance). Ces migrations irrégulières seraient plutôt liées aux conditions environnementales changeantes (Newton 2012, Ramenofsky et al. 2012). En fait, les migrations facultatives seraient favorisées dans les situations où la disponibilité des ressources alimentaires et les conditions environnementales varient fortement entre les années (Wingfield 2003, Newton 2008, Rappole 2013). Deux formes de migration facultatives sont souvent décrites dans la littérature : les migrations irruptives (aussi connues sous les termes *irruptions* ou *invasions*) et le nomadisme (Newton 2006a, 2008, 2012).

Les irruptions sont une forme extrême et souvent spectaculaire de migration facultative caractérisée par un mouvement massif et inhabituel d'un grand nombre de migrants dans un endroit spécifique (Newton 2006a, 2008). Ces mouvements migratoires populationnels sont généralement périodiques et peuvent être très variables en termes de nombre de migrants, leurs distances parcourues, l'aire qu'ils occupent et la durée de leurs déplacements (Newton 2008). Les irruptions sont généralement observées chez les espèces spécialistes de ressources imprévisibles ou pulsées, et sont communes chez au moins deux groupes d'oiseaux : les granivores boréaux et les strigidés (i.e. chouettes et hiboux). Les granivores boréaux sont souvent spécialistes de graines de conifères qui sont généralement produites de façon irrégulière, périodique ou en masse (« mast fruiting » en anglais, Newton 2008). La faible abondance de ces ressources certaines années serait responsable des migrations massives de ces granivores hors de leur aire régulière (Svardson 1957, Bock and Lepthien 1976). Chez les strigidés, plusieurs espèces se nourrissent principalement de petits mammifères dont les populations fluctuent en abondance de façon cyclique dans plusieurs régions nordiques (Stenseth 1999, Korpimäki et al. 2004, Ims and Fuglei 2005, Fauteux et al. 2015a, Fauteux et al. 2015b). Il est donc suggéré depuis longtemps que les mouvements massifs à grande échelle de ces strigidés vers le sud soient liés aux fluctuations d'abondance des petits mammifères dans le Nord (Shelford 1945, Cheveau et al. 2004, Morrissette et al. 2010). Les migrateurs irruptifs peuvent toutefois montrer une certaine régularité de mouvements entre leurs sites de reproduction et d'hivernage, mais migrer massivement vers certains endroits (souvent plus au sud que leur aire d'hivernage habituelle), certaines années, lorsque leurs ressources alimentaires diminuent drastiquement ou que la densité de leurs populations limite la disponibilité des ressources (Lack 1954, Newton 1970, Koenig and Knops 2001).

Le nomadisme, quant à lui, est un comportement migratoire individuel. Tout comme les migrateurs irruptifs, les migrateurs considérés nomades répondent aussi aux fluctuations irrégulières de leur environnement en exploitant des habitats ou des ressources sporadiques (Dean 2004, Newton 2008). Face à cette variabilité environnementale, les migrateurs nomades n'ont généralement pas de sites fixes de reproduction ou d'hivernage (Andersson 1980, Dean 2004) quoique les définitions de nomadisme peuvent varier. Le nomadisme est bien décrit chez les espèces désertiques où les précipitations, qui déterminent les zones de verdissement et les densités d'insectes, orientent souvent leurs déplacements (Dean 1997, 2004, Roshier et al. 2006). Comme pour les irruptions, la disponibilité des ressources alimentaires est aussi un facteur menant au nomadisme chez certaines espèces (Korpimaki and Norrdahl 1991, Brown and Hopkins 1996, Cheveau et al. 2004). Les migrateurs nomades peuvent ainsi parcourir des centaines voire des milliers de kilomètres entre deux sites de reproduction ou d'hivernage consécutifs selon l'abondance de ces ressources (e.g. jusqu'à plus de 3000 km chez le bec-croisé des sapins *Loxia curvirostra*; Newton 2006b). Pour les espèces nomades, les déplacements peuvent se produire à toutes les périodes du cycle annuel, dans toutes les directions et à des distances plus ou moins longues (Dean 2004, Newton 2008). Alors que les migrateurs réguliers pourraient outrepasser une aire où une ressource serait abondante pour atteindre une destination prédéterminée, les migrateurs nomades pourraient s'y arrêter pour l'exploiter (Dingle 1996), ce qui rend leurs mouvements très irréguliers (Dean 2004).

## 1.2. Utilisation de l’habitat et de l’espace

Au courant de leur cycle annuel, les migrateurs aviaires rencontreront un large spectre de conditions environnementales, incluant différents types d’habitats, une disponibilité des ressources variable, des conditions météorologiques changeantes et des environnements sociaux hétérogènes (Newton 2008, Fuller 2012, Rappole 2013). Devant cette variabilité environnementale, les migrateurs devront donc sélectionner à chaque site un habitat approprié à leurs besoins selon les saisons, un processus qui s’effectuerait de façon hiérarchique (i.e. grande à fine échelle spatiale; Johnson 1980).

On définit l’utilisation de l’habitat comme la façon que les individus utilisent les composantes d’un environnement pour répondre à leurs besoins (Block and Brennan 1993, Jones 2001). Les facteurs qui déterminent comment les individus utilisent leurs habitats sont nombreux et varient considérablement durant leur cycle annuel (e.g. saison de reproduction ou période d’hivernage; Hildén 1965, Somveille et al. 2015, Pérez-Moreno et al. 2016). Évidemment, les habitats utilisés par différentes espèces varient énormément et les relations oiseaux-habitats intéressent naturalistes et les ornithologues depuis longtemps (Darwin 1897, Lack 1933, Cody 1985). Chez les individus d’une même espèce, le sexe (Marquiss and Newton 1982, Both et al. 2003, Sunde and Redpath 2006), l’âge ou l’expérience (Kerlinger and Lein 1986, Telleria et al. 2001), la saison (Nakazawa et al. 2004, McClure et al. 2013), l’heure du jour (Gillings et al. 2005, Conklin and Colwell 2007), les conditions météorologiques (Petit 1989, Lehikoinen et al. 2013) ou le niveau de spécialisation individuel (Bolnick et al. 2003) sont autant de facteurs pouvant influencer l’utilisation d’un habitat. L’utilisation de l’habitat peut être mesurée à différentes échelles spatiales telles que celle des domaines vitaux (échelle individuelle) ou de la distribution géographique (échelle populationnelle).

Chez les migrateurs aviaires, la saison de reproduction (été) requiert de trouver un site de nidification propice (e.g. où le risque de prédation est minimisé), un partenaire et des ressources alimentaires adaptées aux besoins des jeunes (Cody 1985, Rappole 2013). En période non-reproductive, l’accès à la nourriture, souvent plus limitée en hiver, et l’évitement de la prédation semblent être les critères principaux utilisés pour la sélection d’un habitat

(Bryant 1979, Brindock and Colwell 2011, Rappole 2013). Entre les sites de reproduction et d'hivernage, les habitats peuvent ainsi différer énormément. Par exemple, le labbe à longue queue *Stercorarius longicaudus*, comme plusieurs espèces d'oiseaux marins, passent la majeure partie de leur cycle annuel en mer, et ne reviennent sur terre que pour se reproduire (Wiley and Lee 1998, Schreiber and Burger 2001, Cherel et al. 2007). Le type d'habitat ou l'abondance des ressources peuvent aussi être des facteurs déterminants du choix de sites à d'autres périodes du cycle annuel telles que la migration ou la mue (Buler et al. 2007, Lewis et al. 2010, Dieval et al. 2011).

### 1.3. Fidélité et dispersion

Les mouvements individuels tels que la dispersion (*i.e.* mouvement d'un individu de son site natal ou de reproduction précédente à un nouveau site de reproduction l'année suivante; Greenwood 1980) et la philopatrie (retour d'un individu à son site natal ou à un site de reproduction précédent; Greenwood 1980), influencent les patrons de distribution ainsi que la taille et la structure génétique des populations (Rockwell and Cooke 1977, Greenwood and Harvey 1982). Beaucoup d'espèces d'oiseaux et de mammifères sont fidèles à leur site de reproduction ou à leur site natal (*e.g.* sauvagine : Anderson et al. 1992; mammifères marins : Pomeroy et al. 2000, rongeurs : Arnaud et al. 2012, ongulés : Tremblay et al. 2007). Cette régularité spatiale et temporelle confère des avantages tels que la familiarité avec le site (*i.e.* l'habitat, la nourriture, les congénères, les prédateurs; Greenwood 1980, Weatherhead et Forbes 1994, Part 1995) ou l'évitement des coûts de dispersion (*i.e.* coûts énergétiques, stress, vulnérabilité à la prédation, etc.; Bengtsson 1978, Greenwood 1980, Bonte et al. 2012), favorisant ainsi l'augmentation du succès reproducteur (Greenwood 1980, Part 1991, Belichon et al. 1996) et la survie (Brown et al. 2008, Johnson and Walters 2008). La fidélité au site chez les migrateurs de longues distances est d'autant plus remarquable vu la grande distance parcourue entre les sites d'hivernage et de reproduction.

Contrairement à la forte fidélité des migrateurs aviaires à leur site de reproduction (*e.g.* Gauthier 1990, Sedgwick 2004, Fowler 2005), la fidélité à leurs aires d'hivernage serait généralement moins prononcée (*e.g.* Mehl et al. 2004; révisé dans Newton 2008). Comme pour la migration, la fidélité à un site est généralement favorisée lorsque les niveaux de ressources sont prévisibles dans l'espace et dans le temps, mais n'est pas optimale lorsque les ressources sont imprévisibles (Newton 2006a, 2008). La priorité durant la saison non-reproductive étant essentiellement la survie, les individus seraient plus libres de leurs mouvements et bénéficieraient d'une plus grande flexibilité dans leur choix d'habitats durant cette période que lorsque leurs activités sont centrées autour d'un nid durant la période de reproduction (Newton 2008).

### 1.4. Effets reportés

Les conditions rencontrées durant toutes les phases du cycle annuel peuvent avoir des conséquences importantes sur les traits d'histoires de vie ou la dynamique de population des espèces (Metcalfe and Monaghan 2001, Norris and Taylor 2006, Harrison et al. 2011). De plus, les décisions de mouvements, de fidélité ou de dispersion prises durant une saison donnée peuvent aussi avoir des répercussions à d'autres périodes du cycle annuel d'un individu. Les effets reportés sont définis comme des évènements qui se produisent à une saison mais qui influencent le succès individuel à une saison subséquente (Fretwell 1972, Marra et al. 1998, Norris 2005). Le succès reproducteur peut ainsi être affecté par la qualité des ressources alimentaires (Sorensen et al. 2009), leur abondance (Davis et al. 2005, Penteriani et al. 2013, Cooper et al. 2015), ou par la qualité de l'habitat (Marra et al. 1998, Norris et al. 2004, Inger et al. 2010) pendant la saison non-reproductive précédente. Par exemple, chez la paruline flamboyante *Setophaga ruticilla*, une espèce qui hiverne dans les tropiques mais se reproduit en milieu tempéré, les individus hivernant dans un habitat de moindre qualité s'établissent plus tardivement sur leur site de reproduction que les individus hivernant dans les habitats de meilleure qualité. De plus, le nombre de jeunes produits qui atteignaient l'envol était plus faible chez ces individus et ces jeunes quittaient aussi le nid plus tardivement (Marra et al. 1998). Cette cascade d'évènements montre que la qualité de l'habitat hivernal a des effets sur le succès reproducteur subséquent, même si le site d'hivernage se trouve à des milliers de kilomètres du site de reproduction. Il est donc important de comprendre toutes les périodes du cycle annuel d'un migrateur et comment elles interagissent dans le temps et l’espace, car les décisions prises hors de la saison de reproduction peuvent avoir des conséquences importantes sur les saisons subséquentes.

## 1.5. Écologie hivernale chez les migrateurs aviaires : la mal connue

Quoique la période non-reproductive (hivernage et migration) compose la majorité du cycle annuel d’un migrateur, il s’avère qu’assez peu d’études se sont penchées sur l’écologie et la fidélité hivernale des migrateurs (Marra et al. 2015). En effet, une brève analyse sur le moteur de recherche *Web of sciences* (couvrant la période de1902 au 5 mai 2017) nous permet d’observer que le nombre d’articles faisant référence aux habitats de reproduction (14 668) sont beaucoup plus nombreux que ceux sur la saison non-reproductive (5 029). Ce résultat pourrait être expliqué par le fait que les impacts individuels et populationnels des évènements qui se produisent en hiver sont moins directs que ceux qui se produisent durant la saison de reproduction. Aussi, il est à noter que durant la période hivernale, les migrateurs peuvent se trouver dans des endroits éloignés, peu accessibles pour les chercheurs, ce qui peut représenter des défis logistiques importants. Toutefois, même si les habitats saisonniers sont souvent géographiquement et écologiquement éloignés, le fait que ces différentes périodes soient liées entre elles par les effets reportés rend primordiale l’étude de l’écologie hivernale d’un migrateur pour comprendre l’espèce dans son ensemble.

## 1.6. Techniques d’étude des espèces migratrices

Établir les liens entre les différentes parties du cycle annuel d’un migrateur est essentiel pour en comprendre son écologie. Cependant, la complexité logistique du suivi des migrateurs, notamment chez les espèces nomades dont les mouvements sont imprévisibles, ou les espèces hivernant dans les endroits isolés et peu accessibles, complique les études. De plus, les prédateurs au sommet des réseaux trophiques sont souvent extrêmement mobiles et peuvent se déplacer sur de longues distances (Akesson and Weimerskirch 2005, Phillips et al. 2007, Egevang et al. 2010, Therrien et al. 2014b). Toutefois, les trois dernières décennies ont vu naître des techniques permettant de surmonter en partie ces obstacles. Entre autres, la télémétrie satellite est maintenant communément utilisée pour suivre les déplacements à fine échelle des oiseaux de grande taille, ce qui a permis de découvrir des patrons, routes et haltes migratoires, en plus de sites d'hivernage et d'alimentation jusqu'alors inconnus chez une multitude d'espèces (e.g. Jouventin et Weimerskirch 1990, Berthold et al. 2001, Ueta et al. 2002, Mansfield et al. 2009).

Les analyses d'isotopes stables sont aussi devenues un outil fort utile pour documenter la distribution géographique (Hobson 1999) ou les régimes alimentaires d'espèces hautement mobiles (Hobson and Wassenaar 2008, Inger and Bearhop 2008, Hobson 2011). Cette technique, basée sur la variation des ratios d'isotopes présents à l'état naturel (e.g. hydrogène $\delta D$, carbone $\delta^{13}C$, azote $\delta^{15}N$) et emmagasinés dans les tissus d'un animal, permet de différencier la zone géographique d'origine ou les sources de nourriture ingérées (e.g. types de proies). Les tissus métaboliquement inertes, comme les plumes, «emprisonnent» l'information isotopique au moment où ce tissu est formé et la conserve indéfiniment (Hobson 1999). Par contre, les tissus métaboliquement actifs conservent l'information isotopique sur différentes échelles de temps, soit de quelques jours (foie, plasma sanguin) à quelques semaines (muscle, sang) ou plusieurs mois (collagène; Newton 2008). Il est ainsi possible de cibler la ressource la plus probable utilisée par les individus au moment de la synthèse de ces différents tissus. Ainsi, comme pour la télémétrie satellite, les analyses d'isotopes stables aident à faire la lumière sur certaines périodes de l'année où les migrateurs aviaires sont moins accessibles, et permettent de faire des liens entre les périodes de reproduction et d'hivernage (Chamberlain et al. 1997, Hobson and Wassenaar 1997, Marra et al. 1998). Cette technique a déjà été appliquée avec succès chez plusieurs espèces de prédateurs arctiques. Par exemple, Roth (2002) et Tarroux et al. (2012) ont pu déterminer que le milieu marin contribuait de façon significative à l'alimentation d'une espèce terrestre, le renard arctique, en hiver.

## 1.7. Le harfang des neiges *Bubo scandiacus*

### *1.7.1. Écologie de la reproduction*

En plus d'être un animal emblématique et indicateur de la santé des écosystèmes arctiques (Holt et al. 2015), le harfang des neiges est un prédateur migrateur dont les migrations irruptives hivernales et le comportement nomade estival sont connus depuis longtemps (Sclater and Salvin 1877, Gross 1927, 1931, 1947, Kerlinger et al. 1985, Therrien et al. 2014b) et médiatisés (e.g. Holland 2013, Kaufman 2013, Mactavish 2013, Leung 2014). Le harfang a une distribution circumpolaire (Holt et al. 2015) et on en connaît une seule espèce (Marthinsen et al. 2009). Durant la saison de reproduction en été, le harfang niche dans la toundra arctique, au nord de la limite des arbres, où il se nourrit presqu'exclusivement de lemmings et de campagnols (Gilg et al. 2006, Therrien et al. 2014a, Holt et al. 2015). Ces petits mammifères sont bien connus pour leurs fluctuations d'abondance qui suivent habituellement des cycles de 3-5 ans dans plusieurs régions de l'Arctique (Elton 1924, Chitty 1950, Gruyer et al. 2008, Krebs 2011). En Amérique du Nord et en Eurasie, les cycles de populations de rongeurs peuvent être synchrones jusqu'à quelques centaines de kilomètres, mais rarement à des échelles plus grandes que 1000 km (Erlinge et al. 1999, Angerbjörn et al. 2001, Predavec et al. 2001, Krebs et al. 2002).

Considéré comme un spécialiste de petits mammifères durant la saison de reproduction, le harfang des neiges est habituellement présent à un site de reproduction seulement durant les années de forte abondance de lemmings, et leur succès reproducteur est hautement dépendant de l'abondance de ces proies (Gauthier et al. 2004, Gilg et al. 2006, Therrien et al. 2014a, Therrien et al. 2014b). De plus, la distance qu'ils peuvent parcourir entre deux sites consécutifs de reproduction (725 km en moyenne; *breeding dispersal* en anglais) est impressionnante (Therrien et al. 2014b) et démontre une absence de fidélité aux sites de reproduction. Cette dispersion extrême est expliquée par la fluctuation et l'imprévisibilité des ressources sur lesquelles le harfang se spécialise durant la saison de reproduction. Contrairement à la plupart des autres espèces aviaires et même des autres strigidés, le harfang peut pondre jusqu'à 14 œufs (moyenne ± ÉT: 7.0 ± 2.1 oeufs; Potapov and Sale 2012) durant les étés de pics de petits mammifères, ce qui nécessite un apport élevé en biomasse de proies (Holt et al. 2015). Le harfang est un prédateur important dans le réseau trophique arctique et peut jouer un rôle clé dans la régulation des populations de petits mammifères (Gilg et al. 2003, Gilg et al. 2006, Therrien et al. 2014a).

### *1.7.2. Écologie hivernale*

Durant l'hiver en Amérique du Nord, on peut retrouver le harfang des neiges à travers tout le Canada et le nord des États-Unis, et différentes tactiques hivernales ont été observées.

Tout d'abord, étant une espèce de milieux ouverts, le harfang est un migrateur régulier des Prairies et Grandes Plaines centrales Nord-Américaines (Boxall and Lein 1982b, Kerlinger et al. 1985, Holt et al. 2015). Dans ces grandes étendues, similaires à la toundra en termes de végétation et d'abondance de proies (Boxall and Lein 1982b, Holt et al. 2015), les harfangs sont présents toutes les années quoique leur abondance peut varier (Kerlinger et al. 1985).

Le harfang est aussi bien connu pour ses irruptions hivernales. Ces migrations massives sont observées le plus souvent aux 3-5 ans (moyenne ± ÉT = 3.9 ± 0.13; Newton 2002) au sud du Canada et au nord des États-Unis, se produisant principalement dans l'est et l'extrême ouest du continent. Il a longtemps été considéré que les harfangs migraient massivement au sud pour fuir les zones arctiques où les proies étaient devenues rares, et donc que les irruptions hivernales de harfangs étaient causées par un manque de nourriture plus au nord (Shelford 1945, Chitty 1950, Lack 1954, Newton 1970). Des migrations irruptives similaires ont d'ailleurs été documentées chez trois espèces de chouettes boréales hivernant dans l'est de l'Amérique du Nord (Cheveau et al. 2004). Cependant, les résultats d'études plus récentes tendraient plutôt à supporter une hypothèse alternative suggérant qu'à l'inverse une grande production de jeunes durant les saisons de reproduction où les petits mammifères sont très abondants serait à l'origine des irruptions hivernales de harfangs (Gross 1947, Fuller et al. 2003, Morrissette et al. 2010, Therrien et al. 2011b, Therrien et al. 2014b). Le fait que durant ces irruptions une prédominance de juvéniles soit observée (Smith 1997) supporterait cette hypothèse. Toutefois, aucune étude n’a testé ces hypothèses alternatives en lien avec l’abondance de la nourriture dans l’Arctique.

La toundra arctique est aussi un habitat hivernal pour le harfang des neiges (Gessaman 1972, 1978, Fuller et al. 2003, Therrien et al. 2011b, Potapov and Sale 2012, Holt et al. 2015). Cette espèce est bien adaptée aux nuits polaires ainsi qu’aux conditions rigoureuses de cette région (Gessaman 1972, 1978), ce qui leur permet d’occuper une niche hivernale généralement peu utilisée par d’autres espèces prédatrices (Sittler 1995, Gilchrist and Robertson 2000, Burnham and Newton 2011, Lai et al. 2016). Dans cet environnement nordique, le harfang peut utiliser à la fois le milieu terrestre et le milieu marin englacé. L’utilisation du milieu marin est connue des peuples nordiques depuis longtemps (Potapov and Sale 2012, Holt et al. 2015) et a déjà été rapportée anecdotiquement dans la littérature scientifique (Irving et al. 1970, McRoy et al. 1971, Gilchrist and Robertson 2000, Robertson and Gilchrist 2003). Toutefois, il a seulement récemment été montré par suivis satellitaires que cette utilisation pouvait être très importante pour les individus (jusqu’à 101 jours consécutifs sur les glaces au nord du Québec durant l’hiver ; Therrien et al. 2011b). À l’inverse des résultats de Therrien et al. (2011b), des suivis satellitaires en Norvège, en Russie de l’est et en Alaska/Yukon ont plutôt révélé une faible utilisation de la glace de mer dans ces régions (Fuller et al. 2003, Jacobsen et al. 2009, Doyle et al. 2017).

### *1.7.3. Mouvements migratoires hivernaux*

Ces résultats démontrent donc une grande variabilité spatiale, inter-annuelle et possiblement inter-individuelle dans les patrons de migration du harfang. Bien que les variations spatiale et temporelle de la nourriture, et en particulier des lemmings, la proie principale des harfangs, puissent être impliquées, les facteurs qui pourraient expliquer cette variabilité dans les patrons de mouvement demeurent largement inexplorés.

Durant la saison non-reproductive, le régime alimentaire du harfang est plus généraliste et diversifié qu’en été, quoique les petits mammifères demeurent les proies principales (Keith 1963, Boxall and Lein 1982a, Detienne et al. 2008). Les harfangs hivernant dans le milieu marin pour une période prolongée pourraient se nourrir d'oiseaux marins (Robertson and Gilchrist 2003). Tel que démontré par Therrien et al. (2011b), les harfangs ayant fait une utilisation extensive de la glace de mer se trouvaient à proximité de polynies, qui sont des trouées d'eau libre dans les glaces de mer créées par les courants marins et la topographie (Barber and Massom 2007). Ces ouvertures dans les glaces sont essentielles dans le paysage arctique car elles offrent des fenêtres d'alimentation pour de nombreuses espèces durant la saison hivernale (Stirling 1997, Gilchrist and Robertson 2000, Mallory and Gilchrist 2005, Heide-Jorgensen et al. 2013). Elles accueillent notamment des concentrations de canards de mer, qui constitueraient les proies potentielles des harfangs à ces sites (Gilchrist et Robertson 2000, Robertson et Gilchrist 2003). Pour les harfangs hivernant en milieu côtier, la disponibilité de ressources à la fois marines et terrestres permettrait une alimentation plus diversifiée aussi, selon la disponibilité (Holt et al. 2015).

Ainsi, durant la période non-reproductive, les harfangs étalent une diversité déconcertante de tactiques d'hivernage. Contrairement à la saison de reproduction, on ignore si les harfangs démontrent une fidélité au site d'hivernage car nos connaissances sur leurs mouvements et patrons d'utilisation de l'espace durant cette période sont très limitées.

## 1.8. Contexte et objectifs de la thèse

Depuis 1989, un suivi écologique exhaustif et longitudinal a été graduellement mis en place à l'Île Bylot, NU (73°08 N 80°00 O), dans le but de mieux comprendre l'écosystème arctique, notamment la dynamique de population de plusieurs espèces, les interactions trophiques et l'effet des changements climatiques sur ces processus. Ainsi, depuis 1993, la population de harfangs nicheurs à l'Île Bylot est suivie, tout comme les populations fluctuantes de leurs proies de prédilection, les lemmings (Fig. 1.1). De plus, en 2007, 12 émetteurs satellites ont été posés sur des femelles nichant sur l'Île Bylot permettant ainsi de suivre pour la première fois les déplacements de harfangs des neiges ayant niché dans le Haut Arctique sur plusieurs années. Une première analyse de ces données a permis de décrire les patrons de mouvements et la phénologie pré-reproduction (Therrien et al. 2014b, Therrien et al. 2015), d'évaluer les distances de dispersion de reproduction (Therrien et al. 2014b), et de découvrir des patrons d'utilisation de l'habitat hivernal jusqu'alors pratiquement inconnus (Therrien et al. 2011b). Ces derniers résultats en particulier ont généré toute une série de nouvelles questions sur les tactiques d'hivernage, de déplacements et de sélection d'habitats de ce prédateur au comportement migratoire unique.

L'objectif général de cette thèse est donc d'améliorer nos connaissances sur l'écologie des espèces qui démontrent des comportements migratoires imprévisibles (e.g. nomade, irruptif), notamment en se penchant sur les patrons de déplacements, l'utilisation de l'espace et les facteurs qui les affectent, et en particulier pendant la saison non-reproductive. Pour se faire, nous avons utilisé le harfang des neiges comme espèce modèle. Plus précisément, les objectifs visent à décrire la variabilité individuelle de leurs mouvements annuels, de leur utilisation de l'habitat hivernal et de leur régime alimentaire, grâce à une approche intégrant plusieurs méthodes d'analyses complémentaires. Cette thèse se divise en 4 chapitres.

Le chapitre 2 a tout d'abord pour objectif de décrire les trajets migratoires et différents paramètres de l'utilisation de l'espace et de l'habitat des harfangs nichant dans l'est du Canada à l'aide de suivis satellitaires. Il vise aussi à évaluer leur fidélité interannuelle aux sites et aux habitats d'hivernage. Finalement, ce chapitre examine l'effet de conditions environnementales comme la couverture de neige ou l'abondance de proies (i.e. lemmings) sur les divers paramètres de l'utilisation de l'espace et de l'habitat.

Le 3$^{e}$ chapitre examine l'influence de l'abondance de proies (i.e. lemmings) mesurées pendant l'été dans l'Arctique sur les irruptions périodiques de harfangs aux latitudes tempérées en hiver à l'aide de données longitudinales de science citoyenne (le Décompte des oiseaux de Noël-*Christmas Bird Count*). Pour ce faire, les deux hypothèses alternatives décrites plus haut, soit l'hypothèse du *manque de nourriture* et celle du *succès reproducteur*, ont été examinées pour expliquer le phénomène des irruptions hivernales.

Suite à la mise en évidence d'une forte utilisation du milieu marin en hiver au chapitre 2, l'objectif du chapitre 4 était de déterminer la contribution de ce milieu au régime alimentaire hivernal des harfangs des neiges. Compte tenu que les oiseaux qui passent l'hiver en Arctique ne peuvent être capturés qu'en été, nous avons premièrement évalué si les valeurs isotopiques ($\delta^{13}$C et $\delta^{15}$N) de différents types de plumes récoltées sur des oiseaux en été pouvaient nous renseigner sur la contribution des milieux marin vs terrestre à leur régime alimentaire hivernal. Nous avons aussi déterminé les facteurs de discrimination isotopiques pour les plumes de harfangs sur des individus en captivité, une information essentielle pour reconstituer le régime alimentaire à partir d'isotopes stables.

Dans le 5$^{e}$ chapitre, l'objectif était d'évaluer si la variabilité interindividuelle de la contribution des ressources marines à l'alimentation estimée par l'analyse isotopique des plumes au chapitre 4 pouvait être expliquée par l'utilisation de l'habitat en hiver. Pour se faire, ce chapitre combine les données spatio-temporelles hivernales d'individus suivis par télémétrie satellitaire¸ aux informations provenant des signatures isotopiques de plumes récoltées sur ces mêmes individus au moment de la capture. Ce chapitre examine aussi si l'utilisation de l'habitat marin en hiver par les harfangs peut avoir des effets reportés sur les performances reproductives subséquentes.

Finalement, le chapitre 6 discute de la portée des résultats présentés dans cette thèse, notamment dans les domaines de l'écologie hivernale et de la migration, et expose des perspectives de recherches potentielles découlant de ces travaux.

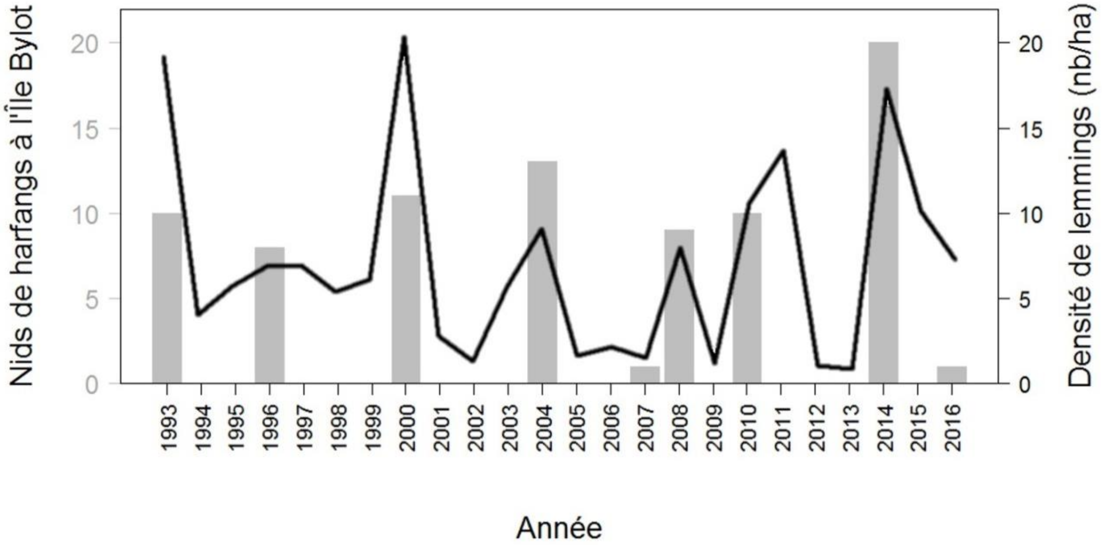

**Figure 1.1**. Variations dans les nombre de nids de harfangs répertoriés et les densités de lemmings (lemmings bruns et lemmings à colliers) à l'île Bylot dans le secteur du camp 1 et de la rivière Oasis entre 1993 et 2016.

# CHAPITRE 2: Wintering space use and site fidelity in a nomadic species, the snowy owl

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## 2.1. Résumé

Les espèces migratrices peuvent exploiter divers habitats sur de vastes étendues géographiques et adopter différents patrons d'utilisation de l'espace et de l'habitat durant leur cycle annuel. Chez les espèces nomades, les déterminants de l'utilisation de l'habitat en dehors de la saison de reproduction sont peu connus à cause de leurs patrons de mouvements souvent imprévisibles. Dans ce chapitre, nous analysons la variabilité dans l'utilisation de l'espace et de l'habitat par une espèce hautement nomade, le harfang des neiges. Grâce au suivi de 31 oiseaux marqués d'émetteurs satellites entre 2007 et 2016, nous avons 1) étudié comment les patrons d'utilisation de l'espace en hiver varient selon l'environnement (marin vs terrestre), la zone latitudinale (Arctique vs tempérée), les conditions de neige locales et les densités de lemmings et 2) évalué la fidélité à l'habitat hivernal et au site. Nos résultats ont confirmé une grande variabilité interindividuelle dans les patrons d'utilisation de l'habitat par les harfangs en hiver. Les aires d'utilisation fréquentes étaient concentrées en Arctique et dans les milieux marins et côtiers. Les harfangs hivernant dans l'environnement marin se sont déplacés sur de plus grandes distances durant l'hiver, avaient de plus grands domaines vitaux et ceux-ci étaient divisés en plusieurs petites zones comparativement aux individus hivernant dans l'environnement terrestre. Lorsque les densités de lemmings étaient élevées, la taille des domaines vitaux diminuait et l'utilisation de l'environnement marin augmentait en hiver. Aussi, un couvert nival relativement épais en automne menait à une installation plus tardive des harfangs sur leurs aires d'hivernage. Contrairement aux prédictions, les harfangs avaient tendance à utiliser davantage l'environnement marin quand l'épaisseur du couvert nival était mince. Les harfangs étaient très constants dans leur utilisation d'un environnement donné et d'une zone latitudinale spécifique en hiver, mais démontraient une certaine flexibilité dans leurs patrons d'utilisation de l'espace et une fidélité au site modeste. La constance des harfangs dans l'utilisation de leurs habitats hivernaux peut fournir des avantages en termes d'expérience, mais leur flexibilité et leur mobilité leur permettraient de surmonter certains défis liés aux conditions environnementales changeantes à plus fine échelle spatiale.

Mots clés: *Bubo scandiacus*, nomadisme, habitat d'hivernage, utilisation de l'espace, fidélité au site, domaine vital, distance de dispersion, couvert nival, densité de lemmings.

### 2.2. Summary

Migratory species can exploit many habitats over vast geographic areas and adopt various patterns of space and habitat use throughout their annual cycle. In nomadic species, determinants of habitat use during the non-breeding season are poorly known due to the unpredictability of their movement patterns. Here, we analysed variability in wintering space and habitat use by a highly nomadic species, the snowy owl. Using 31 females tracked by satellite telemetry between 2007 and 2016, we 1) assessed how space use patterns in winter varied according to the environment (marine vs terrestrial), latitudinal zone (Arctic vs temperate), local snow conditions and lemming densities and 2) investigated winter habitat and site fidelity. Our results confirmed a high inter-individual variation in patterns of habitat use by wintering snowy owls. Highly-used areas were concentrated in the Arctic and in the marine and coastal environments. Owls wintering in the marine environment travelled over longer distances during the winter, had larger home ranges and these were divided in more smaller zones than individuals in terrestrial environments. Wintering home range sizes decreased with high winter lemming densities, use of the marine environment increased following high summer lemming densities, and a relatively thick snow cover in autumn led to later settlement on the wintering ground. Contrary to expectations, snowy owls tended to make greater use of the marine environment when snow cover was thin. Snowy owls were highly consistent in their use of a given wintering environment and a specific latitudinal zone between years, but demonstrated flexibility in their space use and a modest site fidelity. The snowy owls' consistency in wintering habitat use may provide them with advantages in terms of experience but their mobility and flexibility may help them to cope with changing environmental conditions by adapting at fine spatial scale.

Keywords: *Bubo scandiacus*, nomadism, wintering habitat, space use, site fidelity, home range, dispersal distance, snow cover, lemming density.

## 2.3. Introduction

Throughout their annual cycle, migratory species can exploit many habitats over vast geographic areas that may be separated by thousands of kilometers. In doing so, individuals adopt various tactics of movement (Newton 2008, Phillips et al. 2009), foraging (e.g. McClellan et al. 2010) and habitat use (Tranquilla et al. 2014). Many aspects of the wintering ecology can have important carry-over effects in subsequent seasons (Metcalfe and Monaghan 2001, Norris and Taylor 2006, Harrison et al. 2011) but linking events occurring on the wintering ground to the subsequent reproductive period is difficult in most long-distance migrants (Marra et al. 2015).

Habitat use, defined as the way individuals use environmental components to meet their life history needs (Block and Brennan 1993, Jones 2001), can be influenced by multiple factors during the winter. In northern regions, variation in food abundance in combination with environmental factors affecting food accessibility, such as snow cover, can ultimately determine the abundance of wintering birds in a given region (Greenwood and Baillie 1991, Golawski and Kasprzykowski 2010). Despite such environmental variability, some migrating species will show relatively high fidelity to a specific wintering site because familiarity with a given site may improve foraging efficiency, predator avoidance or maintain a dominant status, which ultimately could increase individual fitness (Cresswell 2014, Blackburn and Cresswell 2016, Latta et al. 2016). Site fidelity is generally favoured when resource levels are predictable in space and time (Newton 2006a, 2008).

Nomadic species show highly variable and unpredictable movements, both within and between years, often in response to large-scale fluctuations in food availability (Swingland and Greenwood 1984, Newton 2008, Rappole 2013). In those species, determinants of habitat use during the non-breeding season is poorly known due to the unpredictability of their migratory patterns (Swingland and Greenwood 1984). The snowy owl is one of the most nomadic species of all birds. Extreme breeding dispersal has been documented in snowy owls during the summer (Therrien et al. 2014b) and in winter they can exhibit a bewildering diversity in movement and habitat use. For instance, although snowy owls are regular winterers in the Canadian Prairies and American Great Plains, they also show periodic irruptions throughout the temperate regions of North America (Kerlinger et al. 1985, Kerlinger and Lein 1988, Holt et al. 2015). Many adult snowy owls also remain in the Arctic throughout the winter and can make extensive use of the marine environment (Therrien et al. 2011b, Robillard et al. 2017). However, very little is known about individual consistency and the effect of environmental factors on patterns of space and habitat use during the winter in such nomadic species.

During the summer, snowy owls specialize on lemmings, which show high temporal and spatial variability in abundance (Angerbjörn et al. 2001, Krebs et al. 2002, Gruyer et al. 2008). In winter, they broaden up their diet and become more generalists. In terrestrial environment, small mammals remain their main prey items (Boxall and Lein 1982a, Detienne et al. 2008) but owls wintering in coastal and marine environments can rely on other prey such as water birds (Campbell and Maccoll 1978, Smith 1997, Robertson and Gilchrist 2003, Robillard et al. 2017). Snowy owls wintering in different regions (e.g. Arctic vs temperate areas) and feeding in different habitats can face highly contrasted environmental conditions. Individuals wintering in temperate terrestrial environments are likely to benefit from a more stable and diverse prey base than those wintering in the arctic tundra where small mammal populations show strong fluctuations in density (Boxall and Lein 1982a, Detienne et al. 2008, Fauteux et al. 2015b). In contrast, those wintering in the arctic marine environment concentrate their foraging activities in areas of open water in the sea ice (e.g. polynyas) where seabirds can be found at high density (Gilchrist and Robertson 2000, Therrien et al. 2011b). Although polynyas can be dynamic at a small spatial scale, at a larger scale they are generally recurrent at the same locations and periods each year due to local oceanic and atmospheric conditions (Smith and Rigby 1981, Barber and Massom 2007). Therefore, we could expect prey base to be more predictable from year to year in the marine environment than in the tundra.

We used satellite telemetry to describe the behavior of wintering snowy owls breeding in eastern Canada and we examined factors affecting it. In particular, we 1) assessed how space use patterns in winter varied according to the environment (marine vs terrestrial), latitudinal zone (Arctic vs temperate), local snow conditions and lemming densities and 2) investigated winter habitat and site fidelity. We predicted that snowy owls would show greater fidelity to wintering than to breeding sites due to the relatively higher predictability of food resources in the former. Due to differences in migration length, we also expected individuals wintering in the Arctic to settle earlier on their wintering site in autumn and to depart later in spring than individuals wintering in southern temperate regions. Moreover, in winters with reduced food availability in the terrestrial environment (low small mammal abundance or thick snow), we expected a greater use of the marine habitat.

## 2.4. Material and methods

### *2.4.1. Study area and snowy owl captures*

Between 2007 and 2014, 31 snowy owls were captured at three different sites in the eastern Canadian Arctic: Bylot Island, Nunavut (73°08N 80°00W; High Arctic) in 2007 (n=12) and 2014 (n=10), Mary River, Nunavut (71°10N 79°21W; High Arctic) in 2011 (n=1) and Deception Bay, Nunavik, QC (62°02N 74°49W; Low Arctic) in 2013 (n=8; see Fig. 2.1 for study site locations). Landscapes of Bylot Island and Mary River are similar and dominated by broad river valleys and gently rolling hills with a mosaic of mesic and wet habitats with lush vegetation (see Gauthier et al. 2011 for a detailed description of Bylot Island's study area); these sites belong to the Arctic bioclimate subzone C (Walker et al. 2005). Deception Bay is dominated by mesic habitats and rocky terrains, with small patches of wet habitats scattered in the landscape and lush vegetation along the river banks; the site corresponds to the Arctic bioclimate subzone D. On Bylot Island, nest search of snowy owls was carried out in suitable nesting habitat over a ~450 km$^2$ area of the south plain on foot or with the help of a helicopter. At Deception Bay and Mary River, nest search was carried out along the roads in the vicinity of the mining facilities present at both sites. Captures of snowy owls were performed with bow-nets positioned over the nest or with a bal-chatri between 29 June and 4 August. Almost all of our marked individuals are females (30 out of 31) because males do not brood their chicks, which complicates their capture.

### *2.4.2. Locations of radio-marked individuals*

Snowy owls were fitted with ARGOS satellite transmitters (Microwave telemetry, USA, PTT-100, n=14; North Star Science and Technology, LLC, USA, PTT-30G, n=17). Transmitters were installed on the owls as a backpack using a harness made of Teflon strips and weighed 40g (i.e. 1.8% of the birds' body mass). It has been shown that these transmitters do not significantly impact survival or reproductive performance of owls (Therrien et al. 2012). Between 2007 and 2010, locations were obtained over a 4-6h period at ~2-3d intervals, from mid-June to November and ~5d intervals from December to mid-June. Between 2011 and 2016, locations were obtained more often during the non-breeding period (i.e. at ~2-3d intervals from December to mid-June and ~5d intervals from mid-June to November). Locations were assigned a class corresponding to their estimated precision, which followed a normal distribution with a standard deviation of <1500m, <500m and <250m, respectively, for the classes we retained (i.e. 1, 2 and 3; CLS 2016). Locations with a lower estimated precision (i.e. classes 0, A, B, Z) were excluded.

As multiple locations were recorded for each transmission period, positions were averaged to a single mean daily coordinate to avoid non-independence of spatial data. Distances between consecutive daily locations were estimated using the *as.ltraj* function in the adehabitatLT package (Calenge 2006) in R version 3.2.3 (R Development Core Team 2015) and divided by the number of days between locations to evaluate the daily movement of individuals. The distance from each daily location to the nearest coast was estimated by the Env-Data annotation system in Movebank (Dodge et al. 2013), with positive values when birds were on land and negative values when they were at sea.

### *2.4.3. Environmental covariates*

Small mammal abundance data on Bylot Island was obtained for both summer and winter periods between 2007-2016, as this is the only site in eastern Arctic of North America where it was measured annually. Summer densities of lemmings were estimated using live-trapping and winter abundance of lemmings was measured by sampling remnants of winter nests (see

Annexe S1.1 for details). We considered summer abundance of lemmings because we believed that it could affect owl behaviour in winter through carry-over effects. For snow depth, we obtained data through the Movebank Env-Data system (Dodge et al. 2013) using the NCEP NARR dataset which interpolates the snow depth at small spatial resolution (i.e. 0.3deg = 32km; see Annexe S1.1 for details). A snow depth was associated with each owl location and averaged over specific time-frames (e.g. autumn) but was ignored for owl locations over sea ice because availability of prey in this habitat (primarily seabirds in open water) should not be affected by snow depth.

### *2.4.4. Data analysis*

#### 2.4.4.1. Determination of breeding and wintering periods

Annual settlement and departure dates on the breeding and wintering areas were determined for each individual. The duration of the breeding or wintering period of each individual owl was defined as the difference between its departure and settlement dates. The autumn period corresponded to the period between the departure from the breeding area and the settlement in the wintering area. Throughout the text, we make a distinction between the non-breeding season (i.e. the entire period outside the breeding season, which includes migratory periods in autumn and spring) and the wintering period as defined above. Details of the methods used to estimate settlement and departure dates are presented in Annexe S1.2.

#### 2.4.4.2. Determination of habitat categories

To analyse space and habitat use, each individual location was assigned to one of the two main environments used by owls based on its distance from the closest marine coast: Land (≥ 0 km from coast), and Sea (< 0 km from coast; negative distance values were assigned when birds were at sea, see above). We calculated the proportion of time spent by individuals in each of these environments during the wintering period and assigned birds as being terrestrial when more than 50% of locations were on land (referred to as inland) or marine when more than 50% of locations were at sea. Each bird was also categorized according to a wintering latitudinal zone as Arctic or temperate, depending if they wintered above or below the tree line.

### 2.4.4.3. Determination of space use parameters

Both home range (95% utilization) and core area size (50% utilization) were estimated using the Brownian bridge kernel method with the function kernellbb of the package adehabitatHR (Calenge 2006) in R (R Development Core Team 2015) for each individual, year and period (breeding and wintering). This method takes into account the path travelled between successive locations and not only the static positions recorded (Bullard 1991, Calenge 2006, Horne et al. 2007). The Brownian bridge kernel method requires time-specific locations, a defined distribution of location errors (here assumed to be normally distributed with mean centered on the estimated location), a parameter related to the imprecision of the locations (i.e. the estimated error associated with location data; *Sig2*) and a Brownian motion variance parameter (σ2m; *Sig1*). This latter parameter is related to the tracked individual's mobility and can be estimated with the liker function in package adehabitatHR through maximum-likelihood (Calenge 2006, Horne et al. 2007) based on the *Sig2* parameter. Because this method characterizes individual space use very finely, we also extracted the number of distinct home ranges and core areas used by each individual in each season. Overlaps in home ranges and core areas between year *t* and year *t*-1 were calculated with the Intersect tool in ArcMap 10.2 (ESRI 2013).

Highly–used areas by wintering snowy owls were estimated with Kernel density estimation using mean daily locations for all birds tracked for at least one complete winter (n=21) with the Kernel density tool in the Spatial analyst toolbox of ArcMap 10.2 (ESRI 2013). This tool calculates a density from point features using a kernel function (ESRI 2013). The default search radius (bandwidth) was used as this approach relies on the spatial configuration and number of input points and corrects for spatial outliers, thereby selecting the relevant search radius while minimizing overestimation (ESRI 2013).

Centroids of all locations during the winter and breeding periods were calculated as mean latitude and longitude for each individual and year. Geodesic distances between centroids were measured in ArcMap 10.2 (ESRI 2013) and were used to estimate dispersal distance.

#### 2.4.4.4. Statistical analyses

To assess the effect of latitudinal zone, snow depth, lemming density and, when applicable, wintering environment, on the different wintering space use variables (i.e. marine habitat use, length of stay on a wintering site, distance travelled, winter dispersal distances, distance to the coast, number of core areas, home range and core area size), we used LMMs with bird ID as random effect to account for the multiple winters that an individual could be tracked. We used the same models (LMMs with bird ID as random effect) to analyse differences in annual dispersal distances (between consecutive breeding or wintering centroids), length of stay, home range and core area sizes between summer and winter and differences in migration distances in autumn and spring. For analyses of the marine environment use, defined as proportion of locations of an individual at sea, we used GLMMs with binomial family and bird ID as a random effect. The term *weights* was added to account for the total number of locations per winter and per individual. To meet normality requirements, dispersal distances, distances travelled, home range and core area size were log-transformed while length of stay on a wintering site, migratory distances between breeding and wintering areas and core area numbers were square-root transformed. All means are presented ± SD unless otherwise specified.

We used the package influence.ME (Nieuwenhuis et al. 2012) to investigate whether some individual data points could be over-influential on some parameter estimates. We identified one outlier (i.e. female J; Annexe S1.3) in the analysis linking the marine environment use with summer small mammal abundance based on the Cooks' distances (Cooks' *D* = 16.1; cut-off value = 0.24; Van der Meer et al. 2010), the percentile change between models including and excluding the ID (155%) and the *sigtest* function (which evaluates how an individual affects the significance of the fixed factors; Nieuwenhuis et al. 2012). This specific female spent 87% of her time in the marine environment in year 1 and 0% in year 2. We thus excluded this female in the relevant statistical analysis but nonetheless showed the data points on the graphs.

## 2.5. Results

### *2.5.1. Habitat use and distance travelled*

The 31 owls marked allowed us to track 42 complete wintering periods, 25 of which were spent predominantly inland (16 in the Arctic, 9 in temperate areas) and, 17 in the marine environment (15 in the Arctic, 2 in temperate areas; Annexes S1.3 and S.1.4). Among birds classified as marine, 80 ± 11 % (range 55 to 98%) of their locations in winter were at sea whereas for those classified as wintering in the terrestrial environment, 85 ± 17 % (range 54 to 100%) of their locations were inland. Highly-used areas were concentrated in the Arctic marine and coastal environments, especially in the Hudson strait (i.e. northern Nunavik and southern Baffin areas) and to a lesser extent in the American Midwest (i.e. North and South Dakota; Fig. 2.1).

Mean distance to the coast in winter ranged from -75 km to 1368 km (171 ± 454 km, n=42; negative distance values indicate birds at sea). Individuals wintering in the Great Plains were much furthest inland (distance to the coast: 1267 ± 75 km; n=6) compared to birds wintering inland in the Arctic or in temperate southeastern Canada (i.e. Newfoundland; 7 ± 14 km, n=19; Fig. 2.1). Individuals wintering in the marine environment were at similar distance from the coast in the Arctic (-31 ± 16 km, n=15) and in temperate areas (-45 ± 43 km, n=2; t-test: t=0.46, p=0.7).

Straight-line distances between centroids of breeding and wintering sites (autumn migration) were shorter for birds wintering in the Arctic (831 ± 504 km) than for birds wintering at temperate latitudes (2517 ± 787 km; $\beta = 21.7$; CI: [14.1; 29.2]) but not different for birds wintering in marine (1009 ± 511 km) or terrestrial environments (1451 ± 1132 km; $\beta = 0.7$; CI: [-7.7; 9.3]). On their wintering areas, mean distance travelled by individuals was greater in marine (2729 ± 1378 km) than in terrestrial environments (1190 ± 695 km) but not different between the Arctic (1817 ±1036 km) and temperate areas (1801 ± 1838 km; Table 2.1). Snow depth in winter and summer lemming densities on Bylot did not affect the distance travelled in winter but there was a trend for shorter distances travelled at high densities of lemmings in winter (Table 2.1; Fig. 2.2a).

Individuals that wintered outside the Great Plains were highly variable in their use of the marine environment (i.e. range: 0 – 98%; mean: 48.2 ± 33.5%; n=36). One female (M) spent up to 169 days at sea in the High Arctic and only 4 individuals were never located at sea during a given wintering season. Individuals made a greater use of the marine environment when snow depth on land was low but this relationship was driven by only two data points at very high snow density (Table 2.1, Fig. 2.2b). Use of the marine environment in winter also increased when lemming density in summer was high (Table 2.1, Fig. 2.2c).

### *2.5.2. Settlement and departure dates*

The average settlement and departure dates from the wintering ground were 16 November and 7 April, and from the breeding ground 27 May and 23 August, respectively. Settlement dates on the wintering grounds were on average earlier for birds wintering in terrestrial environment than those wintering in marine environment, and tended to be earlier for birds that wintered in the Arctic than for birds in temperate areas (Table 2.1; Fig. 2.3). Settlement on a wintering site also occurred later when snow on land was deep in autumn (Table 2.1; Fig. 2.2d). Inversely, arctic birds departed later from their wintering area than temperate ones and terrestrial winterers also tended to depart earlier than marine wintering birds (Tables 2.1; Fig. 2.3). Departure dates from wintering areas were not affected by snow depth or lemming density in winter.

Length of stay on the wintering ground for all individuals averaged 142 ± 32 days and was longer than the length of stay on the breeding site (86 ± 22 days; $\beta$=2.7, CI = 2.2, 3.2; n=98). Owls wintering at temperate latitudes tended to have shorter wintering periods than owls wintering in Arctic (Table 2.1), but neither the wintering environment, snow depth nor the lemming density significantly affected length of stay on wintering grounds.

### *2.5.3. Home range size*

The average winter home range size was 7.11 x $10^4$ $km^2$ (± 8.77 x $10^4$; n=42; Fig. 2.4). Home range sizes were greater in winter than summer (Summer = 2.02 ± 4.57 x$10^2$ $km^2$, β= 6.28, 95% CI = 5.71, 6.84, n=52). Home range size was greater for owls wintering in the marine environment (11.6 ± 9.0 x $10^4$ $km^2$, n=17) than inland (4.1 ± 7.4 x$10^4$, n=25) but did not vary among wintering latitudinal zones (Fig. 2.4) and was greater in winters of low lemming density (Table 2.1, Fig. 2.2e). The number of distinct home ranges within a given winter ranged from 1 to 5 (i.e. 1.9 ± 1.0; Annexe S1.5).

Similarly, the mean winter core area size was 9.4 x $10^3$ $km^2$ (± 13.5 x $10^3$; Fig. 2.4) and was also greater in marine habitats than inland as well as in winters of low lemming density (Table 2.1). Generally, multiple core areas were present in individual home ranges (4.6 ± 2.8 core areas per individual; range: 1-12). The number of core areas were greater in the marine (5.8 ± 2.3) than the terrestrial environment (3.8 ± 2.9) and also tended to be greater for birds wintering in the Arctic (5.1 ± 3.0) than in temperate regions (3.3 ± 2.0; Table 2.1). The number of core areas decreased with increasing lemming density in winter (Fig. 2.2f).

### *2.5.4. Fidelity*

Most individuals that were tracked for two consecutive years used the same wintering environment and latitudinal zone (16 out of 21 cases; Table 2.2). Two individuals switched from the marine to the terrestrial Arctic environment the following year whereas one individual switched from a terrestrial to a marine environment and back to a terrestrial environment in the third winter. Only one individual changed latitudinal zone in the following winter, from the Arctic to temperate latitudes.

The mean distance between centroids of wintering locations for individuals tracked in consecutive years was 389 km ± 624km (i.e. winter dispersal; range = 20 – 2731 km, n = 21), and was lower than breeding dispersal which was 710 km ± 466 km (range = 85 – 1617 km, n=35; [β= -1.00, 95% CI= -1.55, -0.44]; Fig. 2.5). However, if we excluded the individual that switched wintering latitudinal zone from one year to the next (Table 2.2), mean distance between centroids of wintering birds was 271 ± 327 km (range = 20 – 1479 km).

Mean home range overlap for individual tracked over two consecutive winters was 29 ± 28% (range 0-100%) and mean core areas overlap was 12 ± 17% (range 0-62%; n = 21; Annexe S1.5). These values remained highly similar if we excluded the five individuals that changed wintering environment or latitudinal zone between consecutive winters. In comparison, breeding home range or core area never overlapped in consecutive summers (n = 29). Neither the wintering environment nor the latitudinal zone affected the level of home range overlap.

## 2.6. Discussion

Our study is the first to examine the large-scale spatial wintering ecology of a highly nomadic species like the snowy owl. We found that space use patterns strongly differed among individuals using different wintering environments (marine vs terrestrial) and latitudinal zones (Arctic vs temperate) and part of this variability could be explained by environmental factors like snow depth and density of their main terrestrial prey (lemmings). We also found that individuals were generally faithful to their wintering environment and latitudinal zone, and to some extent to their specific wintering location.

### *2.6.1. Intraspecific variation in space and habitat use in winter*

Adult female snowy owls that bred in the eastern Canadian Arctic showed a clear latitudinal dichotomy in their use of wintering areas. Most tracked owls wintered in the Arctic (74%) whereas the rest wintered in temperate regions of North America. Wintering in the Arctic rather than at temperate latitudes may confer several advantages. First, travelling distances during migration are shorter for birds wintering in the Arctic and thus such migration should be physiologically less demanding (Pennycuick 1989). The longer migration of birds travelling to temperate areas can explain why they tended to settle later on their wintering site and departed earlier than birds spending the wintering season in the Arctic. This result is consistent with the general pattern of latitudinal variation in timing of migration reported in other bird species (King and Mewaldt 1981, Newton 2008). Second, birds wintering in the Arctic are close to potential future breeding sites, which should facilitate prospection for suitable settling areas in spring (Therrien et al. 2014b) and may ultimately confer reproductive advantages (Mehl et al. 2004, Bregnballe et al. 2006). Third, being an archipelago, the Canadian High Arctic is rich in coastal habitats, which may provide access to both marine and terrestrial food sources. Even though half of the owls wintering in the Arctic were classified as inland birds, most were located close to coasts (Fig. 2.1) and made use of the marine environment (e.g. up to 46% of their locations were there), which likely allowed them to exploit both marine and terrestrial prey (Holt et al. 2015). Despite the availability of marine food sources in the Arctic, the diversity of terrestrial prey may be lower than in temperate regions and snow cover may reduce their accessibility. In contrast, the Prairies and Great Plains are thought to provide snowy owls with a relatively high abundance of potential prey, such as small mammals and birds (Boxall and Lein 1982a, Detienne et al. 2008, Naughton 2012), but further away from their arctic breeding sites.

Exploitation of the marine environment in winter may confer several benefits. First, food supply may be abundant, profitable and accessible as sea birds wintering at northern latitudes are much larger than small mammals and often aggregate at high local densities in small polynyas (Gilchrist and Robertson 2000, Mallory and Gilchrist 2005). Second, the fidelity of sea ducks to wintering sites in ice-free areas provides a potentially predictable prey base in this environment (Petersen et al. 2012). Third, few predators exploit this food source in winter except for Gyrfalcons *Falco rusticolus* (Burnham and Newton 2011) and ravens *Corvus corax* (Gilchrist and Robertson 2000), which should reduce interspecific competition and energetic costs associated with territorial strife.

Variation in climatic conditions and sea ice extent or thickness can influence polynyas and leads within and among years (Barber and Massom 2007). Although polynyas are generally recurrent ice structures at large scale due to local topography, at a smaller spatial scale and within a given winter they may open or close depending on local wind or current, thus forcing seabirds to move among different patches of open water (Gilchrist et al. 2006, Lovvorn et al. 2014). The mobility of large avian predators like owls allows them to move quickly and potentially over large areas to track variations in the distribution of their prey. This may explain why we found that owls wintering in the marine environment travelled over longer distances during the winter, had larger home ranges and used more core areas than those wintering inland.

Home range size of wintering snowy owls in Eastern North America are among the largest ever reported in strigidae, and possibly in all raptors, with a maximum extent of 363 915 km$^2$. This far exceeds the maximum winter home ranges reported for other avian predators such as Gyrfalcons (172 007 km$^2$; Burnham and Newton 2011) or Lesser Spotted Eagle *Aquila pomarina* (22 500 km$^2$; Meyburg et al. 2004), but is surprisingly close to a mammalian predator, the polar bear *Ursus maritimus*, which also predominantly uses the marine environment (367 547 km$^2$; Auger-Méthé et al. 2016). We found a large inter-individual variability in home range size, with some owls having relatively small ranges with few core areas whereas other had large ranges with up to 12 core areas. White and Burnham (1999) also reported a large variability in Gyrfalcon winter home ranges around Greenland where variable ice conditions forced some individuals to track sea bird prey over large areas. Overall, individuals wintering in a marine environment may need to use multiple centers of activities and move more to fulfill their needs than those wintering in a terrestrial environment.

Timing of sea ice formation may also limit the ability of snowy owls to exploit the marine environment. As autumn progresses, sea ice will expand and eventually force sea birds to aggregate in relatively small ice-free areas. Sea ice phenology may therefore explain why owls wintering in the marine environment tend to settle later than birds in terrestrial environments. Similarly, in spring, the persistence of sea-ice and the late onset of sea ducks' pre-breeding migration from polynyas (e.g. King eiders *Somateria spectabilis* in April; Oppel 2008) may extend the time of prey availability and explain the later departure by birds wintering in marine environments compared to terrestrial ones.

### *2.6.2. Fidelity to wintering site and environment*

Migratory birds often show a high level of fidelity to their breeding and even wintering sites (Greenwood 1980, Weatherhead and Forbes 1994). In contrast, snowy owls are considered a nomadic species (Holt et al. 2015), as shown by the extreme breeding dispersal distance between consecutive breeding attempts previously documented in this species (Therrien et al. 2014b) and confirmed here. This extreme behaviour is likely due to cyclic, large amplitude population fluctuations of lemmings in the Arctic, leading to a highly unpredictable summer food supply both spatially and temporally (Krebs 2011).

Because snowy owls show a greater flexibility in their use of prey, habitat and geographical areas in winter than in summer and because the abundance of some of their winter prey is more predictable, we expected a greater fidelity of owls to their wintering areas compared to their breeding areas. This prediction was supported because inter-annual distances between centroids of winter home ranges were about half of the breeding dispersal observed in summer. Nonetheless, these inter-annual distances were still quite lengthy (i.e. of the order of ~200-300 km) and overlap in winter home ranges between consecutive years was moderate (~30%), despite their very large size. We also observed no difference in overlap extent between birds wintering in marine vs terrestrial environments, nor for birds that wintered in the Arctic vs temperate areas. Considering the geographic range and the diversity of environments where snowy owls can be found in winter (see Figs. 2.4 and 2.5; Boxall and Lein 1982b, Fuller et al. 2003, Holt et al. 2015), it is interesting that these birds even overlapped their wintering home ranges and core areas at all. Therefore, although owls showed a propensity to partly reuse the same wintering area from one year to the next, some factors may limit their ability to do so (see below).

At a broader scale, individuals were quite consistent in their wintering habitat use, predominantly using the same environment (marine or terrestrial) and latitudinal zones from one winter to the next (76%). Nonetheless, some individuals switched their use of their main environment between winters and most individuals have been located in both environments each winter. Switching from the terrestrial to the marine environment may be facilitated in the Canadian Arctic because both habitats are highly intertwined and thus often close to each other. Age and experience are other factors that can affect habitat use patterns in birds (e.g. Dolbeer 1982, Cresswell 2014). In snowy owls, it is believed that young and immatures predominantly migrate to temperate areas in winter whereas a high proportion of adult breeders spend the winter in the Arctic (Fuller et al. 2003, Doyle et al. 2017, this study). However, this is unlikely to be a factor in our study because all our birds were experienced breeders and the only switch detected between latitudinal zones was from the Arctic to temperate areas, the opposite of what is expected as birds get older.

### *2.6.3. Environmental determinants of space and habitat use*

In top predators like the snowy owl, variation in food availability is thought to be a major factor affecting space and habitat use pattern (e.g. Schliebe et al. 2008, Trierweiler et al. 2013, Lopez-Lopez et al. 2014). Annual variations in sea ice dynamics may change the spatial distribution of seabirds and could explain the moderate site fidelity shown by snowy owls in the marine environment. Unfortunately, quantitative information on the annual variation in the abundance of seabirds wintering in the Canadian Arctic is too scarce to address this question.

In terms of terrestrial prey, longitudinal data on small mammal densities in winter and summer are rare and Bylot Island was the only site in the whole eastern Canadian Arctic where this information was available. This is clearly a limitation to our analysis because owls range over a large portion of the Canadian Arctic in winter, although we note that lemming population fluctuations may be spatially synchronous at a relatively large scale, (i.e. hundreds of kilometers, Krebs et al. 2002). Despite these limitations, we found evidences that lemming densities on Bylot Island affected some aspects of habitat use by wintering owls. Home range sizes were smaller in years of high lemming densities in winter as found in other predatory birds. For instance, Prairie falcons *Falco mexicanus* dramatically reduced their home range size in years of high ground squirrels *Spermophilus townsendii* densities (Marzluff et al. 1997).

Use of the marine environment increased during winters following high summer densities of small mammals. Fauteux et al. (2015b) showed that lemming populations in the Canadian Arctic often declined during the autumn following peak summer densities to reach very low densities in the subsequent winter. Therefore, low winter lemming abundance after a summer peak may explain the previous result rather than a carry-over effect from the previous summer lemming abundance. A good knowledge of the ecology of prey species in all periods of the annual cycle is thus important when attempting to infer carry-over effects.

Over land, snow cover is another factor that may greatly affect food availability for snowy owls, both directly and indirectly. On the one hand, a thick snow cover may limit the ability of owls to prey on small mammals living underneath (Chamberlin 1980) as it does for other avian predators (Sonerud 1986) or foxes (Duchesne et al. 2011). On the other hand, a thick snow cover offers refuges from predators and a good thermal insulation for lemmings, which should favor their winter survival and positively affect their population (Reid et al. 2012, Bilodeau et al. 2013). A thick snow cover in autumn during the period of settlement for the winter may hinder the ability of snowy owls to find suitable areas, as suggested by their earlier settlement when snow in autumn was thin. Similarly, snow cover and depth have been shown to affect the pre-breeding movements of snowy owls when prospecting for suitable breeding sites (Therrien et al. 2015). However, a thin snow cover through the winter may eventually reduce small mammal populations by limiting their reproduction and reducing their survival, which could explain why snowy owls tended to make greater use of the marine environment under these conditions.

### *2.6.4. Future perspectives in a changing climate context*

Consistency in habitat use may provide advantages in terms of familiarity and experience in exploiting specific prey but some flexibility can also help to cope with changing environmental conditions. Sea ice extent is known to show a long-term decline (Stroeve et al. 2012) and changes in ice structure have already been shown to affect seabirds (i.e. Bump and Lovvorn 2004) and marine mammals (e.g. Hunter et al. 2010, Amstrup et al. 2013; Laidre et al. 2008). The reliance of wintering snowy owls on both the marine and terrestrial arctic environments may expose them to changes occurring in both but their high mobility may also allow them to adapt to changes at a fine scale. Further investigations are needed to understand the effects of changing winter conditions on the survival and subsequent reproductive performances of snowy owls.

## 2.7. Acknowledgments

We thank Glencore for their hospitality and support at the Raglan mine, NU. We also thank Andréanne Beardsell and Yannick Seyer for their help in the field. This study was financially supported by the Natural Sciences and Engineering Research Council of Canada (NSERC), the network of center of excellence ArcticNet, the Polar Continental Shelf Program of Natural Resources Canada, the Fonds de Recherche du Québec Nature et Technologies, EnviroNorth, First Air and the Fonds Écologique Anne Vallée.

## 2.8. Supplementary material

**Annexe S1.1.** Complementary information on estimation methods of lemming abundance and snow depth.

**Annexe S1.2.** Determination of settlement and departure dates on the breeding and wintering sites.

**Annexe S1.3.** Tracking information, wintering environment and latitudinal zones used by 28 snowy owls between 2007 and 2016.

**Annexe S1.4.** Movement of tracked snowy owls and capture sites.

**Annexe S1.5.** Wintering home range contours of tracked snowy owls.

**Annexe S1.6.** Complete statistical results of the relationships between different winter space and habitat use parameters and all explanatory variables examined.

## 2.9. Tables

**Table 2.1.** Statistical results of the relationships between different parameters of winter space and habitat use by snowy owls tracked by satellite telemetry and selected explanatory variables: wintering environment (Environment; marine vs terrestrial), wintering latitudinal zone (LatitudinalZone; Arctic vs temperate), snow depth (SnowAutumn; autumn and SnowWinter; winter) and small mammal abundance on Bylot Island (LemmSummer; summer and LemmWinter; winter). Response variables include: Distance travelled (km; n=42), Marine environment use (n=36; excludes birds wintering in the Prairies), Settlement and Departure dates (n=42), Length of stay (days; n=42), Home range and Core area size (km$^2$; n=42) and Number of core areas (n=42). Bird ID was included in all models as random effect. Latitudinal zone of reference=Arctic zone. Environment of reference = Marine environment. Results with all explanatory variables are presented in Annexe S1.6.

| Response variables | Explanatory variables | β | Lower CI | Upper CI |
|---|---|---|---|---|
| Distance travelled within wintering area | Environment | -0.788 | -1.195 | -0.381 |
|  | LemmWinter | -0.027 | -0.059 | 0.006 |
| Marine environment use | SnowWinter | -0.089 | -0.110 | -0.068 |
|  | LemmSummer[1] | 0.121 | 0.056 | 0.185 |
| Dates of settlement on wintering ground | Environment | -14.393 | -28.025 | -0.761 |
|  | LatitudinalZone | 11.745 | -3.849 | 27.339 |
|  | SnowAutumn | 2.732 | 1.623 | 3.841 |
| Dates of departure from wintering ground | Environment | -8.733 | -21.922 | 4.456 |
|  | LatitudinalZone | -18.812 | -37.397 | -0.227 |
| Length of stay on wintering site | LatitudinalZone | -0.907 | -1.859 | 0.045 |
| Wintering home range size | Environment | -1.452 | -2.229 | -0.675 |
|  | LemmWinter | -0.077 | -0.149 | -0.005 |
| Wintering core area size | Environment | -1.698 | -2.579 | -0.817 |
|  | LemmWinter | -0.083 | -0.161 | -0.005 |
| Number of core areas in wintering area | Environment | -0.571 | -0.977 | -0.165 |
|  | LatitudinalZone | -0.426 | -0.881 | 0.029 |
|  | LemmWinter | -0.044 | -0.082 | -0.005 |

[1] Female J was removed from this model (n=34)

**Table 2.2**. Individual consistency in winter habitat use (main wintering environment and latitudinal zones) by snowy owls tracked over consecutive years.

Winter2

| | | Marine Arctic | Marine Temperate | Terrestrial Arctic | Terrestrial Temperate | TOTAL |
|---|---|---|---|---|---|---|
| Winter1 | Marine Arctic | **4** | | 3 | | 7 |
| | Marine Temperate | | **1** | | | 1 |
| | Terrestrial Arctic | 1 | | **6** | 1 | 8 |
| | Terrestrial Temperate | | | | **5** | 5 |
| | TOTAL | 5 | 1 | 9 | 5 | 21 |

Blue: Environment switch between 2 consecutive winters.
Orange: Latitude switch between 2 consecutive winters.

## 2.10. Figures

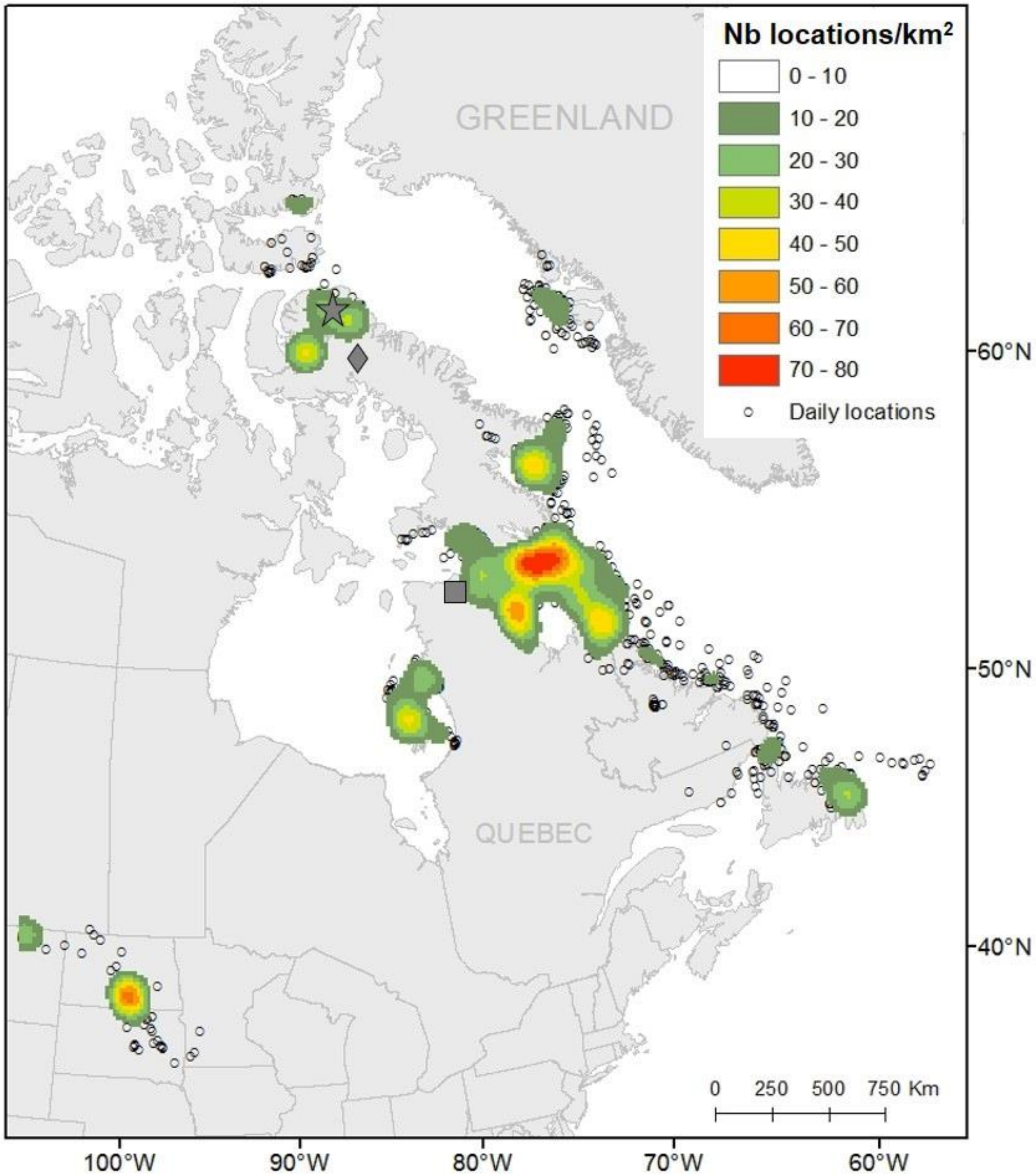

**Figure 2.1**. Highly-used areas by 21 wintering snowy owls tracked between 2007 and 2016 estimated with Kernel densities in ArcMap 10.2. Capture sites (Bylot Island: star; Mary River: diamond; Deception Bay: square) are also depicted.

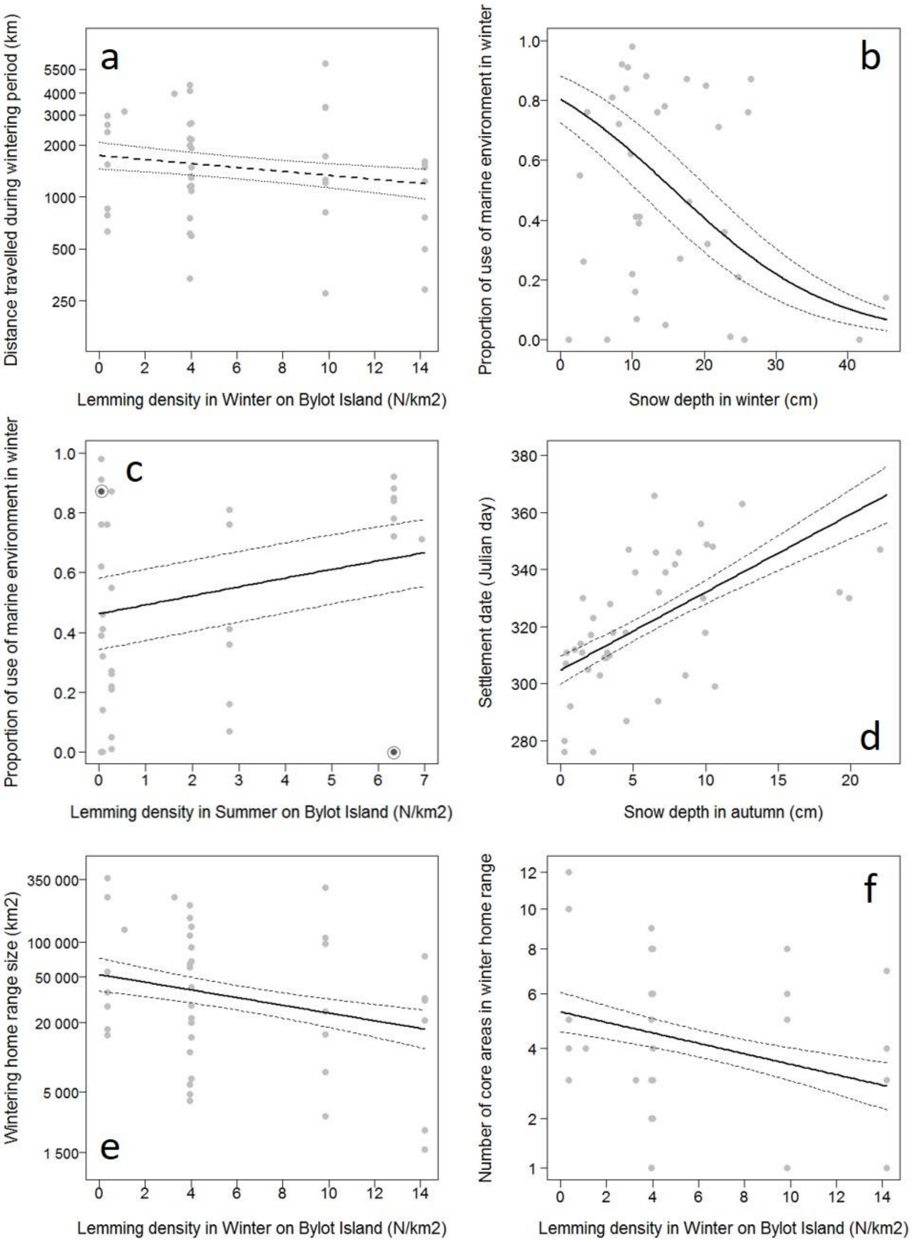

**Figure 2.2.** Relationships between distance travelled (a), proportion of use of the marine environment (b, c), dates of settlement on wintering site (c), wintering home range size (d), number of core areas in winter (e) and lemming densities on Bylot Island (summer or winter) or snow depth (autumn or winter). Coefficients were predicted with LMM or GLMM (from Table 2.1). Regressions with confidence intervals excluding zeros (full lines) and trends (dashed lines) are depicted along with their SE (dotted lines). Confidence levels are 0.95 in all graphs. Raw data points (pale gray dots) and outliers (encircled dark gray dots; removed from analysis) are also depicted.

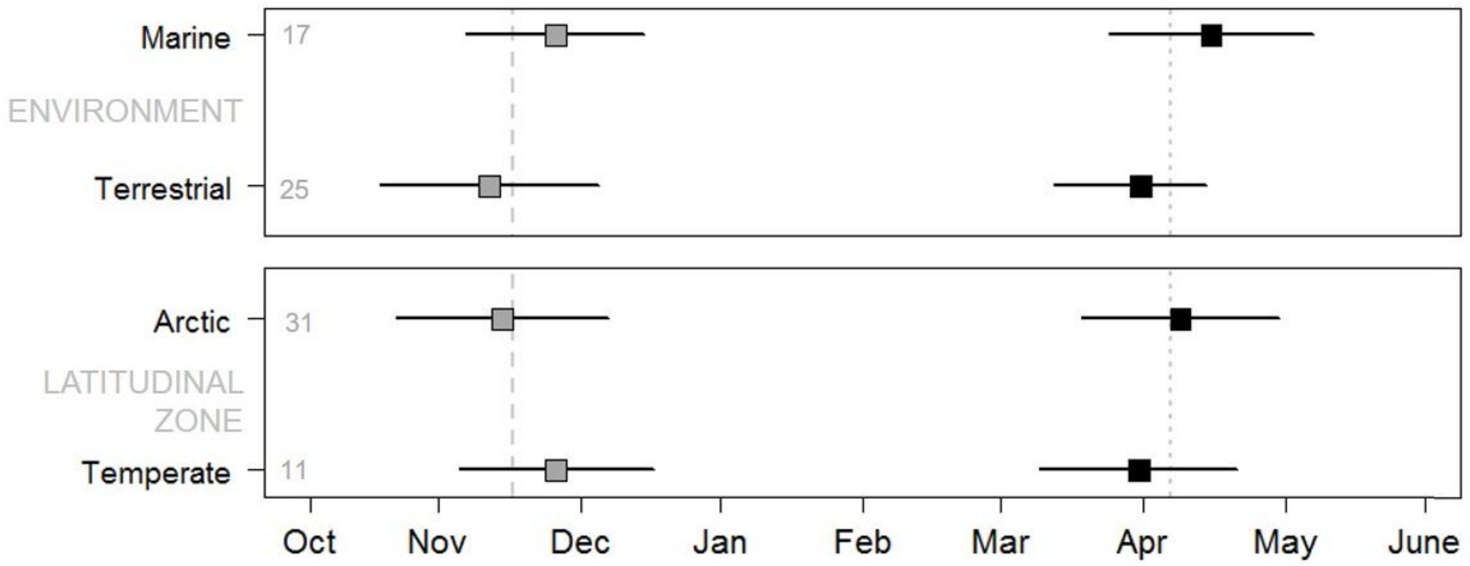

**Figure 2.3**. Settlement (gray squares; mean = dashed line) and departure (black squares; mean = dotted line) dates from wintering areas of snowy owls (n=42) in different wintering environments (top) or at different latitudinal zones (bottom).

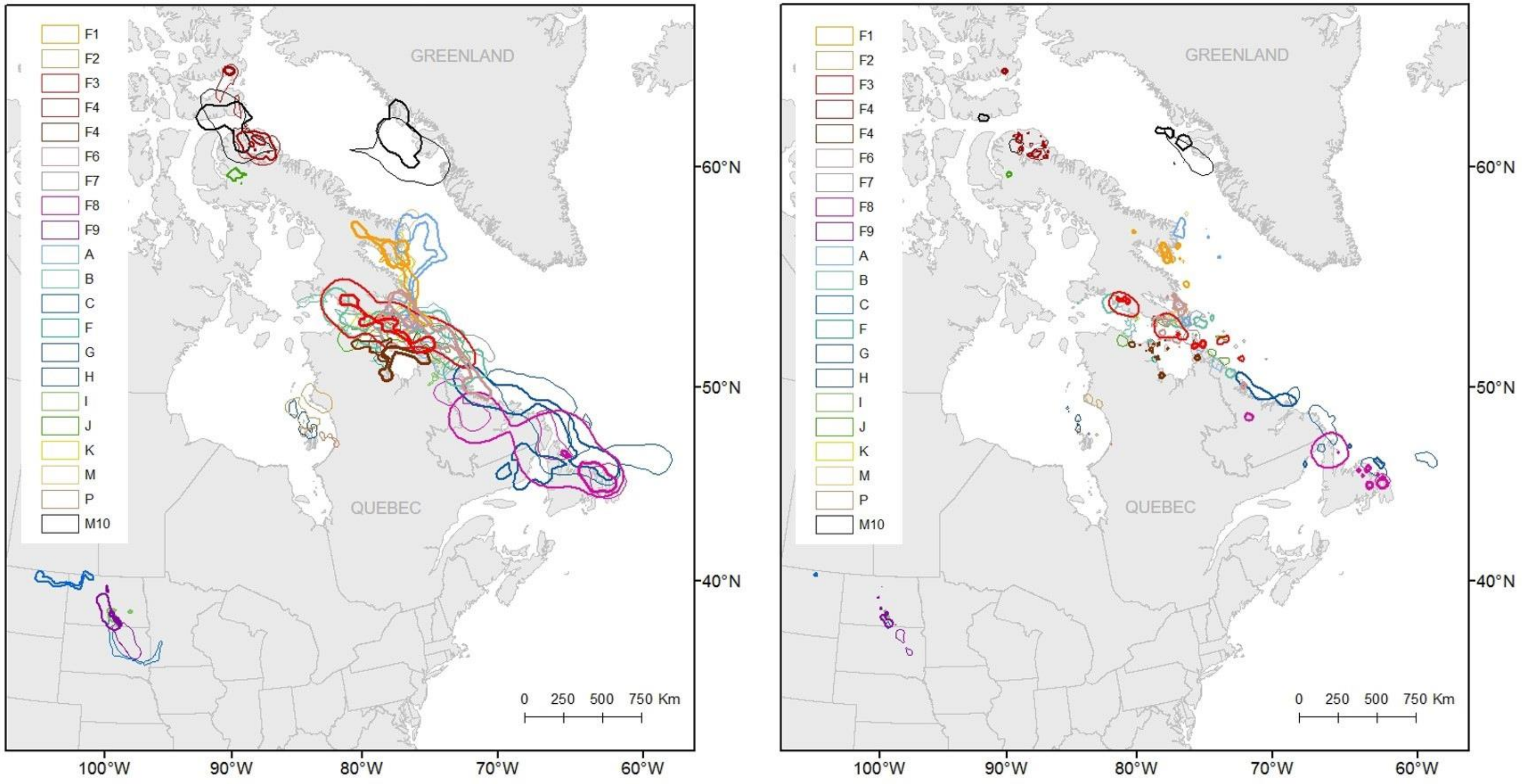

**Figure 2.4.** Wintering home range (a; 95% utilization distribution) and core area (b; 50% utilization distribution) contours of all individuals tracked for at least one winter between 2007 and 2016. Thin line=1st winter, medium line=2nd winter, thick line=3rd winter.

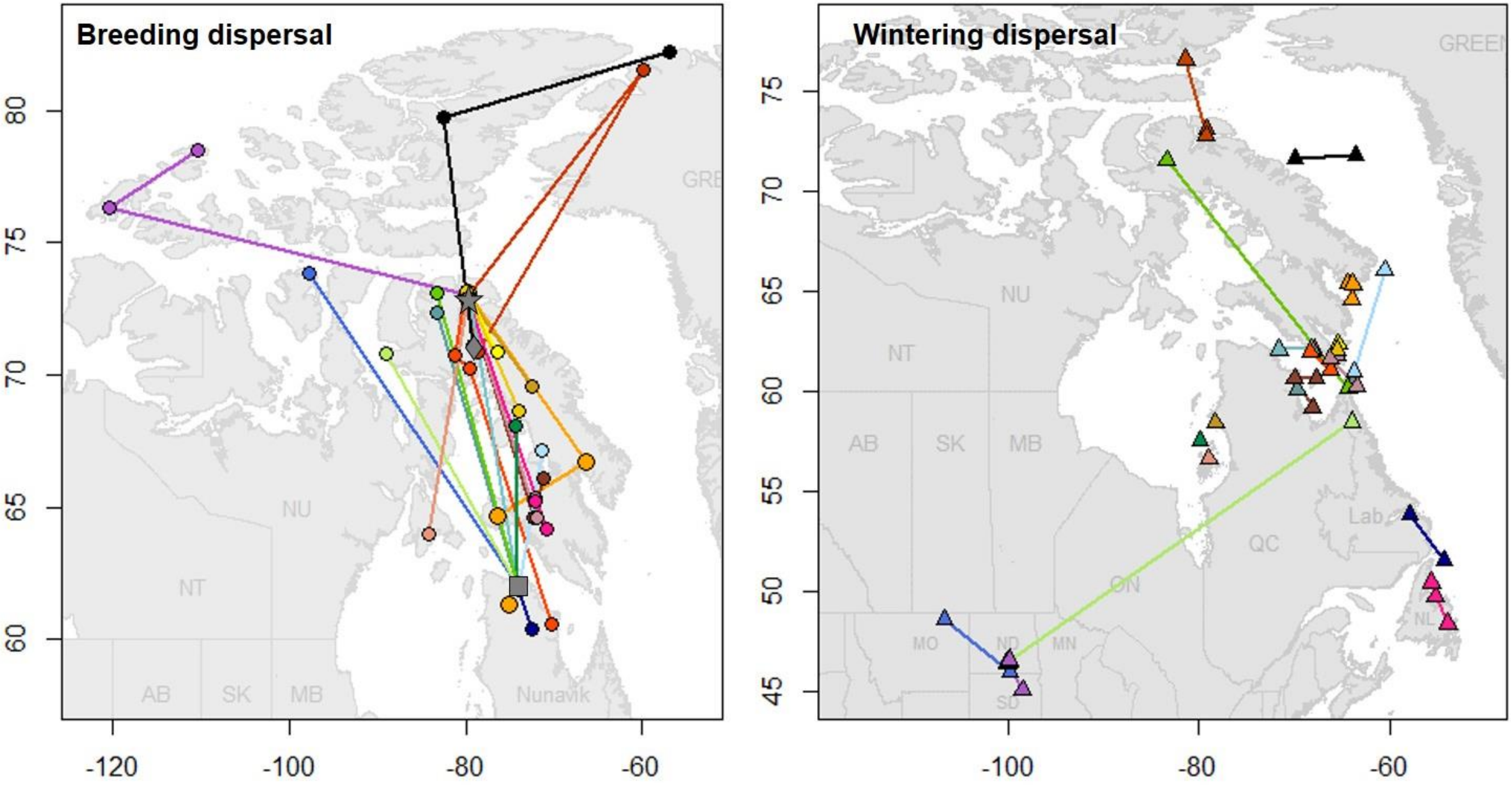

**Figure 2.5.** Summer (circles, LEFT PANEL) and winter (squares, RIGHT PANEL) centroids of locations for individual snowy owls tracked by satellite. The dispersal distance between consecutive seasons (lines) is also indicated for birds tracked over successive years. Capture sites (Bylot Island: star; Mary River: diamond; Deception Bay: square) are also depicted. Individuals' colour identification are the same as in Figure 2.4.

# CHAPITRE 3: Pulsed resources at tundra breeding sites affect winter irruptions at temperate latitude of a top predator: the snowy owl

Référence de la publication:

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## 3.1. Résumé

Les migrations irruptives sont principalement observées chez les espèces spécialistes de ressources pulsées et semblent être en réponse aux variations imprévisibles des ressources alimentaires. Pour expliquer les irruptions hivernales périodiques du harfang des neiges *Bubo scandiacus* tous les 3-5 ans dans les milieux tempérés de l'Amérique du Nord, nous avons évalué deux hypothèses alternatives. La première, l'hypothèse du *manque de nourriture*, suggère qu'un effondrement dans l'abondance de petits mammifères sur les sites de reproduction en Arctique forcerait les harfangs à quitter la toundra massivement à la recherche de nourriture en hiver. La deuxième, l'hypothèse du *succès de reproduction*, suggère plutôt qu'une abondance élevée de petits mammifères sur la toundra durant l'été permet une production élevée de jeunes, augmentant ainsi le nombre de migrants se déplaçant vers le sud à hiver suivant. Nous avons modélisé les irruptions de harfang des neiges en fonction de l'abondance de ressources alimentaires en été et la localisation géographique. Les abondances de harfangs en hiver ont été obtenues à partir de données de suivis citoyens de 1994 à 2011 et les abondances de petits mammifères en été ont été récoltées à deux sites distants dans l'Arctique canadien : Île Bylot, NU (Haut Arctique est) et Daring Lake, TNO (Bas arctique central). L'abondance de harfangs était positivement reliée à l'abondance de proies à l'été précédent et avait tendance à diminuer d'ouest en est sur le continent Américain. Les migrations irruptives de harfang des neiges sont donc davantage expliquées par l'hypothèse du *succès de reproduction* et semblent être causées par les variations de ressources alimentaires à large échelle. Nos résultats, combinés à ceux d'études précédentes, suggèrent que le déterminant principal des irruptions serait spécifique à chaque espèce, même dans une guilde d'espèces en apparence similaires.

Mots-Clés: *Bubo scandiacus*, migration irruptive, étendue de migration, petits mammifères, ZINB.

## 3.2. Abstract

Irruptive migration is mostly observed in species specialised on pulsed resources and is thought to be a response to unpredictable changes in food supply. We assessed two alternative hypotheses to explain the periodic winter irruptions of snowy owls *Bubo scandiacus* every 3-5 years in temperate North America: (1) the *lack-of-food* hypothesis states that a crash in small mammal abundance on the Arctic breeding grounds forces owls to move out of the tundra massively to search for food in winter; (2) the *breeding-success* hypothesis states that high abundance of tundra small mammals during the summer allows for high production of young, thus increasing the pool of migrants moving south the following winter. We modeled winter irruptions of snowy owls in relation to summer food resources and geographic location. Winter abundance of owls was obtained from citizen-based surveys from1994 to 2011 and summer abundance of small mammals was collected in summer at 2 distant sites in Canada: Bylot Island, NU (eastern High Arctic) and Daring Lake, NWT (central Low Arctic). Winter owl abundance was positively related to prey abundance during the previous summer at both sites and tended to decrease from western to eastern temperate North America. Irruptive migration of snowy owls was therefore best explained by the *breeding success* hypothesis and apparently caused by large scale summer variations in food. Our results, combined with previous findings, suggest that the main determinants of irruptive migration may be species-specific even in a guild of apparently similar species.

Keywords: *Bubo scandiacus*, irruptive migration, wintering range, small mammal, ZINB

## 3.3. Introduction

Migrants are found in a wide diversity of taxa in the animal kingdom, from insects (e.g. dragonflies, Wikelski et al. 2006; Dingle 1972) to large mammals (e.g. African elephant, *Loxodonta Africana*, Thouless 1995) and in both terrestrial (e.g. Blackpoll warbler, *Setophaga striata*, DeLuca et al. 2013; caribou, *Rangifer tarandus*, Le Corre et al. 2014) and aquatic species (e.g. eels: Beguer-Pon et al. 2015; humpback whale, *Megaptera novaeangliae,* Zerbini et al. 2006). Despite the fact that animal migration patterns are often characterised by regularity and predictability, they are complex and take many forms. These patterns are often regarded as continuums that vary in terms of distance (short to long distance migration), intensity (partial to complete migration), or obligation to move (facultative to obligate migration; Newton 2006a, 2008). Irruptions (or invasions) are an extreme and often spectacular form of facultative migration characterized by unusual and massive movements of individuals to a given area, a phenomenon that can sometimes attract considerable public attention (Holland 2013, Kaufman 2013). Movement patterns during irruptive migrations can be highly variable in terms of number of migrants, the distance they travel, the area they occupy and the duration of their travel (Newton 2008). Irruptive migration is mostly observed in species that specialise on unpredictable or pulsed resources and their movements are generally thought to be a response to irregular fluctuations in their food supply (Newton 2006a).

Irruptive migration is common in two groups of birds, boreal seed-eating birds and several raptors, especially owls. Seed eaters typically specialise on a limited or a single food plant, which often include mast fruiting species like coniferous trees (Newton 2008). Examples include common redpolls *Acanthis flammea*, which feed primarily on birch and alder seeds (Hochachka et al. 1999), and common crossbills *Loxia curvirostra*, which specialise on conifer seeds, especially spruce (Newton 2006b). Irruptive migrations of these species have been suggested to be related to periodic failure in the seed crop of their preferred food for a long time (Svardson 1957, Bock and Lepthien 1976, Koenig and Knops 2001). Koenig and Knops (2001) pointed out that two hypotheses could actually explain winter irruptions in seed-eating birds: the *seed-crop failure* and the *population density* hypotheses. According to the first hypothesis, a widespread failure of the seed crop on the northern breeding grounds would force individuals to move overwhelmingly to southern areas in winter due to lack of food. Alternatively, a good seed crop could lead to a high survival and especially a high reproductive success, resulting in an unusually large number of first-year birds being produced and moving south in winter. Results presented by Koenig and Knops (2001) for several species of seed-eaters suggest a combination of both hypotheses as irruptions were often best explained by a large seed crop resulting in high population densities due to a high breeding success followed by a poor seed crop the following year but with some species-specific differences.

Among owls, several species feed primarily on small mammals, which show large amplitude, cyclic fluctuations in abundance in many northern areas (Stenseth 1999, Korpimäki et al. 2004, Ims and Fuglei 2005, Fauteux et al. 2015a, Fauteux et al. 2015b). Species like the great gray owl *Strix nebulosa*, the boreal owl *Aegolius funereus* and especially the snowy owl *Bubo scandiacus* exhibit irruptive migration during winter in several areas, sometimes with a periodicity similar to the one of small mammals (Bull and Duncan 1993). It has therefore long been thought that these large-scale movements were related to the periodic fluctuations in small mammal abundance (Shelford 1945, Cheveau et al. 2004, Morrissette et al. 2010). Winter irruptions of several boreal owls were found to be negatively related to abundance of small mammals during the previous summer, suggesting that owl irruptions were a response to a lack of food (Cheveau et al. 2004, Côté et al. 2007), which is analoguous to the *seed-crop failure* hypotheses of Koenig and Knops (2001) for boreal seed-eaters.

The snowy owl is probably the species for which periodic winter irruptions are most spectacular and have been known for a long time in North America (Gross 1927, 1931, Shelford 1945, Kerlinger et al. 1985). This strigidae irrupts in large numbers every 3-5 years (mean ± SE = 3.9 ± 0.13; Newton 2002) in southern Canada and northern United States during winter. Snowy owls breed on the Arctic tundra where they feed primarily on lemmings and voles (subfamily Arvicolinae) and their local breeding density and reproductive success is highly dependent on the abundance of small mammals (Gauthier et al. 2004, Gilg et al. 2006, Therrien et al. 2014b). Unlike many birds, including other owl species, snowy owls can lay clutches of up to 14 eggs in small mammal peak years (mean ± SD: 7.0 ± 2.1 eggs; Potapov and Sale 2012). In winter, their diet is more diversified though small mammals remain a prey of choice (Keith 1963, Boxall and Lein 1982b, Detienne et al. 2008). It has long been thought that snowy owls were also escaping areas where food had become scarce, such as during the low period of lemming cycles, and that winter irruptions were thus caused by a lack of food up north (Shelford 1945, Chitty 1950, Lack 1954, Newton 1970). However, recent evidence has not been consistent with this suggestion. Satellite-tracking revealed that many adult owls remain in the Arctic tundra during the winter, irrespective of lemming abundance in the previous summer (Fuller et al. 2003, Therrien et al. 2011b, Therrien et al. 2014b). During invasion years, a greater proportion of juveniles are observed compared to non-irruptive years and individuals are generally in good body condition (Smith 1997). These observations were more in agreement with the hypothesis that a large production of young due to a high lemming abundance in summer were responsible for winter irruptions of owls, an idea already put forward by Gross (1947).

Our goal was to assess two alternative hypotheses to explain periodic winter irruptions of snowy owls in temperate areas of North America. The *lack-of-food* hypothesis states that a crash in small mammal abundance in the Arctic creates a shortage of food and forces owls to move out of the tundra massively in winter. The *breeding-success* hypothesis states that a peak in small mammal abundance during the summer allows for a production of numerous young in the Arctic tundra, which considerably increases the pool of migrants in the following winter. The *lack-of-food* hypothesis predicts that owl abundance in winter should be negatively related to the abundance of tundra small mammals in the previous summer whereas the *breeding-success* hypothesis predicts a positive relation. Studying irruptive migration is challenging due to the continental scale of this phenomenon but citizen-based survey such as the Christmas Bird Count is a powerful tool to colligate long-term, pan-continental observations (Koenig and Knops 2001), especially for an easily observable species like the snowy owl. Our study combined, for the first time, continental-scale data from the Christmas Bird Count with field data of annual fluctuations of small mammals at two distant sites in the Canadian Arctic to test the contrasting predictions of these two hypotheses.

## 3.4. Methods

### 3.4.1. Snowy owl abundance data

Data on the abundance of wintering snowy owls was obtained from the Christmas Bird Count (hereafter CBC) records for the 1994-2011 period. The CBC is conducted annually across North America by volunteer bird watchers and consists of a one-day survey performed in the weeks around Christmas. Volunteers select a “circle” (i.e. survey site) of 24.1 km (15 mi) in diameter, and report every bird seen or heard while walking or driving routes criss-crossing the survey area (mean = 28.5 volunteers/circle, range = 1 to 200; Butcher 1990). Circle locations are predefined and permanent although each circle may not be visited every year, as the visits depend on the volunteers’ enrollment at each site. They also report the number of hours spent in the field per party (i.e. a group of persons counting birds together), for each transportation method used (e.g. car, foot, boat). Observer effort is thus calculated in party-hours. Among the 2300 circles included in the CBC database, 616 have reported at least one snowy owl observation during the 18 years of our study. To evaluate the influence of small mammal abundance on winter irruptions of owls and reduce the noise resulting from anecdotal observations, we only selected sites that showed irruptive patterns, i.e., at least 3 years with ≥3 owl observations recorded at a site between 1994 and 2011. This allowed us to eliminate sites where presence of owls is only accidental and which are unlikely to show irruptive patterns. The selection was performed prior to any analyses. We found 84 sites that met this criterion. The sites were concentrated in southern Canada and northern United States and spanned the whole continent from east to west (Fig. 3.1; the list of sites is provided in Annexe S2.1).

Previous studies that used CBC data to assess bird population trends have emphasized the need to correct for observer effort (Link and Sauer 1999, Dunn et al. 2005). To evaluate the relevance of accounting for observer effort in our study, we verified the relationship between owl counts and effort (calculated as party-hours; see Annexe S2.2), but we could not detect any trend. We also compared models with and without the effort variable in our subsequent analysis (results not shown). Models not accounting for effort performed better based on AIC and the confidence intervals of the effort variable always included zero when effort was added as a covariate. Therefore, an increased observation effort apparently did not lead to higher owl counts. This counterintuitive result can likely be explained by the fact that snowy owls are large, charismatic and conspicuous birds found in open habitats, which facilitates their observation. Moreover, their presence, like other birds of prey (Dunn et al. 2005), is often known by observers prior to the CBC survey. We thus only report the results based on raw counts.

### *3.4.2. Small mammal abundance data*

Reliable, long-term time series of small mammal abundance in the Arctic tundra of North America, where snowy owls breed, are very scarce. We obtained data on annual small mammal abundance from two Arctic sites from 1994 to 2011: Bylot Island, Nunavut (73°08N 80°00W), and Daring Lake (64° 52N 111°35W), Northwest Territories, separated by 1555 km (Fig. 3.1). These were the only two tundra sites that provided a consistent record of annual abundance of small mammals using standard methods for the whole period. Both sites are known breeding grounds for snowy owls. Bylot Island is a High-Arctic, coastal study site where 2 species of small mammals are found: brown lemmings *Lemmus trimucronatus*, the most abundant species, and collared lemmings *Dicrostonyx groendlandicus*. Ninety-one percent (91%) of individuals caught in peak years were brown lemmings and 31% in crash years (percentages are based on live-trapping data from 2004 to 2011; Fauteux et al. 2015b). The landscape at this site is dominated by herbaceous tundra and composed of a mosaic of mesic (85%) and wet (15%) environments. Snap-trapping has been conducted at the site since 1994 and live-trapping since 2004 (see Gruyer et al. 2008, 2010 and Fauteux et al. 2015b for details of the methods). Snap-trapping provides an index of annual abundance while live-trapping allows accurate determination of densities using capture-recapture method. For our analyses, we used population density estimates (in N/ha), measured directly from 2004 onward and transformed from the annual snap-trap index before 2004 using the equation provided by Gauthier et al. (2013).

Daring Lake is a low-Arctic, continental site where multiple species of small mammals are observed: northern red-backed vole *Clethrionomys rutilus* (68%; percentages are based on snap-trapping captures across the study years), meadow vole *Microtus pennsylvanicus* (15%), collared lemming (12%), brown lemming (3%), and different species of shrews (*Sorex* spp., 1%). Small mammal abundance at Daring Lake were estimated using snap-trapping methods and were provided by the Northwest Territories Small Mammal Survey (Government of the Northwest Territories 2008). Snap-trap indices (expressed as N caught by 100 trap-nights) usually provide a good index of mammal abundance (Gauthier et al. 2013). Small mammal abundance at the two sites were not correlated ($r = -0.03$, $p = 0.9$), which indicates an absence of synchrony in small mammal populations at that spatial scale (1555 km). Although small mammal *density* was estimated on Bylot, the term *abundance* will be used hereafter to simplify the text. However, due to differences of methods, absolute abundance values cannot be compared between the 2 sites.

### *3.4.3. Statistical analyses*

Analyses of count data represent a challenge as they often depart from normal distributions due to the presence of excess zeroes or overdispersion. A visual inspection of the frequency distribution of our count data suggested that an excess of zeroes was the case (Annexe S2.3). Therefore, to assess the predictors of snowy owl irruptions, we used Zero-inflated negative binomial (ZINB) models, a class of generalized linear models (GLMs) that account for data with excess zeroes and overdispersion. ZINB models come from a mixture of two distributions where a logistic regression models the structural zeroes (i.e. presence/absence) and a negative binomial regression is used for the counts (i.e. abundance; $y > 0$; Hilbe 2011). Covariates can be added to each component to model the excess of zeroes and/or the count (see Annexe S2.4 for details).

ZINB models can extend generalized linear models (GLMs) by including random effects to the existing fixed effects in the linear predictor, thus producing mixed-effect models (McCulloch and Searle 2001). To account for the non-independence of data collected annually at a given site in our analyses, we added the site as a random effect. We adjusted models with a random effect on the presence/absence component only, the abundance component only and on both. Models with a random effect on both components performed better than models with random effects on each component separately ($\Delta$ AIC= 123.8) and we therefore retained the site as a random effect on both components. Models were fitted with the NLMIXED procedure of (SAS Inst., 2010, NC, release 9.3). We found no evidence for spatial auto-correlation in our data (Moran's I statistic, p = 0.37; Dormann et al. 2007).

Predictor variables included in the ZINB model were: abundance of small mammals on Bylot Island and at Daring Lake and the longitudinal distance between CBC sites and the center of the North American Prairies (see Fig. 3.1). The latter variable was included to account for the fact that snowy owl irruptions could be asynchronous between eastern and western North America. We chose the center of the Prairies as our reference point (distance = 0) because this region of the continent receives the highest densities of snowy owls in winter and is considered a favourable winter habitat for them (Boxall and Lein 1982b, Kerlinger and Lein 1986). The distance variable was expressed in kilometers and represents the longitudinal distance from each site to the reference point (50.57° N -104.88° W), which was the average coordinate of the 43 CBC sites located in the Canadian Prairies and the US Great Plains and Midwest (gray circles in Fig. 3.1). This distance ranged from -1354 km for our westernmost site to 3589 km for our easternmost site. In the analyses, the distance was divided by a constant (i.e. 100) to minimize the magnitude difference between variables. Because snowy owl's abundance may not be related to prey densities at our tundra sites equally across the continent, interactions between small mammal densities at each site and distance were also tested. Abundance of small mammals were standardized (i.e. $(x - \bar{x})/std$) because they had different units.

Models were built by combining different groups of variables: (1) food resources in the Arctic (i.e. abundance of small mammals on Bylot Island and at Daring Lake), (2) geographic location in winter (i.e. distance of the sites from the center of the Prairies) and (3) the interactions between these two first groups. Each of these effects had to be applied simultaneously on both components (i.e. presence/absence and abundance) of the model. We compared models using Akaike information criterion corrected for small sample size (AICc) and performed multi-model inference following Burnham and Anderson (2002).

## 3.5. Results

Between 1994 and 2011, a total of 1298 counts have been performed at the 84 CBC sites retained in our analysis (mean ± SD = 15.5 ± 3.9 counts per site). Of these counts, 494 reported no owls (38.1%), and 3357 snowy owls were observed during the other 804 counts. Total owl abundance (mean ± SD = 186.5 ± 105.0 owls per year, excluding zeros) fluctuated annually and suggested a cyclical pattern of fluctuations during this period (Fig.3.2). Owl abundance also varied spatially (annual mean ± SD = 2.1 ± 2.0 owls per site, Fig. 3.3). In decreasing order of abundance, SKRE (Regina, Saskatchewan), BCLA (Ladner, British Columbia), ONKG (Kingston, Ontario), MBWI (Winnipeg, Manitoba), and MBOH (Oak Hammock Marsh, Manitoba) were the 5 sites where the most owls have been counted (see Annexe S2.1 for details on each site). However, these values should not be considered representative of the mean winter abundance of owls throughout its range considering that we only selected sites where they occurred regularly and showed an irruptive pattern (see methods).

Model selection provided strong evidence for an effect of lemming abundance at both study sites on the probability of occurrence and abundance of snowy owls in winter and weak evidence for an effect of the distance to the Prairies (Cumulative AICc weight = 0.58, Table 3.1). Probability of occurrence in winter was positively related to small mammal abundance on Bylot Island but confidence intervals of the other model averaged estimates included zero (Table 3.2). Owl abundance in winter was positively related to small mammal abundance the previous summer both on Bylot Island and at Daring Lake, and based on its confidence interval, the distance variable nearly excluded zero (Table 3.2). We based our subsequent interpretations on the abundance data (rather than the probability of occurrence), as we considered those most relevant to our initial hypotheses. Winter abundance of snowy owls increased when summer abundance of small mammals increased at either of the two Arctic sites and the slopes of the relationships were relatively similar at both sites (Fig. 3.4a and

3.4b). Owl abundance at individual sites also tended to decrease with the longitudinal distance from west to east (Fig. 3.4c).

## 3.6. Discussion

Irruptive migration of some bird species in temperate areas is thought to be a response to unpredictable changes in food supply in northern regions. Our study is the first to document conclusively a link between summer abundance of small mammals on the Arctic tundra and the winter irruptions of the snowy owl in North America. Our results showed a positive relationship between summer food resources and winter abundance of owls, thereby supporting the *breeding-success* hypothesis but not the *lack-of-food* one. We also found weak evidence for geographic variation in winter abundance of snowy owls.

### *3.6.1. Owl irruption and small mammal abundance*

The pattern of winter fluctuations of snowy owl abundance that we detected in temperate North America over the past 2 decades showed periodic irruptions every 3 to 5 years, which is similar to observations reported earlier during the 20th century (e.g. Shelford 1945, Gross 1947, Chitty 1950), despite some critics (Boxall and Lein 1982b, Kerlinger et al. 1985). These irruptions have long been thought to be linked to the cyclic fluctuations of small mammal populations on the Arctic breeding grounds of this species (Gross 1927, 1931, 1947). However, the lack of long term monitoring of small mammal abundance in the Canadian Arctic strongly limited the ability of previous studies to formally test hypotheses that could explain this pattern (Morrissette et al. 2010, Potapov and Sale 2012). Our results, based on rare long time series, were not consistent with the most commonly accepted hypothesis, the *lack-of-food*, which suggests that winter irruption of owls in temperate regions is caused by a crash in small mammal populations in the north (Shelford 1945, Chitty 1950, Lack 1954, Newton 1970). On the contrary, we found a positive relationship between summer abundance of small mammals at our two study sites and owl abundance during the following winter.

High abundance of small mammals, and in particular lemmings, is essential for successful owl reproduction (Therrien et al. 2014a, Holt et al. 2015). Lemming abundance typically follows a 3-5 years cycle in many parts of the Canadian Arctic (Elton 1924, Chitty 1950, Gruyer et al. 2008, Krebs 2011) but populations may not fluctuate synchronously over the whole range. Potential asynchrony at relatively large spatial scale was the main reason that led Kerlinger et al. (1985) to conclude that rodent abundance was unlikely to explain fluctuations in winter abundance of owls in North America. However, in both North America and Eurasia, rodent population cycles can be synchronous at the scale of several hundred kilometers, though usually not at scales ≥1000 km (Erlinge et al. 1999, Angerbjörn et al. 2001, Predavec et al. 2001, Krebs et al. 2002). The asynchronous fluctuations in small mammals between our two selected Arctic sites located 1555 km apart are thus in agreement with the scale at which spatial synchrony disappeared in those studies.

Since snowy owls will only settle to breed in areas of high lemming abundance (Therrien et al. 2014a), the average breeding dispersal distance recorded for this species in North America (i.e. 725 km (2007-2010) reported in Therrien et al. 2014b; 710 km (2007-2015, including the same individuals from 2007-10): Chap.2, this thesis) provides an idea of the spatial scale at which they have to move to find a high abundance of lemmings following a crash at their previous nesting site. Considering this high dispersal potential, years of high lemming abundance at either of our two selected Arctic sites should result in a good production of young over a relatively large area, which would explain the occurrence of a winter irruption in the following winter. The previous interpretation is consistent with the predominance of juveniles reported in years of owl irruption (Smith 1997), which would be indicative of a high production of young up north. Moreover, owls observed in winter are generally in good body condition, suggesting that birds moving south in year of irruptions are not starving (Kerlinger and Lein 1988). It is also quite unlikely that an owl in poor condition could even migrate 1000 kilometers. Finally, the temporal variability in the amplitude of irruptions could partly be explained by chance events (e.g. weather; Krebs et al. 2002) that may play a role in synchronizing small mammal populations across distant regions of the Arctic such as between our 2 study sites.

Recent satellite tracking studies in the eastern Canadian Arctic revealed that most adult female owls remain in the Arctic during the winter (>75%; Therrien et al. 2011b, 2014b). These birds spent much of the winter on or near sea-ice and likely had a diversified diet, including marine prey (seabirds). Remaining in the Arctic during the non-breeding season may be beneficial for adults as they are close to the breeding ground in spring and can initiate prospection earlier for a site with high lemming abundance to breed (Therrien et al. 2014b, Therrien et al. 2015). In contrast, young birds, which may not breed before several years, may find it easier to move to southern latitudes where i) conditions are milder, ii) prey may be more abundant and easier to catch, and iii) there is less competition with adult owls that remain in the Arctic. Every year, independently of the phase of the lemming cycle, the onset of the Arctic winter likely results in a reduction of the overall prey abundance or accessibility (due to snow or darkness) which may trigger movements of young owls toward southern latitudes.

### *3.6.2. Geographic variation*

Snowy owls can winter in different places like the Arctic tundra (Gessaman 1972) and on or near sea-ice (Gilchrist and Robertson 2000, Therrien et al. 2011b), but for those that move to temperate areas in winter, the North American Great Plains and Prairies are a prime wintering habitat (Boxall and Lein 1982b, Kerlinger et al. 1985, Holt et al. 2015). The vast, open areas of the Prairies are similar to the tundra in terms of vegetation structure and abundance of rodent species (Boxall and Lein 1982b, Holt et al. 2015). Moreover, the thin snow accumulation in the Prairies, as in the tundra, is likely another factor facilitating capture of small mammals. Indeed, snow cover and depth has been shown to affect hunting efficiency (Chamberlin 1980) as well as movements and settlement decisions in snowy owls (Therrien et al. 2015). It is thus surprising that we only found a weak trend for an increase in abundance from east to west, especially considering that Kerlinger et al. (1985) reported a higher abundance in the Prairies than elsewhere in winter based on an analysis of CBC data. A possible explanation for this discrepancy is that in our study, we only selected sites where snowy owls were regularly observed and showed an irruptive pattern in order to test our main hypotheses (see methods). Based on our criteria, we retained 28% of CBC sites (44/158) located in the Prairies (Central region) but only 12% (35/303) in the Eastern region among sites where owls had been observed at least once (Fig. 3.1). This selection led to the exclusion of a much greater proportion of sites where owls were rarely observed in the East than in the Prairies, thereby dampening the spatial variation in abundance between the Prairies and the Eastern region. This could explain why distance from the Prairies had only a weak effect in our analysis. Therefore, our results should not be considered representative of the mean abundance of snowy owls across their temperate wintering range.

### *3.6.3. Determinants of irruptive migration*

The observed pattern of irruptive migration of snowy owls in temperate North America was most consistent with the *breeding success* hypothesis. This pattern of migration involves a mechanism similar to the one of the *population density* hypothesis of Koenig and Knops (2001), which can explain invasions of the common redpoll and black-capped chickadee *Parus atricapillus*, as well as that of another strigidae, the northern saw-whet owl *Aegolius acadius* (Confer et al. 2014). In contrast, the migration patterns of other seed-eaters like the white-winged crossbill *Loxia leucoptera* appear to be better explained by the *seed-crop failure* hypothesis (Koenig and Knops 2001) and the ones of boreal owl, northern hawk owl and great gray owl by the *lack-of-food* hypothesis as formulated here (Koenig and Knops 2001, Cheveau et al. 2004). Therefore, although several seed-eaters and owls feed on pulsed resources that can fluctuate up to 100-fold from one year to the next, species within each of these groups can apparently respond to these fluctuations in different ways. It thus appears that no unique hypothesis can explain irruptive migrations even in species that specialise on similar food resources. Perhaps the strictness of the specialist behaviour (i.e. high specialist vs mild specialist), the type of food exploited, the flexibility in habitat use, the breeding strategy, and the body size are all factors that could influence the response of irruptive migrant to resources fluctuations (Cheveau et al. 2004). Weather has also been proposed to play a role in explaining irruptive patterns (Kerlinger et al. 1985, Krebs et al. 2002). These factors are perhaps not mutually exclusive, and may interact in shaping the migration patterns of irruptive migrants.

Although our study is the first one to model the influence of summer prey abundance on winter abundance of owls using long term field data, some limitations must also be acknowledged. First, because of the limited availability of long-term monitoring data, only two Arctic small mammal survey sites could be used to assess irruptive patterns of snowy owls. It may look like a sparse dataset considering the size of the Canadian Arctic. Nevertheless, these two sites were far apart and asynchronous, which i) eliminated the problem of pseudo-replication and helped us to determine the response of owls at the continental scale to opposite variations in small mammal abundance. Secondly, working with citizen-based data such as CBC is challenging in many ways. CBC surveys were not initially designed nor intended for scientific purposes, but the interest for these large-scale and long-term data have rapidly grown despite the many sources of variability (e.g. number and experience of participants, weather, habitat, modes of travel, area covered, use of attracting devices; Dunn et al. 2005) that introduce background noise to these data set. Despite these potential sources of variability, CBC data also has some advantages such as the large number of survey sites available and the continental-scale coverage. CBC data therefore offers an enormous and unique potential for large-scale studies, as long as limitations are considered.

Despite all these drawbacks, our analysis revealed unique and novel links between pulsed resources during the summer and irruptive migration in winter of an Arctic-nesting predator. For the first time, we provide direct evidence that a good production of young during the summer due to a high abundance of food rather than a lack of food is the main mechanism leading to periodic irruptions of snowy owls in temperate North America. Future work on irruptive migration should include more birds tracked by satellite telemetry to compare among age and sex-classes, multi-year study of migratory routes and the seasonal dynamic of irruptive movements, an assessment of the geographic origin of irruptive birds and the influence of winter habitat selection on breeding success. Ultimately, combining long-term studies of inter-seasonal prey dynamics and extensive satellite tracking of individuals could unravel the details of inter-annual movements associated with irruptive migration and their determinants.

## 3.7. Acknowledgements

We would like to thank Suzanne Carrière (Northwest Territories Government), and Kathy Dale (CBC) for providing the data sets. We also are indebted to Gaétan Daigle, David Émond, and Dominique Fauteux for statistical assistance. This study was financially supported by the Natural Sciences and Engineering Research Council of Canada, the network of center of excellence ArcticNet, the Polar Continental Shelf Program of Natural Resources Canada, the Fonds de Recherche du Québec Nature et Technologies and EnviroNorth. Finally, this study would not have been possible without the efforts of the numerous volunteers who conducted the CBC counts. We thank them all.

## 3.8. Supplementary material

**Annexe S2.1**. Location of the 84 Christmas Bird Count sites selected in this study.

**Annexe S2.2**. Relationship between the number of snowy owls counted annually during the Christmas Bird Count and the effort of observation reported.

**Annexe S2.3**. Annual abundance of snowy owls at each Christmas Bird Count site.

**Annexe S2.4**. Details on the structure of ZINB models

## 3.9. Tables

**Table 3.1**. Model selection of the effect of small mammal abundance at two Arctic sites in summer and geographic location in winter on the probability of occurrence (presence/absence) and abundance of snowy owls in the Christmas Bird Count in southern Canada and northern USA between the years 1994-2011 using Zero-Inflated Negative Binomial models. ZINB models used for these analyses come from a mixture of 2 distributions where a logistic regression models the structural zeroes (i.e. presence/absence) and a negative binomial regression is used for the counts (i.e. abundance; See methods). The same effects were modeled on the probability of occurrence and abundance. The site ID was entered as a random factor in the analysis.

| Variables | K | -2*Log-Lik. | Δ AICc | $w_i$ |
|---|---|---|---|---|
| mamBylot+mamDaring+Dist | 11 | 5084.5 | 0 | 0.44 |
| mamBylot+mamDaring | 9 | 5088.5 | 0.1 | 0.42 |
| mamBylot+ Dist | 9 | 5091.5 | 3.2 | 0.09 |
| mamBylot+mamDaring+Dist+Dist*mamBylot+ Dist*mamDaring | 15 | 5081.5 | 5.4 | 0.03 |
| mamBylot+ Dist+Dist*mamBylot | 11 | 5091.1 | 6.9 | 0.01 |
| mamDaring+ Dist | 9 | 5117.2 | 28.8 | 0.00 |
| mamDaring +Dist+Dist*mamDaring | 11 | 5114.4 | 30.1 | 0.00 |
| Dist | 7 | 5124.4 | 32.0 | 0.00 |

mamBylot: Small mammal abundance on Bylot Island
mamDaring: Small mammal abundance at Daring Lake
Dist: Distance to the center of the Prairies
K: number of parameters
Log-Lik: Log-likelihood
$w_i$: AICc weight

**Table 3.2**. Factors influencing the probability of occurrence (presence/absence) and abundance of snowy owls in the Christmas Bird Count of southern Canada and northern USA between the years 1994-2011. Model-averaged coefficients of the Zero-Inflated Negative Binomial models (from Table 3.1) are presented along with their unconditional standard error (uncond. SE) and 95% confidence intervals (degrees of freedom = 82). Variables with 95% confidence interval excluding 0 are in bold.

| Model Component | Variable | Coefficient | Uncond. SE | Lower CI | Upper CI |
|---|---|---|---|---|---|
| Occurence | **Intercept** | **1.327** | **0.214** | **0.907** | **1.747** |
| | **MamBylot** | **0.434** | **0.117** | **0.204** | **0.664** |
| | MamDaring | -0.012 | 0.084 | -0.176 | 0.152 |
| | Distance | -0.015 | 0.013 | -0.040 | 0.009 |
| | Dist*mamBylot | -0.002 | 0.007 | -0.017 | 0.013 |
| | Dist*mamDaring | -0.004 | 0.006 | -0.016 | 0.008 |
| Abundance | **Intercept** | **1.202** | **0.075** | **1.054** | **1.350** |
| | **MamBylot** | **0.064** | **0.027** | **0.011** | **0.117** |
| | **MamDaring** | **0.068** | **0.026** | **0.017** | **0.119** |
| | Distance | -0.007 | 0.005 | -0.017 | 0.002 |
| | Dist*mamBylot | -0.001 | 0.002 | -0.005 | 0.003 |
| | Dist*mamDaring | -0.003 | 0.002 | -0.007 | 0.001 |

mamBylot: Small mammal abundance on Bylot Island
mamDaring: Small mammal abundance at Daring Lake
Dist: Distance to the center of the Prairies

## 3.10. Figures

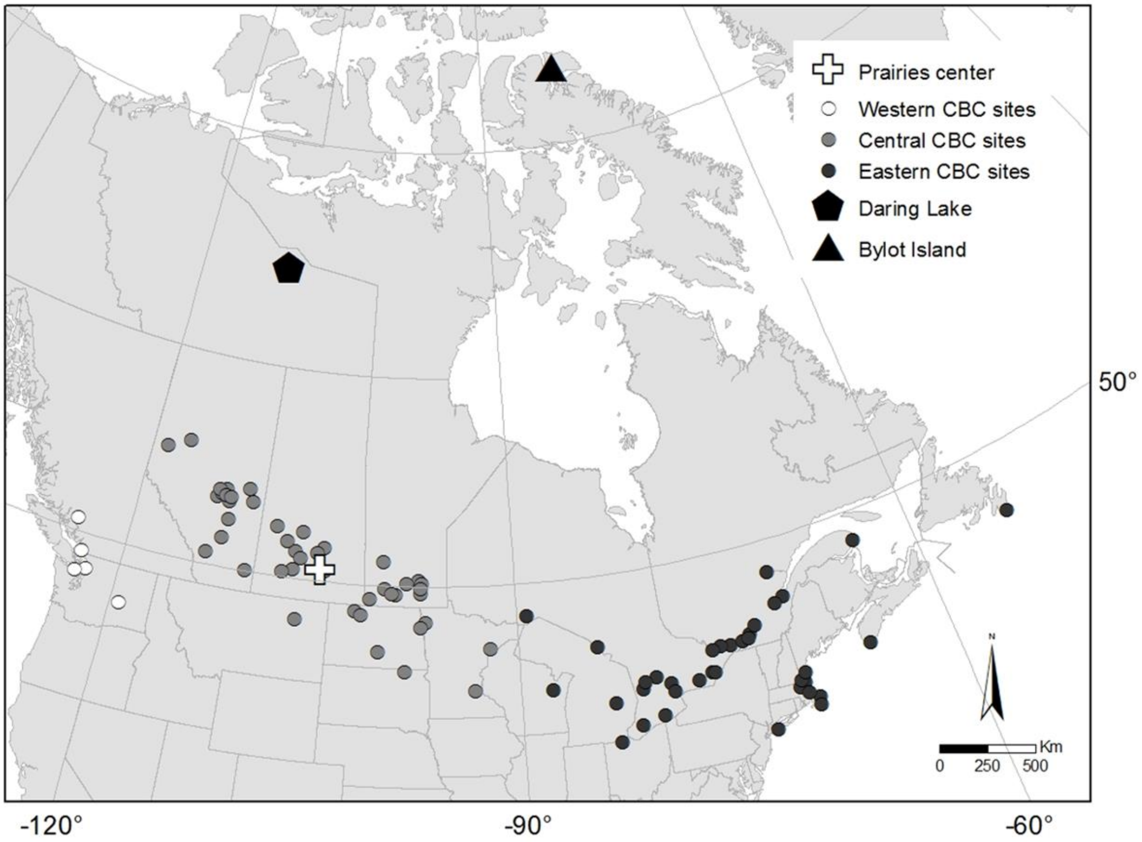

**Figure 3.1**. Location of study sites for summer small mammal abundance in the Canadian Arctic (Bylot Island and Daring Lake), and of Christmas Bird Count (CBC) sites selected to detect an irruptive pattern in winter abundance of snowy owls in temperate North America. The white cross depicts the center of the Prairies calculated as the mean coordinates of CBC sites located in the Canadian Prairies and US Great Plains and Midwest.

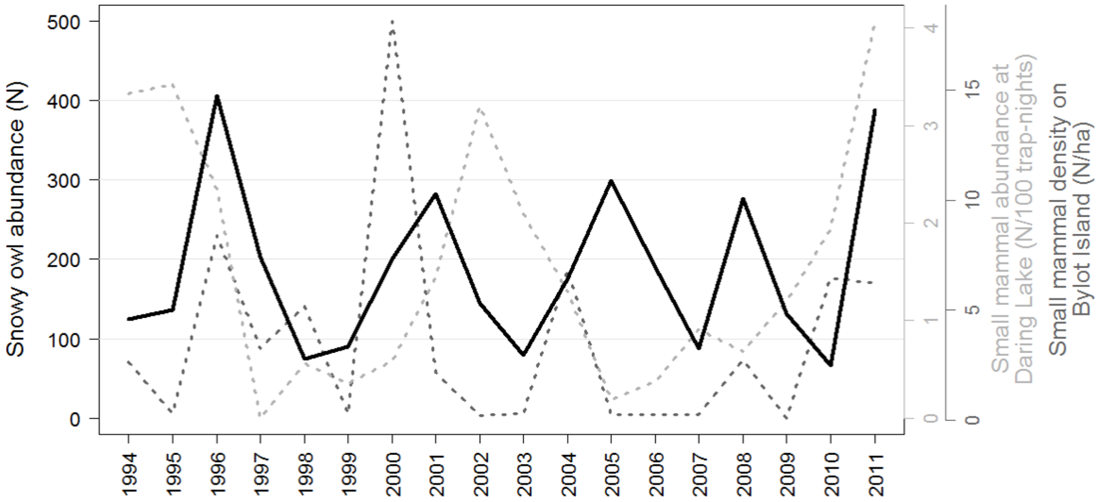

**Figure 3.2**. Annual variation of snowy owl winter abundance at selected Christmas Bird Count sites in temperate North America (black full line), small mammal abundance in summer at Daring Lake, Northwest Territories (light gray dashed line) and small mammal densities on Bylot Island, Nunavut (dark gray dashed line). Notice the different axes scales and units for lemming numbers at each study site. Lemming abundance values are not directly comparable between the two sites because of different units.

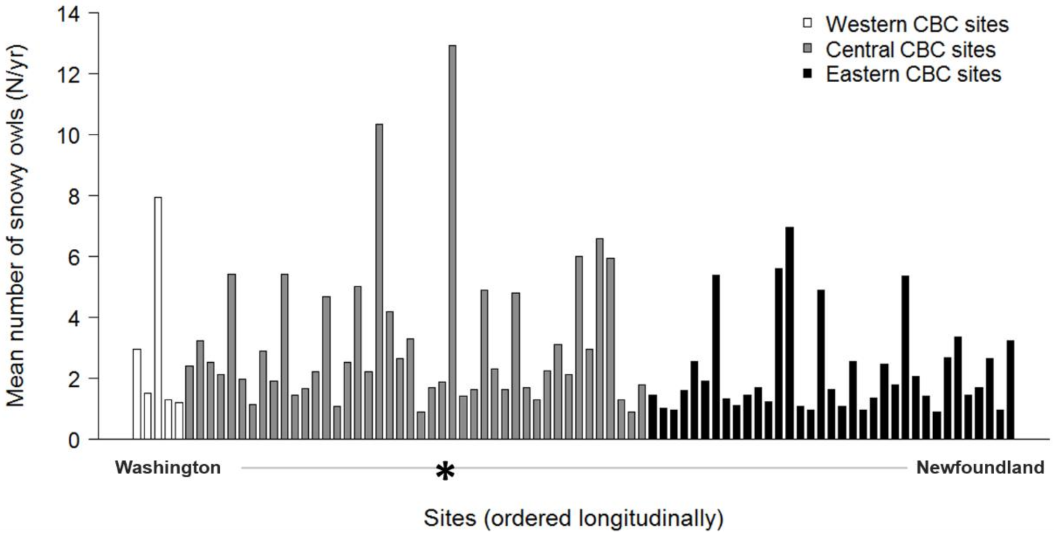

**Figure 3.3**. Mean number of snowy owl observations at each selected Christmas Bird Count (CBC) site for the years 1994 to 2011. Sites are ordered longitudinally, from the westernmost site in Washington State, USA, to the easternmost site in Newfoundland, CAN. These 84 sites were selected based on the presence of irruptive numbers of owls, and exclude sites where the presence of snowy owls was accidental or sporadic (see methods). The center of the Prairies region (see Fig. 3.1) is depicted with the black star.

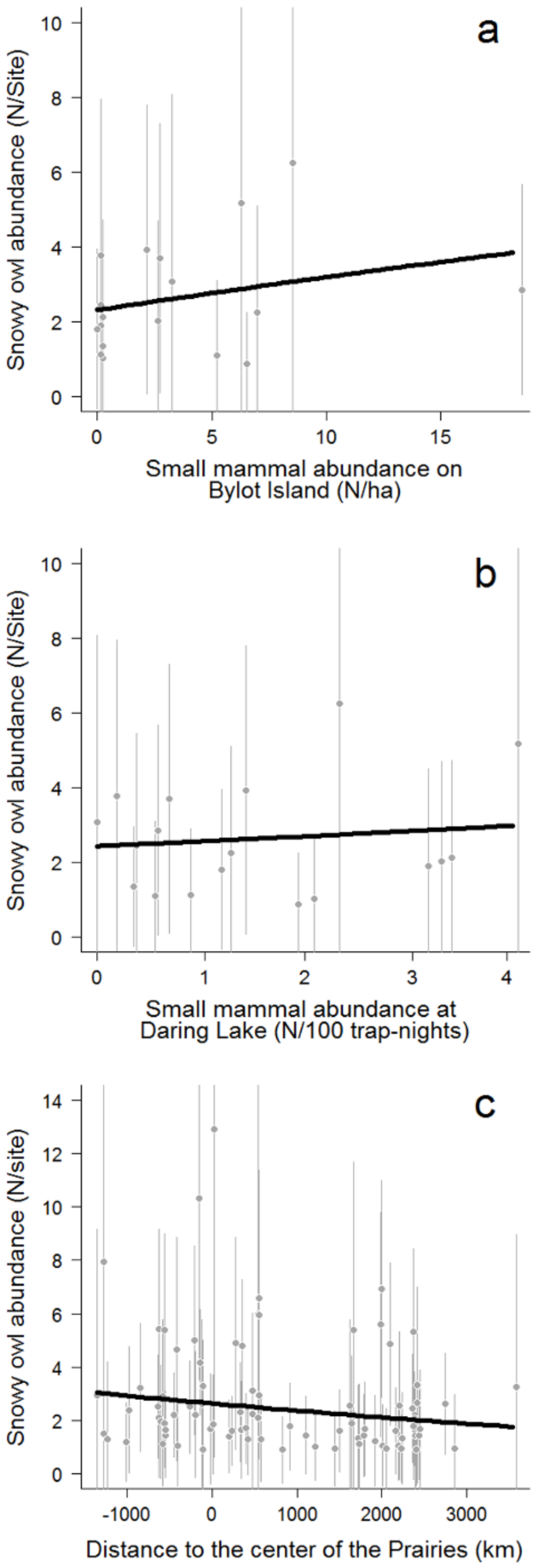

**Figure 3.4.** Relationships between abundance of wintering snowy owls in southern Canada and northern USA predicted by the model-averaged coefficients (from the second component of the Zero-Inflated Negative Binomial model; see Table 3.2) and a) small mammal abundance on Bylot Island, b) small mammal abundance at Daring Lake, and c) longitudinal distance from the Prairies center. Mean ± SD annual abundance of snowy owls is presented to illustrate the fit of the model. Abundance values on the X axis are not directly comparable between the two sites (panels a and b) because of different units.

# CHAPITRE 4: Variability in stable isotopes of snowy owl feathers and contribution of marine resources to their winter diet

Référence de la publication:

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## 4.1. Résumé

Le harfang des neiges est un prédateur arctique reconnu pour son comportement nomade. Des suivis satellitaires ont révélé que certains harfangs adultes utilisaient de façon importante le milieu marin durant la saison non-reproductive. Cependant, la contribution relative des ressources marines à leur régime alimentaire est inconnue. Les analyses d'isotopes stables peuvent être utiles pour documenter le régime alimentaire des espèces animales mobiles durant des périodes de l'année où les individus sont moins accessibles. La présente étude évalue la variation des valeurs isotopiques ($\delta^{13}C$ et $\delta^{15}N$) de différents types de plumes, et l'utilité potentielle de ces plumes pour déterminer la contribution du milieu marin au régime alimentaire hivernal des harfangs des neiges capturés en été. Des plumes de 6 parties du corps ont été échantillonnées sur 18 femelles reproductives à deux sites dans l'est de l'Arctique canadien en 2013 et 2014. Avant d'effectuer les analyses isotopiques, nous avons déterminé les facteurs de discrimination pour les plumes de harfangs sur des individus en captivité. La variabilité des valeurs isotopiques entre les différents types de plumes était relativement faible. Aussi, les corrélations par paires (*pairwise correlations*) des valeurs isotopiques des plumes d'un même individu étaient variables et souvent faibles, suggérant des différences dans le régime alimentaire au moment de la pousse de ces différentes plumes. Les modèles de reconstruction du régime alimentaire (*diet reconstruction models*) ont détecté des contributions de sources marines dans les plumes de harfangs variant de 4% à 19%, entre les différentes parties du corps. Cependant, la contribution marine était très variable lorsque les plumes individuelles étaient examinées sur chaque individu, et variait alors entre 3% et 71%. Ces résultats indiquent qu'aucune plume provenant d'une partie du corps spécifique pourrait être utilisée seule pour inférer la contribution des ressources marine dans le régime alimentaire des harfangs de façon fiable, ce qui serait possiblement expliqué par une grande variabilité dans la séquence et la période de mue. Pour les espèces avec une mue asynchrone comme les harfangs, nous recommandons ainsi l'échantillonnage de plusieurs plumes de différentes parties du corps, en excluant les plumes des ailes, pour étudier le régime alimentaire ou l'utilisation de l'habitat en hiver.

Mots-clés: *Bubo scandiacus*, carbon-13, nitrogen-15

## 4.2. Summary

The snowy owl is an elusive arctic predator known for its nomadic behaviour. Satellite tracking has revealed that some adult snowy owls could make an extensive use of the marine environment during the non-breeding season. However, the relative contribution of marine resources to their diet is unknown. Stable isotope analyses can be useful to document the diet of mobile animals during periods of the year when individuals are less accessible. This study aimed to assess variation in isotopic values ($\delta^{13}$C and $\delta^{15}$N) of various feather types, and the usefulness of feathers to determine the contribution of the marine environment to the winter diet of snowy owls captured in summer. We sampled feathers coming from 6 body regions of 18 breeding females at two sites in the eastern Canadian Arctic in 2013 and 2014. Prior to analyses, diet-tissue discrimination factors of snowy owl feathers were established in captivity. Variability in isotopic values among feather types was relatively low and pairwise correlations in isotopic values between feathers on the same individual were variable and often low, which suggests differences in the diet at the time when various feathers were synthesized. Diet reconstruction models detected a contribution of marine sources to snowy owl feathers ranging from 4% to 19% among feather types. However, the marine contribution was highly variable when single feathers were examined within individuals, ranging from 3% to 71%. This indicated that no single feather type could be used alone to reliably infer the contribution of marine resources to the winter diet of owls, possibly due to a high variability in the timing and sequence of molt. For asynchronous molters like snowy owls, we recommend sampling multiple feathers from various body regions, excluding wing feathers, to investigate winter diet or habitat use.

*Keywords*: *Bubo scandiacus*, carbon-13, nitrogen-15

## 4.3. Introduction

Top predators are often highly mobile and can move over large distances during their life cycle. Examples include seabirds (Akesson and Weimerskirch 2005, Phillips et al. 2007, Egevang et al. 2010) and arctic predators (Tarroux et al. 2010, Therrien et al. 2014b), which can roam over large areas in search of food. To document the diet of highly mobile animals, stable isotope analyses can be useful (Hobson and Wassenaar 2008, Inger and Bearhop 2008, Hobson 2011), especially during periods of the year when individuals are less accessible such as when foraging at sea. Arctic foxes *Vulpes lagopus* (Roth 2002, Tarroux et al. 2012) and long-tailed jaegers *Stercorarius longicaudus* (Julien et al. 2014) are two arctic-breeding species that use the marine environment during the non-breeding season and for which stable isotopes have been used successfully to analyse season-specific diet.

The snowy owl is a tundra-nesting top predator well known for its nomadic and irruptive migratory behaviour (Fuller et al. 2003, Therrien et al. 2014b), which complicates the study of this species during the non-breeding season. Recent evidence based on satellite tracking suggests that in eastern North America, most adults remain in the Arctic in winter and may use the marine environment for several weeks feeding on seabirds (Therrien et al. 2011b). However, the relative contribution of marine resources to the diet of snowy owls is unknown. Stable isotope analyses of animal tissues can be useful to address this question because the isotopic values of potential prey are highly contrasted between the terrestrial and marine environments (Deniro and Epstein 1978, 1981, Hobson and Clark 1992a). However, capturing snowy owls during the non-breeding season in the Arctic to obtain samples for isotopic analyses is extremely difficult, especially in the marine environment. In contrast, capturing owls at nests during the summer is relatively easy (Therrien et al. 2012), and thus offers an opportunity to obtain samples for isotopic analyses provided that some tissues can retain isotopic information on prey ingested during the winter period when birds are at sea.

Feathers collected during the breeding season represent a potential tissue to investigate winter diet because isotopic ratios of keratin, the structural component of feathers, are determined when the tissue is synthesized (i.e., during the period of feather growth) and remain fixed thereafter (Hobson and Clark 1992a, Hobson 1999, Bearhop et al. 2002). In most bird species, feathers are synthesized during the non-breeding season to limit overlap between moult and reproduction (Payne 1972, Howell 2010), two energetically-costly activities, and hence could provide information on the diet during this part of the annual cycle. Unfortunately, moult patterns and timing of feather growth are poorly known in most species. Moult of flight feathers in snowy owls probably starts on the breeding grounds and may extend into the fall or winter period but body feathers can potentially moult year-round (Pyle 1997b). Moult patterns may also vary between sexes and with prey abundance on the breeding grounds (Solheim 2012). Variable moulting patterns of body and flight feathers has the potential to create within-individual heterogeneity in isotopic ratios of feathers (Carravieri et al. 2014), but few studies have looked at those variations within individuals and most of them were carried out on seabirds (e.g., Bond and Diamond 2008, Jaeger et al. 2009, Brasso et al. 2013, Carravieri et al. 2014).

Our aims were therefore to 1) assess the intra-individual variation in feather and blood isotopic values ($\delta^{13}$C and $\delta^{15}$N) of snowy owls captured during the summer, 2) assess if feather $\delta^{13}$C and $\delta^{15}$N could be useful tools to assess the contribution of the marine resources to the winter diet of owls, and 3) assess the average contribution of the marine ecosystem to the diet of snowy owls. We expected variations in $\delta^{13}$C and $\delta^{15}$N values of feathers from different body regions of the same individual because snowy owls are considered asynchronous moulters (i.e., feathers should be synthesized at different places or times, when diet is potentially different; Pyle1997b). In contrast, blood $\delta^{13}$C and $\delta^{15}$N values should show less variability because of the terrestrial-dominated diet of owls during breeding. Using isotopic mixing models, we then investigated the intra- and inter-individual variability in the contribution of marine resources to the diet of owls. For these calculations, we experimentally determined the discrimination factors of $\delta^{13}$C and $\delta^{15}$N owl feathers (Hobson and Clark 1992b), and obtained isotopic values of potential prey items of non-breeding owls. We expected marked inter-individual variations in the marine contribution to the diet of owls because the use of marine environments during the winter is highly variable among individuals (Therrien et al. 2011b).

## 4.4. Methods

### *4.4.1. Study system*

Tissue sampling of wild snowy owls was carried out at two different sites in the eastern Canadian Arctic: Deception Bay, QC (62°02N 74°49W; Low Arctic) in 2013 and Bylot Island, NU (73°08N 80°00W; High Arctic), in 2014 (Fig. 4.1). Deception Bay is located at the northern tip of the Nunavik region of the province of Quebec, and characterised by a rugged and largely rocky terrain with lush tundra vegetation in river valleys. Ungava lemmings *Dicrostonyx hudsonius* and meadow voles *Microtus pennsylvanicus* were the main small mammal found at this site, and lemmings in particular were abundant in the region in 2013 (Robillard unpubl. data). In Nunavik, nest searches for owls were carried out along the 97 km-long road from the Raglan mine settlement (Katinik) to the coastal port of Deception Bay.

Bylot Island is a coastal study site dominated by herbaceous tundra and composed of a mosaic of mesic (85%) and wet (15%) environments where 2 species of small mammals are found: brown lemmings *Lemmus trimucronatus*, the most abundant species, and collared lemmings *Dicrostonyx groendlandicus* (see Gauthier et al. 2011 for a description of the study area). Nest searches for owls took place on the south plain of the island over an area of ~450 km$^2$. We aimed to capture birds in the late incubation period or soon after hatching to limit nest abandonment by the parents. All captures of snowy owls were performed with bow-nets set at the nest (but one was performed using a bal-chatri, i.e. a noose-covered cage with a live bait), from 8 to 18 July 2013 at Deception Bay, and 29 June to 5 July 2014 on Bylot Island. The later capture dates on Deception Bay was due to our delayed arrival to the site because of logistic constraints, and not due to differences in breeding phenology, which was similar at both sites (laying date expressed as julian day: Bylot Island: mean = 152, range = 144 – 164, n = 6; Deception Bay: mean = 146, range = 137 – 153, n = 10; p = 0.08 [t-test]).

### *4.4.2. Tissue sampling in the field and preparation*

Snowy owl feathers and blood were collected on 10 nesting females in 2013 and 8 females in 2014. We plucked or cut feathers from 6 different body regions: top of head, rear of neck, breast, flank, rump and wing (secondaries) and stored them in individual envelopes at room temperature. For wing feathers, 1 new feather (dark brown) and 1 old feather (worn, pale brown) were collected from either the right or left wing. In the laboratory, feathers were washed with a 2:1 chloroform: methanol solution, oven dried at 50°C for 24 hours, and homogenized by cutting them with scissors into approximately 1-3mm fragments. Feather shafts were excluded from homogenization (except for very small ones like head feathers) to limit within-feather variability (Grecian et al. 2015).

We took a 1-ml blood sample from the brachial vein of each individual with a syringe and immediately transferred it to a 70% ethanol-filled Eppendorf tube kept frozen at -20°C. Ethanol does not significantly alter carbon and nitrogen isotopic composition of tissues (Hobson et al. 1997, Therrien et al. 2011a). In the laboratory, blood samples were freeze-dried at -50°C for 72 hours and ground to a fine powder with mortar and pestle. For stable isotope analyses, ~0.7 mg of feathers (n=146) and ~1 mg of blood (n=16) were subsampled, weighed to the nearest 0.001 mg and packed into tin capsules.

To evaluate the proportion of marine sources in the diet of snowy owls, we obtained isotopic values via tissues of potential prey items from different locations and environments within their known winter range (Fig. 4.1). In eastern North America, adult snowy owls winter mainly in south Baffin and Nunavik and in the surrounding marine environment in Davis Strait/Labrador Sea, Hudson strait and eastern Hudson Bay (Therrien et al. 2011b). Thus, we included the following prey groups in our analyses: (1) breast muscles from seabirds, i.e., common eider *Somateria mollissima*, thick-billed murre *Uria lomvia*, common murre *Uria aalge*, razorbill *Alca torda* and long-tailed duck *Clangula hyemalis* (liver in this case) collected in winter; (2) breast muscles from terrestrial birds, i.e., rock ptarmigan *Lagopus muta*; (3) muscles from terrestrial small mammals, i.e., brown, collared and Ungava lemmings and meadow vole. We collected Ungava lemmings and meadow voles in the field near Deception Bay, samples of seabirds were accessed via the Seabird Research Team at Environment and Climate Change Canada (Annexe S3.2) and rock ptarmigans were given to us by Inuit hunters (see Fig. 4.1 and Annexe S3.2 for exact sampling locations). Sources were pooled in 2 groups: marine (n = 5 species) and terrestrial sources (n = 5 species) for stable isotope mixing models, given equal weight to each species within group.

Tissue samples collected in the field were stored frozen at -20°C. In the laboratory, samples were freeze-dried at -50°C, ground to a fine powder with mortar and pestle and lipid were extracted with chloroform using a Soxtec apparatus (Tecator system 1043) before isotopic analyses. Lipid extraction reduces the risk of introducing significant biases in $\delta^{13}C$ values, which often differ between lipid and non-lipid fractions (Tieszen et al. 1983), and is especially important when comparing sources with variable lipid content (Post et al. 2007). For stable isotope analyses, ~1 mg of sources tissue were subsampled, weighed to the nearest 0.001 mg and packed into tin capsules. All values reported are lipid extracted values. Because of the difficulty of obtaining prey tissues from all the different sources, prey tissues came from different years depending on the species and often from a single year for a given species. Therefore, we assumed that prey isotopic ratios did not vary significantly from year to year. However, even if this assumption was not entirely met, annual variation in isotopic values within prey species (e.g. collared lemmings, Annexe S3.2) is likely to be small compared to the large differences between the terrestrial and marine prey (Fig. 4.2) and thus should have little impact on our results.

### *4.4.3. Diet-tissue discrimination*

We assessed the diet-tissue discrimination factors of feathers using 3 captive snowy owls (2 females and 1 male) from a rehabilitation center affiliated with the Faculté de médecine vétérinaire of the Université de Montréal in Saint-Hyacinthe, Québec, Canada. The birds were found injured in the wild and taken to the centre for treatment where they had been in captivity for at least one year prior to the start of our experiment. At the start of the experiment, a tail feather was removed from each bird (R5 or R6 on the right side) under general anaesthesia to allow for a regrowth of the feather under a known diet. Birds were put on a pure diet of mice several weeks before the start of the experiment and maintained on it thereafter. Mice came from a single source (Charles River Canada, Saint-Constant, Quebec, Canada) and were reared on standard commercial feed (Purina 50 –75). All the mice used in this experiment came from the same batch and were kept frozen at the rehabilitation centre until offered to the birds. Birds ate 4–6 mice every day and ingested individual mice whole. Feathers regrowth started 1-2 month after extraction and lasted between 2 and 3 months.

The newly grown tail feathers were removed from each bird when it was fully grown. Five randomly picked mice from the frozen batch were also sampled. Samples of captive owl feathers were cut into tiny pieces and white mice leg muscles were homogenized and prepared for isotopic analyses using the same methods used for potential prey described above. The mean $\delta^{13}$C and $\delta^{15}$N values of prey items were subtracted from the $\delta^{13}$C and $\delta^{15}$N values of each individual's feather ($\Delta X = \Delta_{tissue}-\Delta_{diet}$) to obtain the resulting discrimination factor of feathers ($\Delta$X). For blood, discrimination factors from Therrien et al. (2011a) were used.

All animal manipulations were approved by the the Animal Care Committees of Université Laval and the Faculté de médecine vétérinaire of Université de Montréal.

### *4.4.4. Isotopic analyses*

Isotopic analyses were performed at the Laboratoire d'Océanographie of Université Laval, Québec, Canada. Stable carbon and nitrogen isotope ratios were measured by continuous-flow isotope ratio mass spectrometer (Thermo Electron Delta Advantage) in the continuous-flow mode (Thermo Electron ConFlo III) using an ECS 4010 Elemental Analyzer / ZeroBlank Autosampler (Costech Analytical Technologies). Samples were loaded into tin capsules and combusted (localized temperature up to 1800°C) for the simultaneous determination of carbon and nitrogen isotopic ratios. Two laboratory standards, USGS40 and USGS41 (Qi et al. 2003), were analysed for every 12 unknown samples in each analytical sequence, allowing instrument drift to be corrected if required. Stable isotope ratios were expressed in $\delta$ notation as parts per thousand (‰) deviation from the international standards

V-Pee dee belemnite (carbon) and AIR (nitrogen). Measurement precision of both $\delta^{15}N$ and $\delta^{13}C$ was estimated to be ≤0.2‰.

To validate the consistency in isotopic analyses among laboratories, 15 of our samples were duplicated and ran at another facility (SINLAB, University of New Brunswick, Fredericton, Canada), where the samples of Tarroux et al. (2012) and Gauthier et al. (2015) had been previously analysed. Mean differences of isotopic ratios between the two labs were small (mean ± SD: $\delta^{13}C$ = 0.25‰ ± 0.14‰; $\delta^{15}N$ = 0.14‰ ± 0.53‰) and within (for $\delta^{15}N$) or very close (for $\delta^{13}C$) to the experimental uncertainty estimated for the standards and spectrometer (see above). Values from corresponding samples were also highly correlated between each laboratory (Pearson correlation, $r = 0.96$; $p = <0.001$; df = 13; for both isotopes).

### *4.4.5. Statistical analyses*

Intra-individual variability of $\delta^{13}C$ and $\delta^{15}N$ values in snowy owl tissues was analysed using linear mixed models (LMM; R, package lme4; Bates et al. 2015). The effects of year, type of tissue (i.e., feathers vs blood) and their interaction on $\delta^{13}C$ and $\delta^{15}N$ values were tested using ANOVAs (R, package car; Fox and Weisberg 2011). Bird identity was included in the model as random effect to account for non-independence of data (i.e. repeated measures) within a given bird. We analysed $\delta^{13}C$ and $\delta^{15}N$ values separately because MANOVA does not allow for inclusion of random effects. Where relevant, post hoc tests using differences in least square means (R, package lmerTest; Kuznetsova 2016) were performed to discern more precisely the differences among various tissues.

To determine the contribution of marine prey to the isotopic ratios of snowy owl tissues, we used stable isotopes mixing models (R, package SIAR; Parnell and Jackson 2013). Models used to infer the intra-individual contribution were run using the following parameters: iterations = 500,000, burnin = 50,000 and flat priors with the function siarmcmcdirichletv4 (for inter-tissue analyses; n=17 or 18 values for each of the 8 tissues). This function runs Markov chain Monte Carlo (MCMC) on stable isotope ratios of individual tissues from each bird to determine its dietary habits (Parnell et al. 2010, Parnell and Jackson 2013). We also determined the contribution of each feather type for each individual using the function siarsolomcmcv4, as only one feather type was available for each individual, with the same parameters as above.

Discrimination factors for feathers (this study) and blood (Therrien et al. 2011a) were accounted for in all models and statistical analyses were performed using R 3.2.2 software (R Development Core Team 2015). Results are presented as means ± SD, unless otherwise stated.

## 4.5. Results

### *4.5.1. Isotopic values of owls' tissues*

Overall mean $\delta^{13}C$ and $\delta^{15}N$ values for wild snowy owl tissues collected during the summer were respectively -23.1 ± 0.6 ‰ and +7.5 ± 1.9 ‰ for feathers and -24.8 ± 0.3 ‰ and +4.9 ± 0.8 ‰ for blood (Annexe S3.2). Generally, we observed a greater variability in isotopic values among individuals than among tissues within individuals (Inter-tissues = $\delta^{15}N$: 3.3 ± 0.3, $\delta^{13}C$: -25.0 ± 0.2; Fig. 4.2a; Inter-individuals = $\delta^{15}N$: 3.3 ± 1.2, $\delta^{13}C$: -25.0 ± 0.4; Fig. 4.2b).

Analyses among feather types showed that pattern of variation in $\delta^{15}N$ values differed between the two years of the study (interaction Year x Tissue; Table 4.1). Post-hoc comparisons indicated little variation among feather types except for flank and head feathers in 2013, which had higher $\delta^{15}N$ values than new wing, and tended to have higher values than neck feathers (Annexe S3.3). In 2014, $\delta^{15}N$ values were generally lower than in 2013 except for new wing feathers (Fig. 4.3, Annexe S3.3). Values of $\delta^{13}C$ showed little variations among feather types (Fig. 4.3) and were slightly but significantly higher in 2013 than in 2014 (mean ± SE: -24.8 ± 0.2 ‰ vs 25.2 ± 0.2 ‰, respectively; Table 4.1, Fig. 4.3).

Pairwise correlations in $\delta^{15}N$ and $\delta^{13}C$ values between body regions on the same individual were quite variable but often low (Table 4.2). Neck and new wing feathers isotopic values did not correlate with any other body region whereas head, rump, flank and breast were the body regions that had isotopic values most often correlated to each other (Table 4.2). Overall, this suggests some differences in the diet at the time when various feathers were synthesized, and that these differences were greatest between new wing or neck feathers and other body regions.

When blood was included in the comparisons, there was again an interaction between year and tissue type for $\delta^{15}N$ values (Table 4.1). Post-hoc comparisons indicated that blood $\delta^{15}N$ values were not significantly different from any feather in both 2013 and 2014, but tended to be lower than head and flank feathers in 2013, and new wing feathers in 2014 (Fig. 4.3 a,d, Annexe S3.3). Again, $\delta^{13}C$ values did not differ among tissues when blood was included in the comparisons but differed between years (Table 4.1). Coefficients of variations of isotopic values were much lower for blood than for feathers for both $\delta^{15}N$ (blood: 15.3%, feathers: 25.3%, range: 20.6% to 32.9%) and $\delta^{13}C$ (blood: 1.1%, feathers: 2.6%, range: 1.8% to 4.7%) values.

### *4.5.2. Discrimination factor and marine contribution to owl diet*

The mean $\delta^{13}C$ and $\delta^{15}N$ values of captive owl feathers were respectively -18.5 ± 0.2 ‰ and +12.1 ± 0.2 ‰ and mean values for white mouse muscles were -20.4 ± 0.04 ‰ and +8.0 ± 0.3 ‰. Diet-tissue discrimination factors ($\Delta^{13}C$ and $\Delta^{15}N$) for snowy owl feathers were therefore respectively +1.9 ± 0.04 ‰ and +4.1 ‰ ± 0.3 ‰ (see Annexe S3.1 for details).
Isotopic values of marine and terrestrial sources differed considerably: marine sources were markedly enriched in $^{13}C$ (marine: -19.5 ± 0.7 ‰, terrestrial: -26.2 ± 1.2 ‰) and in $^{15}N$ (marine: +13.7 ± 1.2 ‰, terrestrial: +3.3 ± 1.8 ‰; Fig. 4.2, Annexe S3.2).

The mean proportions of marine sources in feathers from the 6 body regions of snowy owls varied from 0.037 to 0.188 (Fig. 4.3 c, f) and were greater in 2013 (0.151 ± 0.024) than 2014 (0.074 ± 0.039; t = 4.5, df = 10, p = 0.001). Consistent with $\delta^{15}N$ and $\delta^{13}C$ values, mean proportions of marine sources appeared greater for flank, head and used wing feathers in 2013 and for new wing feathers in 2014, but overall, the variation in marine contribution among feathers was relatively low (Fig. 4.3 c, f). Proportions of marine sources in blood were also generally low (Fig. 4.3 c, f). When we combined the information from all feathers collected on each individual, the mean proportions of contribution of marine sources to feathers ranged from 0.04 to 0.23 among our 18 individuals (Fig. 4.4). However, if we look at the value for each feather in each individual, we found a considerable variability in the marine contribution, ranging from 0.03 to 0.71 (Fig. 4.4). For some individuals, the marine contribution was uniformly low for all feathers sampled (e.g., individuals C, K, and M; Fig. 4.4) but for others, the variability among feathers was very large (e.g., especially individuals G and N; Fig. 4.4).

## 4.6. Discussion

Contrary to our expectations, we did not find large and consistent differences in the nitrogen and carbon isotopic values among feathers coming from various body regions of snowy owls. Nonetheless, diet reconstruction using isotopic mixing models detected a significant contribution of marine sources to snowy owl feathers, which supports the hypothesis that these predators feed in this environment at some point during their annual cycle. Moreover, examining these patterns at the individual level also revealed a large variability, with some individuals showing little contribution of the marine resources to their diet during feather growth, whereas others showing large isotopic differences among feathers. To our knowledge, this is the first study documenting intra- and inter-individual heterogeneity in isotopic ratios and diet of an arctic predator using multiple tissues.

### *4.6.1. Variation among feather type and individuals*

In general, whole blood reflects the diet of animals during the previous few weeks (Hobson and Clark 1992a). Because snowy owls appear strictly terrestrial during the breeding season (Holt et al. 2015), we expected isotopic values of blood samples collected in summer to mainly reflect a terrestrial diet. Diet reconstruction models generally confirmed this result but nonetheless indicated a modest contribution of the marine environment to the blood (8% on average). The marine contribution detected in blood samples could be due to the use of endogenous body reserves acquired at other time of the year by breeding females (Cherel et al. 2005, Fox et al. 2009) to meet some energetic shortfalls (Brodin and Jonsson 2003). It could also originate from marine or coastal prey consumed shortly before breeding. However, considering that blood isotopic values did not totally overlap those of terrestrial prey, we preferred to retain all sources in our analyses to avoid exclusions that may have led to dietary proportion biases (Phillips et al. 2014).

Because snowy owls are considered asynchronous moulters (Pyle 1997b), we expected large and possibly consistent variability in isotopic ratios among feathers coming from various body regions as previously shown in other asynchronous moulters such as the Arctic tern (*Sterna paradisaea*), common tern (*Sterna hirundo*), Leach's storm petrel (*Oceanodroma leucorhoa*), and Antarctic prions (*Pachyptila desolata*; Bond and Diamond 2008, Carravieri et al. 2014). However, the pattern of relatively low variability among feather types that we observed across individuals was shown in synchronous moulters like Sphenisciformes and Procellariiformes (Jaeger et al. 2009, Brasso et al. 2013) in which all feathers moult over a short time period. Pairwise correlations in isotopic values between feathers on the same individual were low for some body parts, which suggest differences in the diet at the time when various feathers were synthesized. As a consequence, marine proportions in the diet of snowy owls inferred from isotopic analyses showed large variations among different feathers within the same individual. At least two hypotheses can explain these patterns.

A first hypothesis may be that timing or sequence of moult among various body regions vary considerably among individuals. Flight feathers in snowy owls are only partially replaced every year with a complete moult spanning a period of 3 to 5 years in a relatively predictable replacement sequence (Pyle 1997b, Solheim 2012). On the other hand, body feathers of all owls undergo a complete annual moult (Forsman 1981), but the sequences and timing of body feather moult is poorly known. While diet can be studied in captivity, molt cannot due to different stress and environmental conditions, therefore very little is known for this species, even if captive birds are available. Body feathers are most often replaced during the pre-basic and/or pre-alternate moults depending on the species but year-round moult of some body feathers has been documented in a few species of birds of prey, including the snowy owl, Swainson's hawk Buteo swainsoni and great horned owl Bubo virginianus (Pyle 1997b, Pyle 2008). In seabirds, random sequences and extent of body feather moult have been reported to cause large within-individual variability in the concentration of contaminants deposited in body feathers during their growth (Bond and Diamond 2008, Carravieri et al. 2014). Therefore, the protracted moult of flight feathers and a highly variable moult of body feathers in snowy owls could explain why some feathers in the same individual showed a very large contribution from the marine environment and others very little, and why feathers with a high marine contribution were not found in the same body regions of all individuals.

A second hypothesis may be that the type of environments used (i.e., marine vs terrestrial) may not only vary among individuals (Therrien et al. 2011b) but also that the period of use of the marine environment (i.e., fall, winter or spring) varies among individuals. A seasonal variability like this would explain why some feathers, which could have grown at different times of the year but in a regular or specific sequence in all individuals, exhibit a variable contribution of marine environment among individuals. However, results from radio-tracking studies do not support this hypothesis because owls that use the marine environment tend to do so at about the same time of the year (i.e., from late December to late March; see Therrien et al. 2011b, chapter 2 in this thesis).

### *4.6.2. Inter-annual differences*

The marine contribution to the diet of owls inferred from feathers was twice as high in 2013 than 2014. This inter-annual variability may reflect geographic variation as owls sampled in 2013 were captured in the Low Arctic whereas owls from 2014 were captured in the High Arctic. Therefore, individuals from each sampling site may have had different diets driven by differences in migration or wintering strategies. For instance, birds collected in 2013 were closer to the marine areas used by wintering owls in the eastern Canadian Arctic (Hudson Bay and Hudson and Davis Straits, Therrien et al. 2011b), which could partly explain these inter-annual differences. However, because each site was sampled in a different year, we cannot identify with certainty the source of variation.

### *4.6.3. Discrimination factor*

Discrimination factors established in this study for feathers are similar to Great skua (lipid-extracted samples) values ($\Delta^{13}C$: 2.21 ± 0.07 ‰; $\Delta^{15}N$: 4.8 ± 0.28 ‰; Bearhop et al. 2002), and are in the higher range of values reported for feathers ($\Delta^{13}C$: 0‰–2‰, $\Delta^{15}N$: 2‰–5‰; Peterson and Fry 1987, Kelly 2000; Annexe S3.1). Discrimination factors are known to vary among species and body tissues for the same species (Deniro and Epstein 1981, Vanderklift and Ponsard 2003, Caut et al. 2009). Thus, establishing these factors in captive experiments is important considering that stable isotope mixing models are sensitive to these values (Bond and Diamond 2011). In this study, the $\Delta_{\text{feathers}}$ differ substantially from the $\Delta_{\text{blood}}$ determined on the same species: $\Delta^{13}C_{\text{feathers}}$ is 1.58 ‰ greater than $\Delta^{13}C_{\text{blood}}$ and $\Delta^{15}N_{\text{feathers}}$ is 2.22 ‰ greater than $\Delta^{15}N_{\text{blood}}$. Moreover, had we used discrimination factors established for another avian predator, e.g., the peregrine falcon *Falco peregrinus* (Hobson and Clark 1992b), as a proxy in our analyses, $\Delta^{15}N$ would have been more enriched in blood than in feathers, the reverse of snowy owls, which would have yielded erroneous conclusions. This emphasizes the need to use tissue-specific discrimination factors and refrain from using other species as proxy. It must however be noted that discrimination factors may also vary with prey type (Caut et al. 2009), an element that could not be taken into account in this study (i.e., captive owls could not be fed with sea ducks). Although it could be a source of variability in our analysis, it probably had a negligible impact on our main conclusions because doubling the error of our discrimination factors in SIAR changed the results by <2% for feathers.

### *4.6.4. Usefulness of snowy owl feathers to infer winter diet*

A limitation of this study lies in the fact that moult patterns in snowy owls, especially of body feathers, are poorly known. The approach we used (i.e., the analysis of feathers from different body regions) nonetheless allowed us to detect a significant marine signal in some feathers of several individuals, which supported our original hypothesis. The use of multiple feathers likely provided a general but conservative estimate of marine resource contribution to snowy owl winter diet, and could potentially help in assessing habitat use. On the other hand, the lack of consistency among feathers also complicates their use as a biomonitoring tool for wintering snowy owls, at least until sequence and timing of body feather moult in snowy owls are better established. Our study could not discriminate a single body region from which we sampled feathers that could be reliably used alone to infer habitat use of snowy owls in winter. Flank feathers were the body feathers that yielded isotopic values with the highest marine contribution on average, but this was not always true at the individual level. Flight feathers should be especially avoided because new wing feathers showed opposite patterns between our 2 years (i.e., their isotopic ratios yielded the lowest marine contribution in 2013 among all body regions but the highest in 2014). This may not be surprising considering the protracted moult of flight feathers in owls and that the last juvenal feathers may not be replaced until the fourth prebasic moult (i.e., fourth year) or later (Pyle 1997a, Pyle 1997b, Solheim 2012). Temporal resolution, however, is likely to be low if moulting patterns are as variable as our data implies. For asynchronous moulters like snowy owls, we thus recommend sampling multiple feathers in different body regions to obtain some information on the animal diet at different periods of its life cycle. Future studies should also examine factors (e.g. age, sex, wintering strategies and habitat use or body condition) that could explain the large inter-individual variations in isotopic values that we found.

## 4.7. Conclusion

Despite some limitations, isotopic analyses of feathers collected during the summer allowed us to uncover a significant contribution of the marine environment to the diet of at least some individuals during the non-breeding season. The consumption of marine environment by snowy owls can have important consequences at the individual level, for instance on their body condition, subsequent reproductive success through carry-over effects or increased exposure contaminants present in marine prey (Harrison et al. 2011, Provencher et al. 2014). At the ecosystem level, the use of marine resources by a top predator of the arctic tundra can also have some implications for cross-system exchanges and allochtonous subsidies (Polis and Hurd 1996), especially for the relatively unproductive terrestrial food web (Gauthier et al. 2011). Future studies should concentrate on addressing these issues.

## 4.8. Acknowledgments

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## 4.9. Supplementary material

**Annexe S3.1.** Isotopic ratios of captive snowy owl tail feathers, of their food, and diet-tissue discrimination factors of feathers and blood.

**Annexe S3.2.** Isotopic ratios of wild snowy owl feathers and blood, and of their potential marine and terrestrial prey.

**Annexe S3.3.** Pairwise comparisons of the $\delta^{15}$N isotopic values among various tissues.

## 4.10. Tables

**Table 4.1**. Results of the ANOVA testing for the effects of the year, tissue type (i.e., feather from various body regions or feather from various body regions+ blood) and their interaction on $\delta^{15}N$ and $\delta^{13}C$ isotopes. The female ID was entered as a random factor in the analysis. Degrees of freedom of the error term for models with feathers only was 94 and 108 for feather types+blood.

| Models | | Factor | F | p-val | df |
|---|---|---|---|---|---|
| Intra-tissue (feather types) | | | | | |
| | $\delta^{15}N$ | | | | |
| | | Year | 2.71 | 0.12 | 1 |
| | | Tissue | 0.72 | 0.64 | 6 |
| | | **Year*Tissue** | **2.37** | **0.04** | **6** |
| | $\delta^{13}C$ | | | | |
| | | **Year** | **4.54** | **0.05** | **1** |
| | | Tissue | 2.05 | 0.07 | 6 |
| | | Year*Tissue | 0.91 | 0.49 | 6 |
| Inter-tissue (feather types+blood) | | | | | |
| | $\delta^{15}N$ | | | | |
| | | Year | 2.79 | 0.11 | 1 |
| | | Tissue | 0.67 | 0.70 | 7 |
| | | **Year*Tissue** | **2.22** | **0.04** | **7** |
| | $\delta^{13}C$ | | | | |
| | | **Year** | **5.18** | **0.04** | **1** |
| | | Tissue | 1.80 | 0.09 | 7 |
| | | Year*Tissue | 0.92 | 0.49 | 7 |

**Table 4.2.** Spearman’s rank-order correlation tests between pairs of tissues collected on the same individual (Wn: wing new, Wu: wing used, R: rump, Fl: flank, Br: breast, N: neck, H: head, Bl: blood) for nitrogen (top) and carbon (bottom) isotopes. Significant correlations are in bold. (*) = $0.05 < p < 0.1$, * = $0.01< p < 0.05$, ** =$p < 0.01$.

| $\delta^{15}N$ | Wu | N | R | Fl | Br | H | Bl |
|---|---|---|---|---|---|---|---|
| Wn | -0.07 | -0.10 | 0.13 | 0.08 | 0.15 | -0.07 | -0.21 |
| Wu | 1.00 | 0.31 | **0.59*** | 0.30 | **0.54*** | **0.48*** | 0.23 |
| N | | 1.00 | 0.01 | 0.14 | 0.12 | 0.22 | -0.22 |
| R | | | 1.00 | 0.46 | **0.81**** | **0.66**** | 0.18 |
| Fl | | | | 1.00 | **0.79**** | **0.87**** | -0.08 |
| Br | | | | | 1.00 | **0.87**** | -0.14 |
| H | | | | | | 1.00 | -0.10 |
| Bl | | | | | | | 1.00 |

| $\delta^{13}C$ | Wu | N | R | Fl | Br | H | Bl |
|---|---|---|---|---|---|---|---|
| Wn | -0.21 | -0.23 | 0.07 | 0.21 | 0.39 | 0.12 | 0.17 |
| Wu | 1.00 | -0.08 | **0.63**** | **0.48*** | 0.27 | **0.47(*)-** | -0.02 |
| N | | 1.00 | 0.07 | 0.21 | -0.04 | -0.12 | -0.12 |
| R | | | 1.00 | **0.72**** | **0.77**** | **0.79**** | 0.12 |
| Fl | | | | 1.00 | **0.63**** | **0.78**** | 0.16 |
| Br | | | | | 1.00 | **0.67**** | 0.05 |
| H | | | | | | 1.00 | 0.22 |
| Bl | | | | | | | 1.00 |

### 4.11. Figures

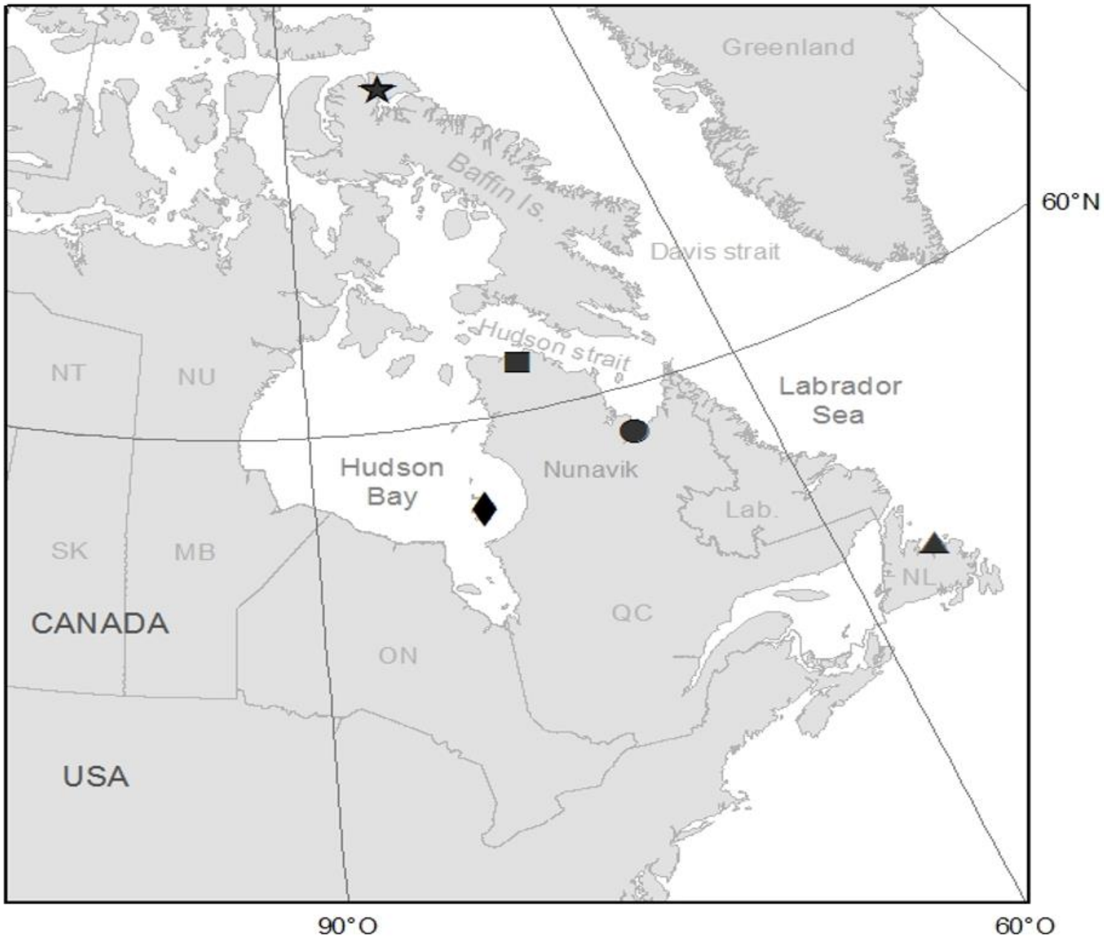

**Figure 4.1**. Sampling locations of snowy owl tissues and potential prey items in eastern North America. Bylot Island, NU (star): feathers and blood of owls (2014), brown and collared lemmings (2007-09); Deception Bay, QC (square): feathers and blood of owls, Ungava lemmings and meadow vole (2013); Belcher Islands, NU (diamond): common eiders (2012) and long-tailed ducks (2000); Kuujjuaq, QC (circle): Rock ptarmigans (2013); Twilingate, NL (triangle): Common murres, thick-billed murres and razorbills (2011-12).

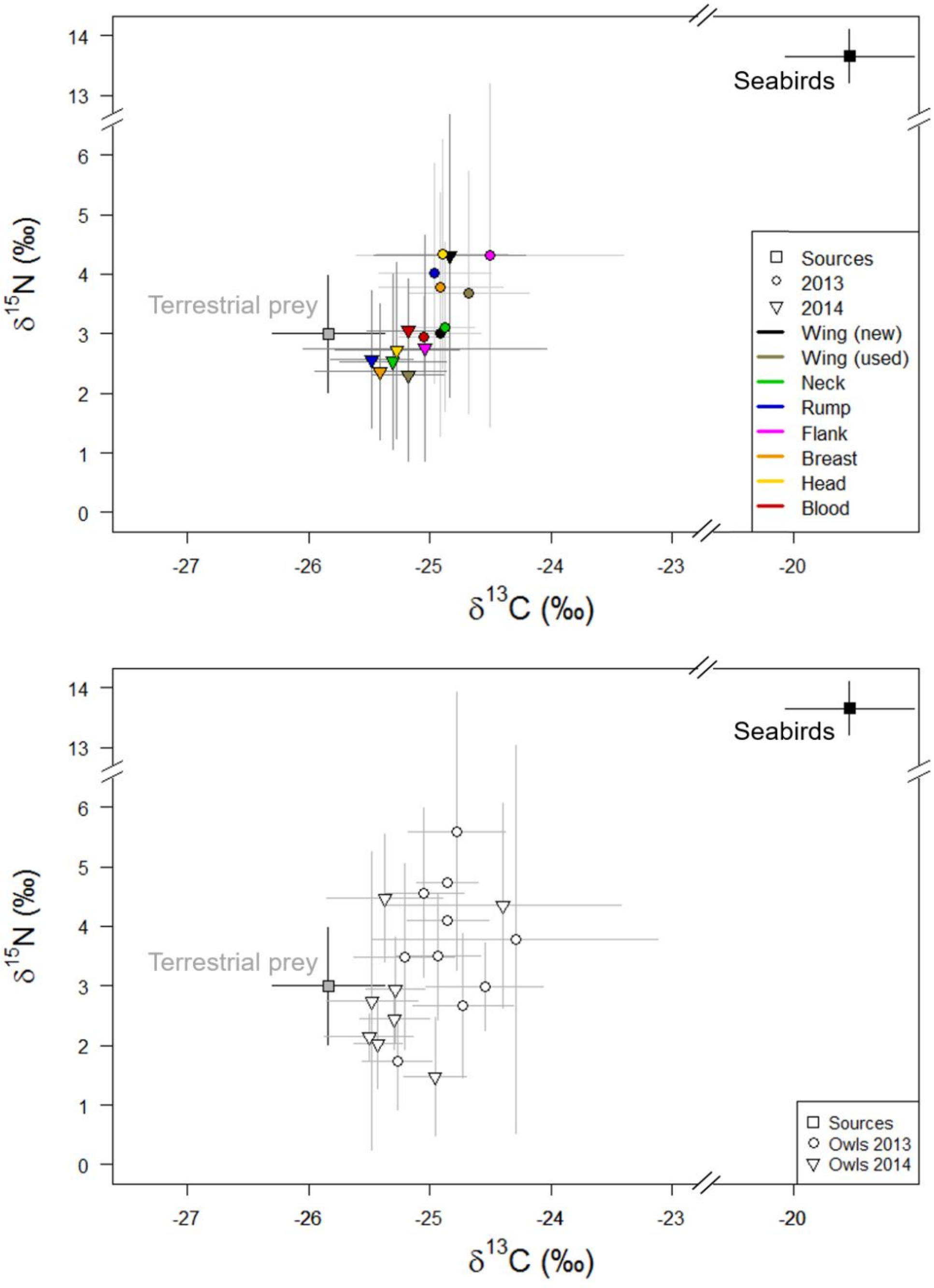

**Figure 4.2**. Relationships between $\delta^{13}$C and $\delta^{15}$N of snowy owl tissues showing (a) the low inter-tissue variability (among 7 feather types and blood) and (b) the greater inter-individual variability in feathers (i.e., 18 females) for 2013 (circles) and 2014 (triangles) presented as means ± SD. Isotopic values of potential prey items are plotted as raw data but values of snowy owl tissues are corrected for their respective discrimination factors.

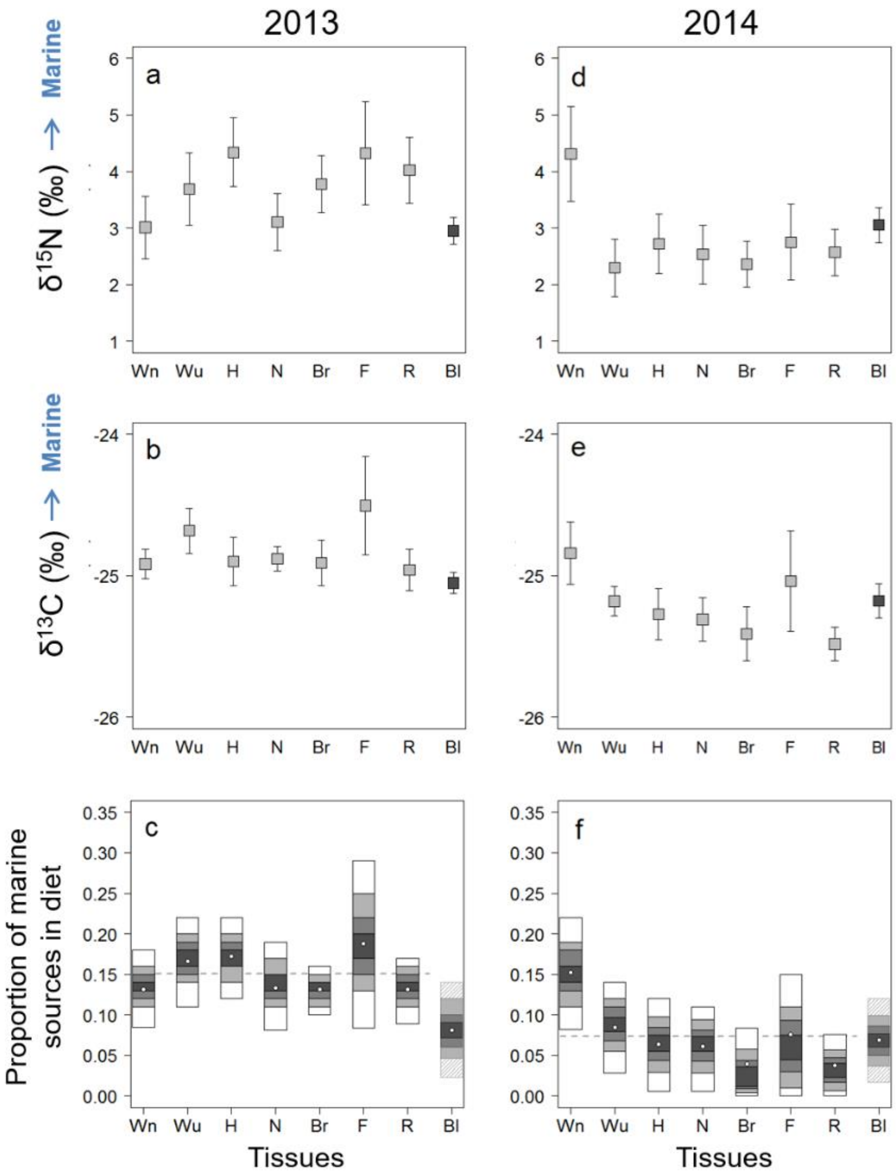

**Figure 4.3.** Variation in $\delta^{15}$N (a,d) and $\delta^{13}$C (b,e) isotopic ratios (mean with SE) in 2013 (a,b) and 2014 (d,e) among snowy owl feather types (gray) and blood (Bl; black). Feather sampled are wing (new=Wn; used=Wu ), neck (N), rump (R), flank (F), breast (Br), and head (H). Proportions of marine sources in different tissues of snowy owls (c,f) are presented with their means (dot) and the 25%, 50%, 75% and 95% credible intervals (dark gray, medium gray, pale gray and white boxes respectively) from the SIAR posterior probability distributions. Dashed lines represent mean proportions of marine sources across all feathers. Isotopic ratios (a, b d and e) were corrected with respective discrimination factors for $\delta^{15}$N and $\delta^{13}$C of blood and feathers to allow a comparison between these 2 tissues.

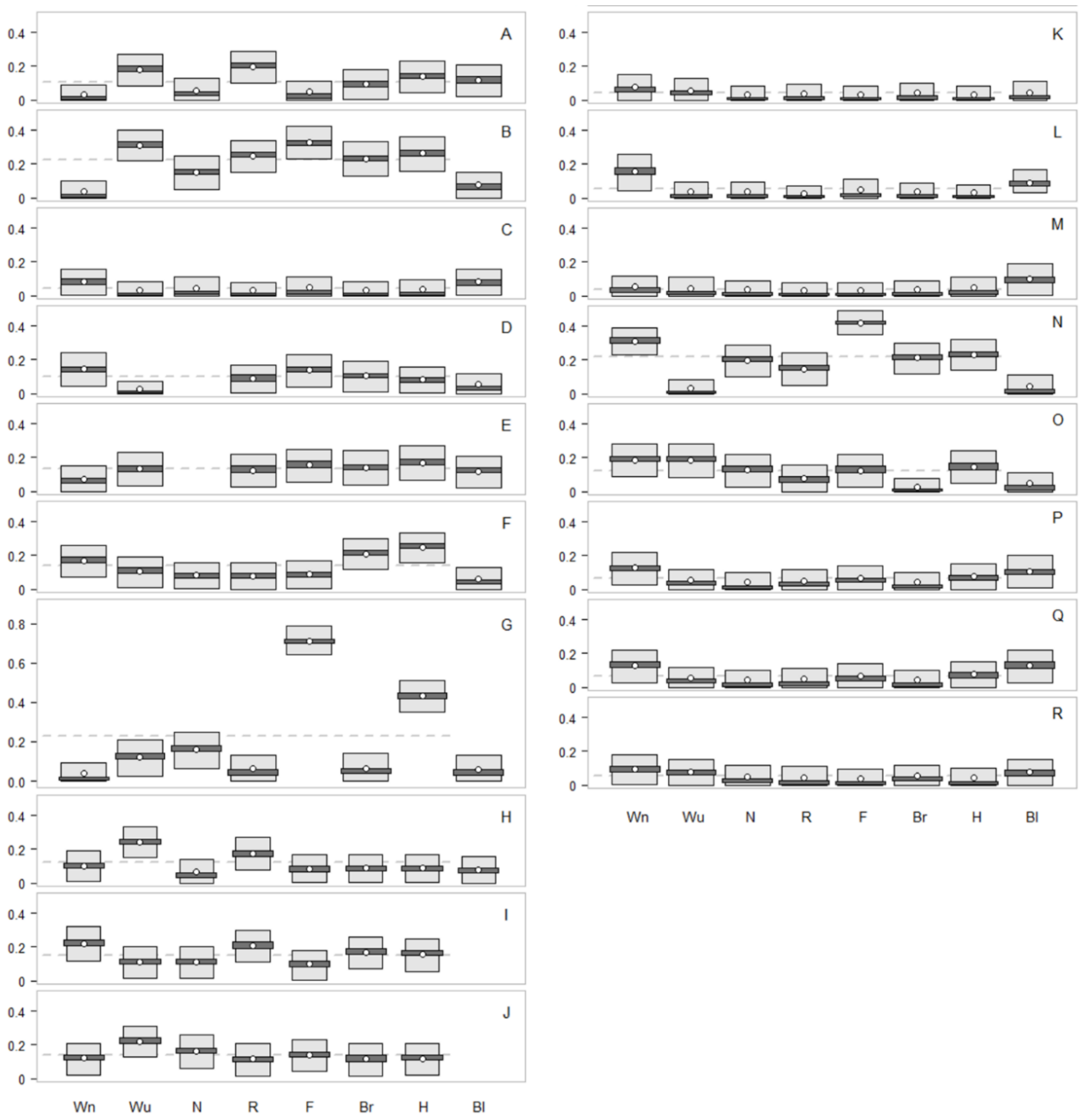

**Figure 4.4.** Mean (dot) proportion of marine sources in different tissues of individual snowy owls and their 25% and 95% credible intervals (dark gray and pale gray boxes, respectively) from the SIAR posterior probability distributions, showing considerable variability in the contribution of marine sources when feathers are analysed independently. Dashed lines depict individual mean proportions of marine sources in diet across feathers. Individuals A to J were captured in 2013 at Deception Bay, QC and individuals K to R in 2014 on Bylot island, NU.

# CHAPITRE 5: Combining satellite tracking and stable isotope analyses of feathers to link winter habitat use, diet and reproduction of snowy owls

En préparation:

Robillard A, Therrien J-F, Gauthier G, Bêty J. *Combining satellite tracking and stable isotope analyses of feathers to link winter habitat use, diet and reproduction of snowy owls.*

## 5.1. Résumé

Combiner les signatures isotopiques de plumes et les suivis satellitaires d'individus marqués a le potentiel de révéler des liens multi-saisons entre l'utilisation de l'espace en hiver, le régime alimentaire et les effets reportés sur les paramètres de reproduction. Les harfangs des neiges utilisent plusieurs tactiques d'hivernage mais leur comportement nomade complique l'étude de leur écologie hivernale. Ils peuvent utiliser les ressources terrestres et marines durant la saison non-reproductive. Nous avons combiné la télémétrie satellite et les analyses isotopiques de plumes pour évaluer si la variabilité interindividuelle dans les contributions marines du régime alimentaire pouvait être liée à l'utilisation de l'habitat hivernal par les harfangs. Nous avons aussi évalué si les variations dans les contributions marines du régime alimentaire influençaient les performances reproductives et la condition corporelle des harfangs par des effets reportés. Dix-sept femelles harfangs ont été capturées sur leur site de reproduction, équipées d'émetteurs satellites et échantillonnées pour les analyses d'isotopes stables ($\delta^{13}$C et $\delta^{15}$N) sur les plumes de 5 parties du corps. Les femelles suivies ont exploité différentes aires d'hivernage : 12 femelles sont restées en Arctique, 3 femelles se sont déplacées jusqu'aux Prairies, et 2 femelles ont migré jusqu'aux côtes de Terre-Neuve et Labrador. Nous avons observé une relation positive entre l'utilisation des environnements marins et côtiers et la contribution des ressources marines dans le régime alimentaire des harfangs. Nos résultats fournissent aussi des estimés quantitatifs de la variation interindividuelle dans le régime alimentaire et l'utilisation de l'habitat des harfangs durant la saison non-reproductive. Nous n'avons cependant trouvé aucune évidence d'effets reportés de la proportion de contribution marine au régime alimentaire sur les performances reproductives subséquentes ou sur la condition corporelle estivale. Notre approche intégrant plusieurs méthodes d'analyses permet d'allonger la couverture temporelle de l'utilisation de l'habitat précédant l'échantillonnage et l'identification d'habitats importants pour la conservation des espèces.

*Mots-clés*: carbone-13, azote-15, harfang des neiges, *Bubo scandiacus*, régime alimentaire, SIAR, environnement marin, habitat d'hivernage

## 5.2. Summary

Coupling isotopic signatures of feathers and satellite tracking of individuals have the potential to reveal multi-season linkage between wintering habitat use, diet and carry-over effects on reproductive parameters. Snowy owls have multiple wintering tactics as they can use both terrestrial and marine resources during the non-breeding season, but their nomadic behaviour complicates their study. We combined satellite telemetry and feather isotopic analyses to assess if inter-individual variability in marine contribution to the diet was a good proxy of their wintering habitat use. We also examined if variations in winter diet can affect the subsequent reproduction performance and body condition through carry-over effects. Seventeen female snowy owls were captured at their breeding site, equipped with satellite transmitters and sampled for stable isotope analyses ($\delta^{13}C$ and $\delta^{15}N$) of feathers from 5 body regions. Tracked snowy owls exploited different areas in winter: 12 females stayed in the Arctic, 3 travelled to the Prairies and 2 to the coast of Newfoundland and Labrador. We found a positive relationship between the use of the coastal and marine environments in winter and the contribution of marine resources to the diet of snowy owls. Our results also provide quantitative estimates of inter-individual variation in diet and habitat use of owls during the non-breeding season. No evidence of carry-over effects of the proportion of marine contribution to the winter diet on subsequent reproductive performance or body condition was found. The integrated approach used in our study allows an extension of the temporal coverage of habitat use prior to sampling and the identification of important habitats or food resources for conservation purposes.

*Keywords*: carbon-13, nitrogen-15, snowy owl, *Bubo scandiacus*, diet, SIAR, marine environment, wintering habitat

## 5.3. Introduction

Intra-population variability in resource use is ubiquitous (Bolnick et al. 2003, Newton 2011). However, for many migratory species, inter-individual variability in diet and habitat use is still poorly documented over the course of their annual cycle (Marra et al. 2015). This is especially true for nomadic species showing complex and irregular patterns of annual movements, often associated to cyclic or fluctuating resources (Newton 2006a, 2008). Variability in resource use during the non-breeding period can have important fitness consequences in migratory animals, including carry-over effects on subsequent breeding performance (Metcalfe and Monaghan 2001, Norris and Taylor 2006, Harrison et al. 2011). Indeed, reproductive success may be affected by diet quality (Sorensen et al. 2009), food abundance (Davis et al. 2005, Penteriani et al. 2013, Cooper et al. 2015) and habitat quality (Marra et al. 1998, Norris et al. 2004, Inger et al. 2010) during the previous non-breeding season. The different wintering tactics may thus have significant impact on fitness but few studies have been able to address those links at the individual level (Marra et al. 2015). The complexity of tracking individuals from wintering sites to distant breeding grounds makes it difficult to link intra-population variability in winter resource use to subsequent breeding performance.

The snowy owl is an Arctic top predator known for its nomadic and irruptive behavior and for the diversity of its wintering tactics (Holt 2015). In North America, some snowy owls migrate from their tundra breeding grounds to temperate sites far inland in the Canadian Prairies and American Midwest, while others stay in the Arctic during the winter and make extensive use of the marine environment (i.e. sea ice and coasts; Therrien et al. 2011b, Chapter 2 in this thesis). The shift to the marine environment is especially surprising for a species that strongly specialises on small mammals during the breeding season (Therrien et al. 2014a, Holt et al. 2015). Owls using the marine environment are exposed to environmental conditions and food resources radically different from those encountered in terrestrial environment.

Using stable isotope analyses of two elements (N and C), we recently showed that a significant contribution of marine resources to the diet of snowy owl could be detected in feathers of individuals captured in summer, indicative that some owls were at least partly relying on marine resources during the non-breeding season (Robillard et al. 2017). Diet reconstruction models showed that the level of marine resource contribution also varied greatly among individuals (Robillard et al. 2017). In this study, we examine the hypothesis that inter-individual variability in diet during the non-breeding season, inferred using feather isotopic signatures, is linked with individual wintering habitat use. To test this hypothesis, we related habitat use of individual female owls tracked with satellite telemetry during the non-breeding season with the contribution of marine sources in their diet. A secondary objective was to investigate potential carry-over effects of the diet and habitat use during the non-breeding season on their subsequent reproduction performance and body condition of females. Considering the large diversity of wintering tactics observed in this species, the snowy owl is a good study model to link inter-individual variability in resource use to subsequent reproduction in nomadic animals.

## 5.4. Methods

### *5.4.1. Study system*

Snowy owls were captured at two different sites in the eastern Canadian Arctic: Deception Bay, QC (62°02N 74°49W; Low Arctic) in 2013 and Bylot Island, NU (73°08N 80°00W; High Arctic), in 2014. Deception Bay is situated in the Nunavik region of the province of Quebec and characterised by mesic tundra and rocky terrain with lush tundra vegetation in river valleys. Nest search at Deception Bay was carried out along the road from the coastal port of Deception Bay to the Raglan mine. Bylot Island is a coastal study site composed of a mosaic of mesic (85%) and wet (15%) habitats (see Gauthier et al. 2011 for a detailed description of the study area). Nest search was carried out in an area of ~450 km$^2$ on the south plain of the island. Captures of snowy owls were performed with bow-nets positioned over the nest or with a bal-chatri trap (one case) set a few meters away from their nest from 8 to 18 July 2013 at Deception Bay and 29 June to 5 July 2014 on Bylot Island. Differences in capture dates between the two sites are explained by logistic constraints that delayed our arrival at Deception Bay, and not due to differences in breeding phenology (see Robillard et al. 2017 for details).

### *5.4.2. Capture and marking of owls*

We captured 10 breeding females at Deception Bay and 8 on Bylot Island. We fitted each owl with an ARGOS satellite transmitter (Microwave telemetry, USA, PTT-100, (N=2); North Star Science and Technology, LLC, USA, PTT-30G (N=16)). The transmitter and harness weighed 40g, which corresponds to 1.8% (range 1.6% to 2.1%) of the birds' body mass and have been shown to have no significant effect on their survival or reproductive performances (Therrien et al. 2012). Transmitters were installed on the owls as a backpack using a harness made of Teflon strips.

Locations were obtained over a 4-6h period at ~2-3d intervals, from December to mid-June and ~5d intervals from mid-June to November. Locations were assigned a class corresponding to their estimated precision, which followed a normal distribution with a standard deviation of <1500m, <500m and <250m respectively for the classes we retained (i.e. 1, 2 and 3; CLS 2016). Positions were averaged to a single mean daily coordinate to avoid non-independence of spatial data (see Chapter 2 for details).

### *5.4.3. Feather and prey sampling and isotopic analysis*

For each snowy owl captured on the breeding ground, we collected one or multiple feathers from each of the 5 following body regions: head, neck, breast, flank and rump. For 2 individuals, neck feathers were missing, so analyses were performed on 4 body regions for these birds.

To reconstruct snowy owl diet, we obtained muscle and liver samples of potential prey items from different locations and environments (see Robillard et al. 2017 for details on how these samples were obtained). They included: (1) marine birds collected in winter (common eider *Somateria mollissima*, thick-billed murre *Uria lomvia*, common murre *Uria aalge*, razorbill *Alca torda* and long-tailed duck *Clangula hyemalis*), (2) terrestrial birds (i.e. rock ptarmigan *Lagopus muta*), and (3) terrestrial small mammals (i.e. brown *Lemmus trimucronatus*, collared *Dicrostonyx groenlandicus* and Ungava *Dicrostonyx hudsonius* lemmings, and meadow vole *Microtus pennsylvanicus*). For stable isotope mixing models, sources were pooled in 2 groups: marine (N = 5 species) and terrestrial sources (N = 5 species), given equal weight to each species within group. We also assumed that prey isotopic ratios did not vary significantly from year to year, based on the high winter site fidelity of some prey species (e.g. Petersen et al. 2012, Tranquilla et al. 2014, Blackburn and Cresswell 2016) or small and overlapping home ranges of others (e.g. Blackburn et al. 1998, Predavec and Krebs 2000, Schmidt et al. 2002), which suggest that these prey feed on similar resources inter-annually.

Prior to stable isotope analyses, feathers were washed with a 2:1 chloroform: methanol solution, homogenized by cutting them with scissors into approximately 1-3mm fragments, subsampled (i.e. ~0.7 mg of feathers) and packed into tin capsules. Muscle and liver samples of prey were freeze-dried, ground to a fine powder with mortar and pestle and lipid-extracted with chloroform using a Soxtec apparatus (Tecator system 1043) before isotopic analyses to reduce the risk of introducing significant biases in $\delta^{13}$C values (Tieszen et al. 1983, Post et al. 2007). Isotopic analyses were performed at the Laboratoire d'Océanographie of Université Laval, Québec, Canada. Details of laboratory techniques for isotopic analyses are presented in Robillard et al. (2017).

### *5.4.4. Habitat use data*

We used locations of snowy owls provided by the transmitters to characterize habitat use. First, we measured the distance to the coast for each location with the nearest-neighbor interpolation method of NASA available in the Movebank Env-Data system (Dodge et al. 2013). Distances (d) to the coast were signed (positive values on land, negative values at sea) and were averaged to a mean daily distance. Each location was then assigned to a habitat class: marine ($d < -5$km), terrestrial ($d > 5$km) or coastal (i.e. marine coasts only; 5km > d >

-5km). The width of the coastal habitat (i.e. 10km) was chosen based on the mean daily distance covered by individuals in this study (i.e. 7.3 ± 2.8 km, n = 1949 locations for 11 individuals) during the winter (i.e. January-February-March), which was less than the width of our coastal strip. Nonetheless, we ran sensitivity analyses by using a coastal width of 15km and 20km. We obtained very similar results (not shown) and thus presented only analyses based on the 10km width. Proportions of locations at sea (i.e. number of locations at sea/total number of locations) and proportions of locations at sea or in the coastal area (i.e. (number of locations at sea + number of locations along the coast)/total number of locations) were calculated.

### *5.4.5. Statistical analyses*

To infer the contribution of marine prey to the isotopic ratios of each individual, we used stable isotopes mixing models (R, package SIAR; Parnell and Jackson 2013). We determined the marine contribution to each feather in each individual using the function siarsolomcmcv4 in R, which is based on a Markov chain Monte Carlo (MCMC) procedure. Models were ran using the following parameters: iterations = 500,000, burnin = 50,000 and flat priors (Parnell et al. 2010, Parnell and Jackson 2013). Diet-tissue discrimination factors estimated for snowy owl feathers ($\delta^{13}C$: 1.88 ± 0.04 ‰; $\delta^{15}N$: 4.12 ± 0.26 ‰; Robillard et al. 2017) were used as trophic enrichment factors in the models.

A limitation of our study is that movements of snowy owls and the marine contribution to their diet could not be estimated over the same time period. Indeed, feathers collected during the summer reflect the diet of owls at the time when feathers were grown in the previous year (i.e. prior to capture) whereas tracking of individuals took place after capture (Fig. 5.1). However, Therrien et al. (2011a) and Robillard et al. (2017) found that individuals were highly consistent in their habitat use over successive winters. Hence, we assumed that the proportion of locations at sea and along the coast is highly correlated from year to year at the individual level (see also Discussion section). We analysed the link between the inferred marine proportion in the diet and wintering habitat use variables at different periods of the year using linear models. In a previous analysis, we found large intra- and inter-individual variability in marine proportion among body feathers possibly linked to variable timing of molt among body parts and individuals (Robillard et al. 2017). To account for that, we used two response variables in our analyses: mean marine proportion across all feathers (n = 5 per individual) and mean marine proportion in the two feathers with the most marine signal (hereafter called marine feathers). To obtain the latter, we selected the two feathers with the highest C and N values. This category allowed us to target feathers that most likely grew during the previous winter when owls potentially fed on marine prey (Therrien et al. 2011a, Robillard et al. 2017). All marine proportions were log-transformed to meet normality requirements.

To examine inter-individual variability in the marine contribution to feather isotopic signatures, we ran linear models using four explanatory variables: 1) proportion of all locations at sea, 2) proportion of all locations at sea and along the coast, 3) mean distance to the nearest coast (km) and 4) latitude, as conditions experienced by birds wintering in Arctic are different than those at more southern latitudes. Each explanatory variable was tested in separate models to avoid over-parametrization and because most of them were highly correlated. We examined these relationships over 3 general periods of the annual cycle: 1) autumn (1 Sept. - 31 Dec.), 2) winter (1 Jan. – 31 March) and 3) all year (starting at capture date and including all locations until the next breeding season). To ensure enough temporal coverage of each period used in the analyses (autumn, winter and entire year), we selected individuals that were tracked during more than half of the period for the autumn and winter periods (autumn: N=17; winter: N=12 individuals), and individuals that were tracked from summer (capture date) to 1 May or later for the entire year period (N=11 individuals). For all models, collection year was also entered as a fixed effect because this variable affected both $\delta^{13}$C and $\delta^{15}$N values of snowy owl feathers from which the diet was inferred (Robillard et al. 2017). Models with year as a fixed variable always performed better than models without it in terms of AICc. Statistical analyses were performed using R 3.2.0 software (R Development Core Team 2015). Results are presented as means ± SD, unless otherwise stated.

## 5.5. Results

### *5.5.1. Habitat use*

Among the 18 marked owls, 17 females were tracked for extended time periods, ranging between 132 and 714 days (mean = 411 ± 222 days), which allowed the recording of 18 to 256 daily locations (mean = 154 ± 87 locations) after location-class filtering. One transmitter emitted for only 2 weeks, and hence one individual was excluded from analyses.

Owls tracked during our study period exploited different areas throughout the years. In winter, 12 owls stayed in the Arctic (e.g. Hudson Bay, Hudson and Davis straits) while 3 travelled to the southern Canadian Prairies and northern US Midwest and 2 to the coast of Newfoundland and Labrador. In winter, the mean distance of daily locations to the nearest coast (175 ± 461 km) was greater than in autumn (89 ± 280 km) or throughout the year (104 ± 330 km; Table 5.1), consistent with the fact that some females wintered far inland while others made extensive use of sea ice and coast. Proportion of locations at sea and along the coast also exhibited a large variability among individuals in winter, ranging from 0 to 1 (Table 5.1).

In terms of time spent in the marine environment (i.e. number of days between the first and last location at sea), one female spent the whole winter (i.e. 186 days) at sea, while 4 others spent a considerable amount of time there (respectively 143, 141, 138 and 122 days). For females that spent a large proportion of their time (>50%) at sea in winter, their average distance to the coast ranged from -7 to -68 km (negative values were used when they were at sea). At the opposite end, two females that travelled to the central part of the continent spent 100% of their time inland in winter and their average distance to the coast were 617 km and 1214km.

### *5.5.2. Link between diet and habitat use*

Mean proportion of marine sources in the diet of individual owls ranged from 0.04 to 0.29 when using all feathers and from 0.04 to 0.57 when using the 2 marine feathers (Fig. 5.2). Coefficients of variation were large (55% when using all feathers and 69% with the marine feathers), indicating marked inter-individual variability in the use of marine resources.

We found no link between marine proportions in the diet and habitat use during the autumn period (Table 5.2). In winter however, we found a negative relationship between the proportion of marine sources in the diet of snowy owls and the distance to the coast when using either all body feathers or marine feathers (Table 5.2). Feathers of birds wintering far from the coast (i.e. far inland in the Prairies and Midwest) had a relatively low contribution of marine resources in their diet compared to birds that were close to or in the marine environments, though we noted a large variability in the latter group (Fig. 5.3). The relationships were significant even if we excluded the 2 most extreme inland birds (i.e. the two birds wintering at an average of 617 and 1214 km from the coast; All feathers: Est.: -2.30, CI low: -6.03, CI up: 1.43; Marine feathers: Est.: -4.01, CI low: -8.00, CI up: -0.002; Fig. 5.3). In addition, we also found a positive relationship between the proportion of marine sources in the diet and the proportion of locations at sea and along the coast, and a near significant relationship when using the proportion of locations at sea (Table 5.2, Fig. 5.3). When using locations throughout the year, we also found an inverse relationship between marine proportions estimated in feathers and distance to the coast (Table 5.2).

### *5.5.3. Carry-over effects on reproduction*

Clutch size of individuals at the time of capture ranged from 1 to 9 eggs (mean: 6.1 ± 1.8 eggs) and their body mass at capture varied from 1.92 to 2.49 kg (mean: 2.18 ± 1.12 kg). The mean laying date in 2013 was 31 May (n=10) and 25 May in 2014 (n=6) but ranged from 17 May to 13 June in both years. Clutch size and laying date were not related to inferred marine proportions in the diet but a trend for an inverse relationship was found for body mass (Table 5.3). Birds with a high proportion of marine source in their feathers tended to be lighter than those with a low proportion (Annexe S4.1) and we observed the same trends if we used all feathers or only the two marine feathers (Annexe S4.1).

## 5.6. Discussion

By combining data on habitat use derived from satellite transmitters with those on the diet inferred by stable isotope analyses of feathers, we showed a link between the intra-population variability in the use of the coastal and marine environments in winter and the contribution of these environments to the diet of snowy owls. This confirms our hypothesis that inter-individual variability in diet during the non-breeding season is linked with individual wintering habitat use. However, we found no evidence of carry-over effects on subsequent reproduction of variability in the contribution of the marine environment to the diet inferred from feathers.

### *5.6.1. Seasonal habitat use and diet*

Our study confirms previous reports that snowy owls breeding in the eastern North American Arctic can winter in a wide spectrum of habitats, including the arctic tundra, the arctic marine environment and the North American Prairies (Therrien et al. 2011b, Chapter 2 in this thesis). In this study, most owls (i.e. 80%) used the marine environment in winter with some individuals (i.e. 8/12 owls) spending over 95% of their time over sea ice or along the coast. Our isotopic analyses showed that a significant part of the owls' diet comes from the marine environment. This clearly establishes that marine prey are a major food source for wintering owls in the eastern Canadian Arctic. Although owls also used the marine and coastal environments to some extent during autumn, we found no relationship between the use of this habitat in autumn and the marine contribution to their diet as inferred from the isotopic composition of feathers. It is possible that none of the feathers that we sampled grew in autumn and thus none of them provided information on the diet at that time of the year (Robillard et al. 2017). Alternatively, and perhaps more likely, the relative availability of marine prey to owls are lower in autumn than in winter in the Arctic.

Indeed, although the total abundance of marine prey like seabirds may be greater in autumn than in winter, before many of them migrate south, they may be harder to catch at that time. In autumn, sea ice only began to freeze and therefore seabirds are likely still scattered over large expanses of water, rendering prey catching more difficult for owls. On the other hand, snow cover is still low or inexistent during the autumn season, which allows owls to easily prey on terrestrial prey like small mammals or land birds (Potapov and Sale 2012). In winter, ice cover becomes more extensive, leaving only small areas of open-water (i.e. polynyas and leads) where seabirds often concentrate in dense aggregations (Gilchrist and Robertson 2000), thereby facilitating prey capture by owls. Robertson and Gilchrist (2003) reported that the number of snowy owls near polynyas of the Belcher Island in Hudson Bay where positively related to the local abundance of sea ducks in winter. In contrast, the availability and vulnerability of prey in the tundra, primarily lemmings, decrease between autumn and winter. Lemming populations are often at their lowest seasonal density at the beginning of the snow season after suffering intense predation pressure during the summer and autumn season (Gilg et al. 2003, Therrien et al. 2014a, Fauteux et al. 2015b). In addition, catching lemmings may become harder once snow covers the ground (Chamberlin 1980, Therrien et al. 2015). Snowy owls using mainly the marine environments also tended to settle later during the non-breeding season than birds using terrestrial environments (Chapter 2). Therefore, some owls may progressively switch from a primarily terrestrial-based diet in autumn to a predominantly marine one during winter.

Our results confirm that snowy owls can show a great flexibility in their diet during the non-breeding season, and possibly more than previously recognized (Holt et al. 2015), in response to variations in prey availability. However, the extensive use of sea ice and reliance on marine prey observed in owls wintering in the eastern Canadian Arctic contrast with observations made in Norway, Russia and western North American Arctic. In those areas, use of the sea ice by owls in winter is limited or negligible (Fuller et al. 2003, Jacobsen et al. 2009, Doyle et al. 2017). These differences may arise due to variability in prey availability or accessibility among these regions in winter. For instance, the marine environment of the eastern Canadian Arctic is more productive than the western Arctic (Frey et al. 2015) and may thus harbour a higher density of seabirds in winter (e.g. Fort et al. 2010, Hunt et al. 2013). Alternatively, other continental areas may offer a higher density and diversity of prey for owls such as high density of snowshoe hares and ptarmigans in Alaska and Yukon (Doyle et al. 2017).

### *5.6.2. Potential limitations of the study*

An important assumption in our analyses was that individuals were consistent in their winter habitat use from year to year because feather stable isotopes reflected diet prior to the period of satellite tracking (Fig. 5.1). Changes in wintering habitats between years (i.e. individual wintering in the marine/coastal environment one year and far inland the next year or vice versa) could partly explain some of the unexplained variability in our relationships. Such habitat shifts may be more likely for young individuals that breed for the first time because immature individuals generally move to southern inland areas rather than remaining in the Arctic (Smith 1997, Robillard et al. 2016). In our study system, most individuals (81%; n=21; Chapter 2) were quite consistent in their use of marine/coastal and inland environments over successive winters, so we can conclude that the assumption of fidelity to their wintering strategy was largely met. However, the possible occurrence of environmental shifts observed in a few birds likely rendered our analyses more conservative because the “wrong” wintering habitat would have been associated with the isotopic signatures of feathers recorded in the previous year. The fact that we still find several significant relationships despite such potential limitation suggests that they are robust.

Another factor that may have contributed to unexplained inter-individual variability in marine contribution to the diet of owls wintering near the coasts is differential prey selection. Among snowy owls’ potential marine prey items, long-tailed ducks, common murres and thick-billed murres, which feed mainly on crustaceans and fish (Gaston and Hipfner 2000, Jamieson et al. 2001, Robertson and Savard 2002), are considered higher trophic-level prey than common eiders that feed on bivalve and mollusk (Hobson 1993, Goudie et al. 2000). If some individuals specialised on marine prey at specific trophic levels, this could have affected our estimation of the marine contribution to their diet. For instance, high $\delta^{15}N$ value in the feathers of some owls could be due to those individuals feeding on prey of higher trophic level at the time of feather growth (Hobson 1993), and this greater ratio would bias our estimates of marine proportion in their diet.

Another potential limitation of the study is that we have sampled terrestrial prey from northern sites only, although 3 owls have wintered in the continental Prairies where prey species differ. Thus, we may not have covered adequately the range of isotopic signatures of prey base for these birds. However, although the reported isotopic values of small mammals in the Prairies (e.g. Deer mice *Peromyscus maniculatus* in Saskatchewan $\delta^{15}N$: 7.6 ± 1.6 ‰, $\delta^{13}C$: -23.4 ± 1.0; White et al. 2012) are greater than isotopic values of small mammals in Arctic ($\delta^{15}N$: 3.4 ± 4.1 ‰, $\delta^{13}C$: -26.5 ± 2.6; Robillard et al. 2017), and these differences are small compared to those between terrestrial and marine prey. Hence, such limitation should not affect our main conclusions.

### *5.6.3. Winter diet and carry-over effects*

We did not find evidence that variability in the winter habitat use of owls inferred from their diet affected subsequent reproduction. Carry-over effects of wintering conditions on subsequent reproduction have been shown in several migratory avian species (Norris et al. 2004, Inger et al. 2010, Legagneux et al. 2012, Gurney et al. 2014, Paxton and Moore 2015) but not in others (Oppel and Powell 2009, Drake et al. 2014). Similar to our results, no impact of the winter habitat use was found on the breeding phenology and productivity of Yellow warblers *Setophaga petechia* breeding in High Arctic as opposed to those breeding in Low Arctic, and the authors suggested that the increased migration distance dampened carry-over effects rather than penalizing long-distance breeders (Drake et al. 2014).

Differences in the quality of habitat used in winter among individuals is often a key factor leading to reproductive carry-over effects in migratory birds (Norris et al. 2004, Studds and Marra 2005, Inger et al. 2010). In the case of snowy owls however, it is unclear whether the arctic marine environment is of higher quality than the terrestrial one in winter, especially when the latter is located much further south (i.e. the Prairies). Wintering conditions in the Arctic or over sea ice are likely more rigorous than in the Prairies and increase physiological costs but it also reduces migration distance and may allow individuals to arrive earlier on the breeding site in spring (Therrien et al. 2014b). Overall, it is possible that the advantages of wintering in one habitat or the other may not differ much for owls, which may explain the absence of reproductive carry-over effects and the persistence of such diverse strategies. Moreover, a limiting factor in this analysis was that sample size was small. Further investigations would be needed to confirm the lack of association between wintering strategy and subsequent breeding.

## 5.7. Conclusion

Coupling feather isotopic signatures and satellite tracking of individuals have revealed multi-season linkage and provided detailed information on intra-population variability in resource use over a relatively large spatio-temporal scale in a nomadic species. Merging these two techniques allowed us to explain some of the variability in wintering diet based on the relative use of two contrasted habitats, the terrestrial and marine environment. Caron-Beaudoin et al. (2013) also showed the usefulness of combining such approaches in a population of ring-billed gull *Larus delawarensis* showing large inter-individual variability in foraging behaviours, but in general, few avian studies coupled those techniques to explore linkage between seasons (Furness et al. 2006, Danckwerts et al. 2016, Pillar et al. 2016). This integrated approach could have interesting ecological implications, such as extending the temporal coverage of resource use prior to sampling and allowing the identification of habitat types or important food resources for species targeted by conservation measures. We also encourage future work aimed at assessing the diet, habitat use and carry-over effects in males and young snowy owls as these may potentially differ from adult females.

## 5.8. Acknowledgments

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## 5.9. Supplementary material

**Annexe S4.1**. Effect of proportion of marine sources in the diet on the body weight of snowy owls estimated by linear regression.

**Annexe S4.2**. Variability in the proportions of marine sources in the diet of individual snowy owls inferred from each individual feather.

## 5.10. Tables

**Table 5.1**. Mean, SD, minimum and maximum values (in parentheses) of parameters describing habitat use for each period analysed (N = number of individual snowy owls tracked by satellite). Negative distances represent locations at sea and positive distances, locations on land.

| Habitat parameter | Autumn Sep.-Dec. N = 17 | Winter Jan.-Mar. N = 12 | All year N = 11 |
|---|---|---|---|
| Number of locations | 53 ± 20 (18 – 77) | 63 ± 20 (28 – 83) | 213 ± 38 (153 – 256) |
| Proportion of locations at sea (< -5 km) | 0.09 ± 0.10 (0 – 0.32) | 0.43 ± 0.31 (0 – 0.83) | 0.24 ± 0.15 (0 – 0.44) |
| Proportion of locations at sea + along the coast (< 5 km) | 0.41 ± 0.24 (0 – 0.82) | 0.71 ± 0.43 (0 – 1) | 0.49 ± 0.25 (0.04 – 0.85) |
| Distance to the coast (km; signed) | 89 ± 280 (-201 – 1490) | 175 ± 461 (-369 – 1480) | 104 ± 330 (-369 – 1490) |
| Distance to the coast (km; absolute) | 96 ± 278 (0 – 1490) | 223 ± 440 (0 – 1480) | 127 ± 322 (0 – 1490) |
| Latitude | 62.7 ± 6.3 (43.7 – 75.7) ° | 58.1 ± 6.4 (44.2 – 71.7) ° | 61.8 ± 6.9 (43.7 – 75.7) ° |

**Table 5.2**. Coefficients (β with their 95% confidence intervals) of linear regressions relating the mean marine proportions in the snowy owl diet inferred from all body feathers sampled or the two feathers with the highest marine contribution to different habitat use variables (**Prop_locSea**: proportion of locations at sea; **Prop_LocSea+Coast:** proportion of locations at sea and along the coast, **DistcoastSTD**: standardized mean distance to the coast (km; positive value over land, negative value over the sea); **DistcoastAbsSTD**: absolute standardized mean distance to the coast (km); and **Latitude** (°)) and for different periods of the annual cycle. Year was added as fixed effect in all models. Significant relationships are shown in bold (N = number of females).

| Explanatory variables | Autumn<br>1Sep. - 31Dec.<br>N=17 | | | Winter<br>1Jan. - 31March<br>N=12 | | | All year<br>N=11 | | |
|---|---|---|---|---|---|---|---|---|---|
| | β | LowerCI | UpperCI | β | LowerCI | UpperCI | β | LowerCI | UpperCI |
| **All feathers** | | | | | | | | | |
| Prop_locSea[1] | -0.28 | -3.13 | 2.56 | 0.72 | -0.32 | 1.76 | 1.93 | -0.52 | 4.38 |
| Prop_locSea+Coast[2] | 0.64 | -0.77 | 2.06 | 0.68 | -0.15 | 1.51 | 1.10 | -0.63 | 2.84 |
| DistcoastSTD | -0.21 | -0.48 | 0.05 | **-0.34** | **-0.62** | **-0.06** | **-0.36** | **-0.68** | **-0.04** |
| DistcoastAbsSTD | -0.22 | -0.48 | 0.04 | **-0.33** | **-0.62** | **-0.04** | **-0.35** | **-0.68** | **-0.02** |
| Latitude | 0.03 | -0.04 | 0.09 | 0.02 | -0.04 | 0.09 | 0.01 | -0.10 | 0.13 |
| **Marine feathers** | | | | | | | | | |
| Prop_locSea[1] | -0.12 | -3.48 | 3.25 | 0.96 | -0.22 | 2.15 | 2.48 | -0.26 | 5.23 |
| Prop_locSea+Coast[2] | 1.09 | -0.52 | 2.70 | **0.95** | **0.04** | **1.85** | 1.55 | -0.35 | 3.46 |
| DistcoastSTD | -0.28 | -0.59 | 0.02 | **-0.41** | **-0.74** | **-0.07** | **-0.44** | **-0.80** | **-0.08** |
| DistcoastAbsSTD | -0.29 | -0.59 | 0.01 | **-0.38** | **-0.73** | **-0.03** | **-0.42** | **-0.80** | **-0.05** |
| Latitude | 0.03 | -0.05 | 0.11 | 0.02 | -0.06 | 0.10 | 0.00 | -0.14 | 0.14 |

[1] locSea: < -5km

[2] SeaCoast: < 5km

**Table 5.3.** Coefficients (β with their 95% confidence intervals) of linear regressions relating clutch size, laying date and body mass (kg) of snowy owls to the mean marine proportions in their diet inferred from all body feathers sampled or the marine feathers only (N = number of females).

| Dependent variables | β | Lower CI | Upper CI |
|---|---|---|---|
| **All feathers** | | | |
| Clutch size (N = 18) | 0.24 | -1.22 | 1.70 |
| Laying date (N = 16) | 4.07 | -1.09 | 9.23 |
| Body mass (N = 17) | -0.81 | -0.17 | 0.01 |
| **Marine feathers** | | | |
| Clutch size (N = 18) | 0.28 | -0.98 | 1.54 |
| Laying date (N = 16) | 3.34 | -1.16 | 7.83 |
| Body mass (N = 17) | -0.07 | -0.15 | 0.01 |

## 5.11. Figures

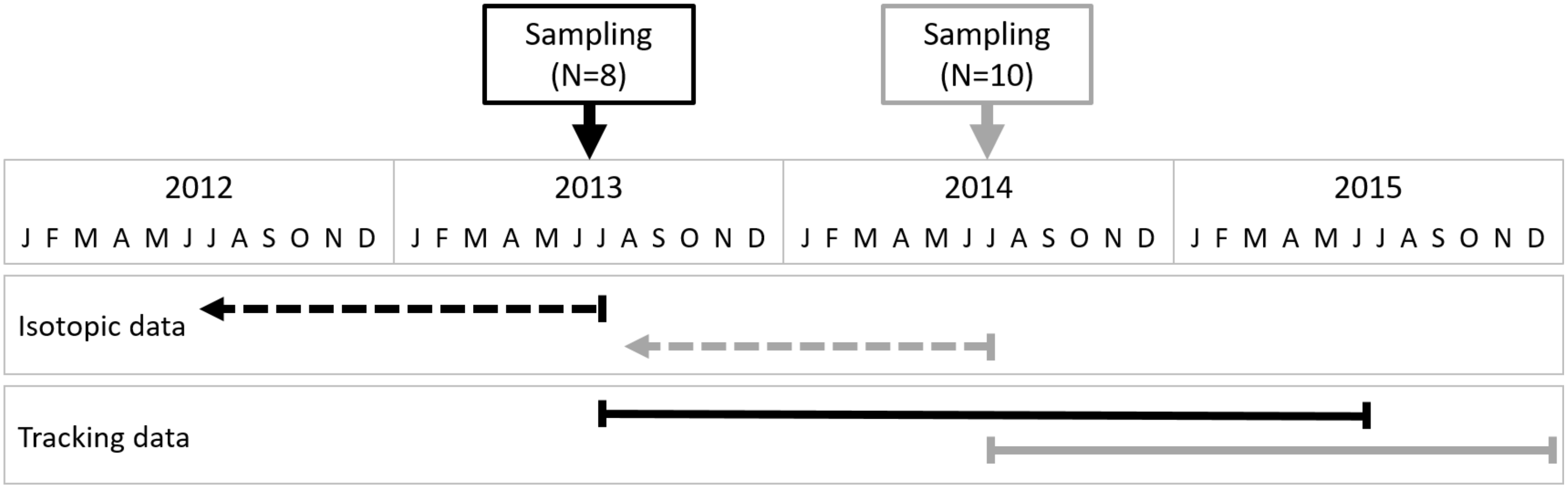

**Figure 5.1**. Schematic timeline depicting the sampling of snowy owl tissues in Deception Bay, QC, 2013 (black box) and on Bylot Island, NU, 2014 (gray box) along with the potential period (months of the year, indicated by uppercase letters) from which isotopic data may origin (dashed arrows) and the period when owls were tracked by satellite telemetry (solid lines).

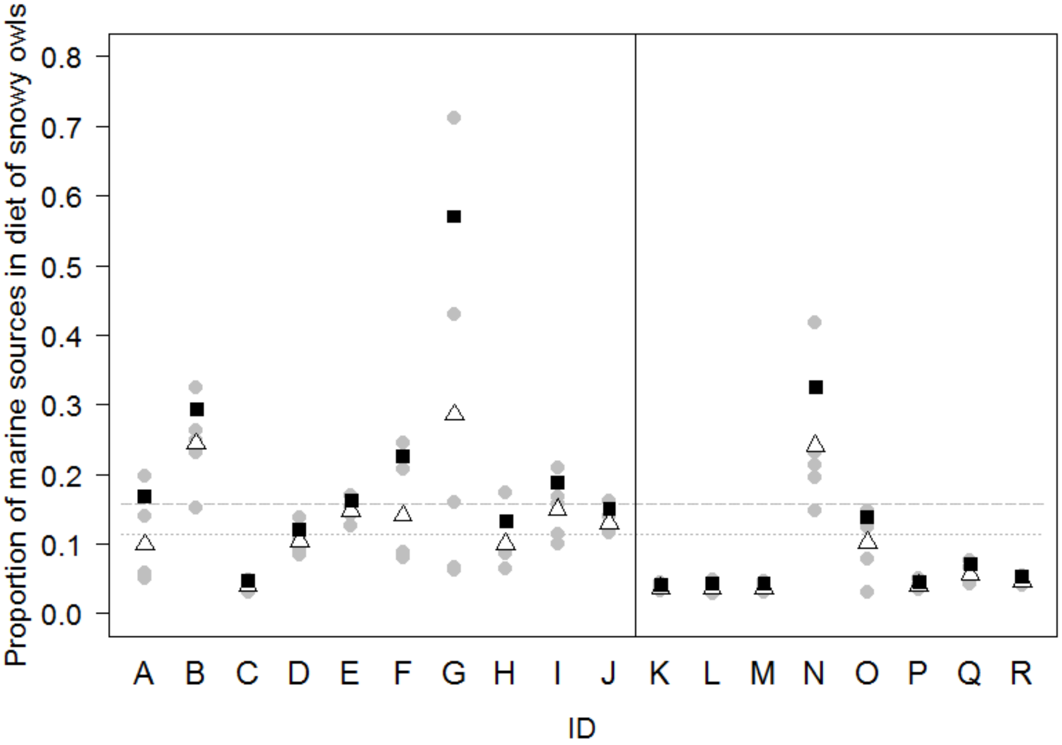

**Figure 5.2.** Proportions of marine sources in the diet of individual snowy owls (ID) inferred from each feather (gray circles) using the SIAR posterior probability distributions. Mean proportion of marine sources for each owl based on all feathers (white triangle) and from the two marine feathers (black square) are also shown. Dotted and dashed gray lines depict respectively mean marine proportions of all feathers and the two most marine feathers. See Annexe S4.2. for variability of individual feathers.

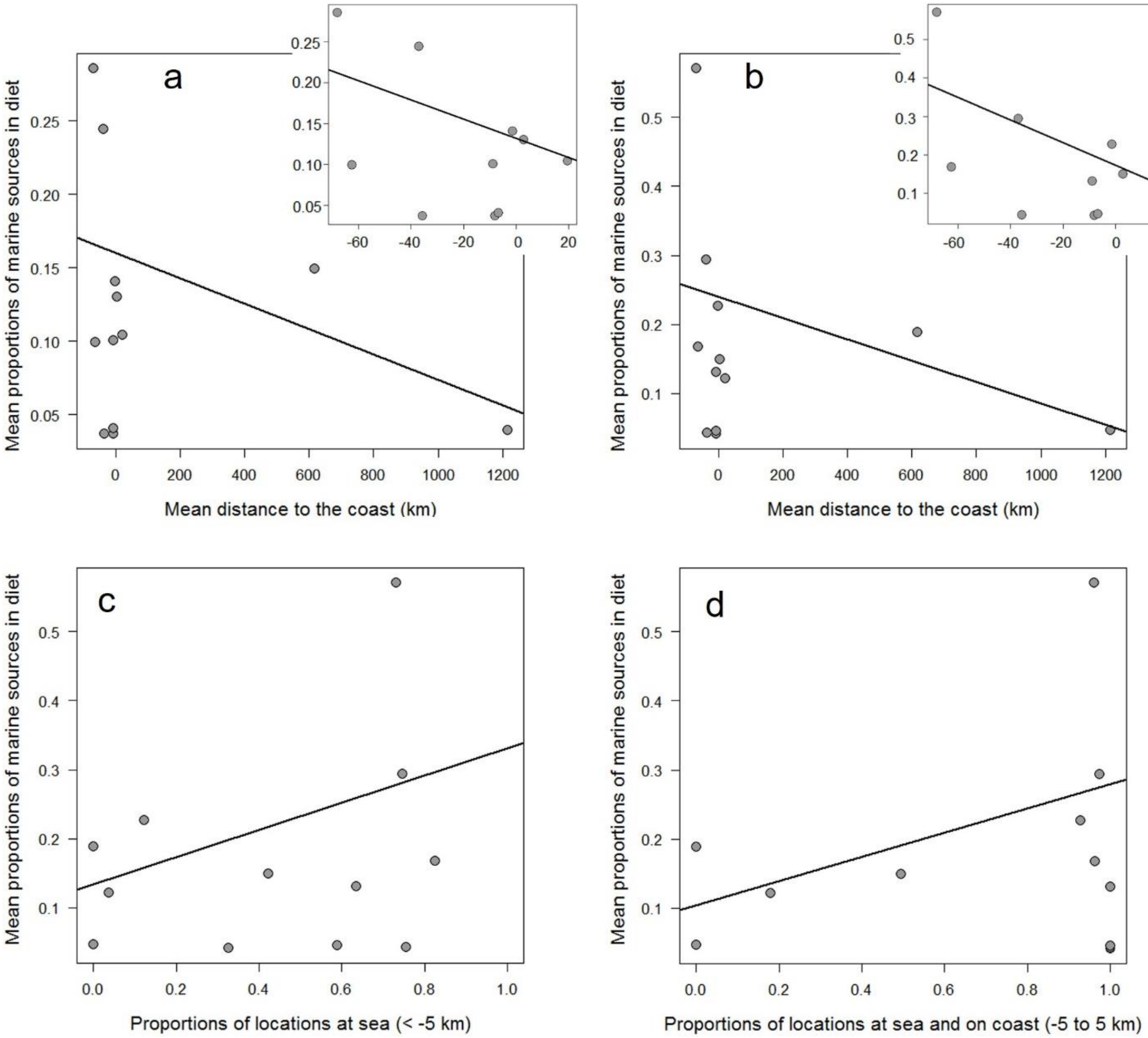

**Figure 5.3**. Relationships between proportion of marine sources in the diet inferred from all body feathers (a) or the two most marine feathers (b,c,d) and distance to nearest coast (a,b), proportions of locations at sea (c) and proportions of locations both at sea and along the coast (d) during winter. Insets represent the relationships between proportion of marine sources in the diet inferred from feathers and distance to the coast excluding the 2 individuals wintering far inland. Regression lines are from models in Table 5.2. Positive distance values represent locations on land, while negative distance values are associated to locations at sea.

# CHAPITRE 6 : Conclusions générales

Mon projet de thèse s'insère dans un effort de recherche pour mieux comprendre l'écologie des espèces qui démontrent des comportements migratoires de type nomade ou irruptif, en particulier pendant la saison non-reproductive. Pour se faire, mon projet s'est penché sur le harfang des neiges, un prédateur aviaire dont les migrations suscitent un énorme intérêt à la fois scientifique et populaire. Cependant, comme pour plusieurs autres espèces aux déplacements imprévisibles, nos connaissances sur son écologie en dehors de la période reproductive étaient très limitées et principalement centrées dans les Prairies canadiennes et les Grandes Plaines américaines (e.g. Boxall et Lein 1982a, b, Kerlinger et Lein 1988, Detienne et al. 2008). Cette thèse offre donc une nouvelle perspective à grande échelle des mouvements et de l'utilisation de l'habitat hivernal des harfangs (chapitre 2) et de leurs migrations irruptives (chapitre 3), en plus d'une évaluation de la contribution du milieu marin à leur régime alimentaire hivernal en lien avec leur utilisation de l'habitat (chapitres 4 et 5).

## 6.1. Écologie hivernale : Migration, utilisation de l'habitat et fidélité

Une partie importante de cette thèse repose sur le suivi par satellite de 31 harfangs marqués dans l'est de l'Arctique canadien. À ce jour, ces oiseaux constituent le plus grand groupe de harfangs des neiges suivis par télémétrie depuis leurs sites de reproduction en Arctique, et a permis une avancée considérable dans nos connaissances spatiales sur cette espèce en période hivernale. Nous avons pu confirmer la grande variabilité intra-spécifique dans les mouvements et l'utilisation de l'espace et des habitats en hiver par le harfang des neiges. Les résultats montrent que la majorité des femelles adultes suivies ont hiverné en Arctique, ce qui confère à ces individus une distance de migration plus courte, une plus grande proximité aux futurs sites de reproduction et un accès aux ressources alimentaires terrestres et marines à travers les nombreux habitats disponibles de l'archipel arctique canadien. Les résultats ont aussi confirmé l'importance du milieu marin et côtier pour cette espèce déjà soulevée par Therrien et al. (2011b).

Le harfang est aussi une espèce plutôt unique considérant sa propension à utiliser à la fois des habitats d'hivernage terrestres, côtiers et marins dans la même saison. Même lorsqu'ils hivernent aux latitudes tempérées, les harfangs font usage de plusieurs types d'environnements (Therrien et al. 2017). De plus, les analyses du chapitre 2 ont permis de déceler des différences dans les patrons d'utilisation de l'espace par les harfangs qui variaient entre les individus hivernant majoritairement en mer ou sur terre, et entre les individus hivernant en Arctique et dans les zones tempérées. Entre autres, les individus hivernant en milieu marin se sont déplacés sur de plus longues distances et avaient des tailles de domaines vitaux plus grands que les individus terrestres. Ces résultats concordent avec des ressources plus dispersées spatialement en milieu marin (Gilchrist et al. 2006, Lovvorn et al. 2014), ce qui pourrait nécessiter des dépenses énergétiques plus grandes pour exploiter les proies dans ce milieu (Mace et al. 1984).

L'épaisseur de neige au sol et la densité de leurs proies terrestres principales (les lemmings) ont permis d'expliquer une partie de la variabilité dans les patrons d'utilisation de l'espace. Nos résultats montrent qu'une épaisse couche de neige peut compliquer les décisions d'installation sur une aire d'hivernage, que la taille des domaines vitaux des harfangs diminuait lors des années de forte abondance de lemmings mais, contre-intuitivement, que leur utilisation du milieu marin augmentait lors de ces années. Ceci suggère que le couvert neigeux pourrait affecter le comportement des harfangs de façon directe et indirecte car une épaisse couche de neige peut d'une part limiter l'accès aux proies qui vivent sous la neige pour les prédateurs (Chamberlin 1980, Sonerud 1986, Duchesne et al. 2011). D'autre part, un couvert de neige épais favorise la survie des lemmings en offrant un refuge contre les prédateurs et une meilleure isolation thermique (Reid et al. 2012, Bilodeau et al. 2013) ce qui peut contribuer à augmenter l'abondance des proies pour les harfangs.

Nous avons également montré que les harfangs étaient plus fidèles à leurs aires d'hivernage qu'à leurs sites de reproduction, ce qui est à l'opposé de ce qui est le plus souvent rapporté chez les oiseaux (Newton 2008). Ces différences saisonnières pourraient être liées au caractère plus prévisible des ressources alimentaires durant la saison hivernale. En effet, les proies du harfang durant la saison hivernale (e.g. petits mammifères dans les Prairies, proies marines), quoique sujettes aux variations environnementales (e.g. couvert neigeux, dynamique des glaces), semblent tout de même plus stables et prévisibles que les fluctuations cycliques de lemmings durant la saison de reproduction (Andersson 1980, Newton 2008, Holt et al. 2015). Considérant l'étendue géographique et la diversité des environnements où les harfangs ont le potentiel d'hiverner (Boxall and Lein 1982b, Fuller et al. 2003, Holt et al. 2015), il est intéressant, voire fascinant, de constater que leurs domaines vitaux se superposent même un peu. Les individus ont montré une forte fidélité à leur zone latitudinale d'hivernage et, dans une mesure un peu moindre, à leur habitat (terrestre vs marin) entre les années. Toutefois, leur grande mobilité leur permet vraisemblablement aussi de répondre aux variations environnementales qu'ils rencontrent en changeant de zone latitudinale ou d'habitat au besoin.

## 6.2. Nomadisme et irruptions

Le nomadisme des harfangs sur leurs aires de reproduction a déjà été documenté (Therrien et al. 2014b) et les distances de dispersion observées dans cette étude ont permis de le confirmer basé sur une taille d'échantillon accrue. Par contre, la fidélité relative au site d'hivernage que nous avons observé nous amène à nous questionner sur l'à-propos de l'utilisation du terme nomadisme pour cette espèce en hiver. En fait, il existe un large éventail de définitions pour le nomadisme, dont les patrons peuvent varier de façon interspécifique (voir plusieurs exemples dans Andersson 1980; Dean 2004) ou intraspécifique (Singh et al. 2012, Wheat et al. 2017) et selon plusieurs facteurs tel que l'abondance de ressources, les conditions environnementales (Dean 2004) et la saison (Lenz et al. 2015; cette thèse). Le terme *nomadisme* est donc large et peut parfois porter à confusion. De plus, certains migrateurs facultatifs peuvent préparer leur migration comme des migrateurs de type obligatoire (e.g. Cornelius et Hahn 2012). Chez ces derniers, la préparation migratoire peut inclure des changements physiologiques et comportementaux (e.g. hyperphagie, accumulation de graisses; Odum 1960, Blem 1976) et se base généralement sur des facteurs endogènes (e.g. rythmes circadiens et circannuels; Gwinner 1996). Comme les harfangs semblent montrer une certaine régularité dans leurs mouvements migratoires malgré la variabilité spatiale que nous avons observée, il pourrait être intéressant de vérifier si certains facteurs endogènes sont en partie responsables de la phénologie de la migration chez le harfang.

Les irruptions périodiques de harfangs dans les zones tempérées sont une autre facette des patrons migratoires hivernaux de cette espèce. Nos analyses ont permis de déboulonner un mythe bien ancré dans les croyances ornithologiques, celui suggérant que les harfangs migrent au sud en masse quand la nourriture vient à manquer au nord, par exemple lors du creux des cycles de populations de lemmings. Au contraire, nos résultats montrent que l'abondance de harfangs aux latitudes tempérées en hiver est plutôt liée à une abondance de proies sur les sites de reproduction en Arctique en été, en accord avec l'hypothèse du *succès reproducteur*. Les résultats du chapitre 2 viennent aussi réfuter l'hypothèse que le manque de nourriture en Arctique serait la cause des irruptions vers le sud. En effet, le suivi de harfangs adultes sur 10 années, dont certaines ont été des creux de lemmings, n'a permis d'observer qu'un seul changement de latitude (i.e. individu hivernant en Arctique une année et au sud à l'année suivante). Si le manque de nourriture était la cause première des irruptions dans le sud, alors nous nous serions attendus à observer ce changement à plus d'une reprise. Il semble donc que même en présence de faible abondance de lemmings, les harfangs adultes demeurent en Arctique. L'utilisation de la glace de mer n'est probablement pas étrangère à ce comportement car cela offre aux harfangs des proies alternatives en arctique quand les lemmings sont absents ou inaccessibles en hiver. Ces résultats sont aussi en accord avec les ratios d'âges observés durant les irruptions (i.e. majoritairement des jeunes de l'année; Smith 1997), et concordent du même coup avec l'hypothèse du *succès reproducteur* comme cause des irruptions.

Il est intéressant de noter que chez plusieurs espèces de strigidés qui s'alimentent toutes de proies généralement pulsées (i.e. populations cycliques), certaines espèces ont des irruptions qui s'expliqueraient de façon similaire aux harfangs (e.g. petite nyctale *Aegolius acadius*) alors que d'autres semblent plutôt migrer massivement suite à un manque de nourriture (e.g. nyctale de Tenglmalm *Aegolius funereus*, chouette épervière *Surnia ulula*; Confer et al. 2014). Les raisons qui pourraient expliquer ces différences sont encore mal connues mais pourraient être liées au degré de spécialisation du migrateur irruptif (i.e. très spécialiste vs peu spécialiste), au type de proies exploitées, à la flexibilité de l'habitat utilisé, la stratégie de reproduction ou la taille corporelle (Cheveau et al. 2004). Par exemple, tout comme le harfang, la petite nyctale peut utiliser des habitats variés et s'alimenter de proies diverses durant la saison non-reproductive (Rasmussen et al. 2008) alors que la nyctale de Tengmalm est restreinte aux forêts anciennes et mature, donc généralement plus limitée dans ses choix de proies (Hayward and Hayward 1993, Cheveau et al. 2004).

À la lumière de ces résultats, il apparaît que sur le spectre des patrons migratoires, le harfang pourrait être un cas particulier de par la diversité de ces mouvements. En effet, les adultes semblent démontrer une phénologie de migration qui s'apparente à ce qu'on observe chez les migrateurs réguliers (chapitre 2), mais sont aussi des migrateurs hautement nomades d'un été à l'autre. Les juvéniles quant à eux pourraient présenter des patrons migratoires et d'hivernage bien différents de ceux des adultes. Les harfangs immatures sont notamment prédominants durant les migrations irruptives cycliques en hiver (Smith 1997, Robillard et al. 2016) alors que les adultes demeurent majoritairement en Arctique et montrent une certaine fidélité d'hivernage (chapitre 2). Cependant, durant les travaux de cette thèse, il n'a pas été possible de suivre des juvéniles.

## 6.3. La difficulté de documenter le régime alimentaire hivernal du harfang

Du suédois *harfang* qui signifie « mangeur de lièvres », l'importance des proies pour le harfang des neiges est à la base même de son nom. Plutôt connu comme un spécialiste de lemmings durant la saison de reproduction, le harfang devient plus généraliste en dehors de la saison de reproduction comme le montre plusieurs études (Gross 1944, Keith 1963, Boxall and Lein 1982a, Smith 1997, Detienne et al. 2008, Potapov and Sale 2012, Holt et al. 2015). De plus, comme la majorité du cycle annuel des migrateurs se trouve en dehors de la saison de reproduction, il importait de s'y attarder.

Suite aux découvertes récentes sur l'importance des milieux marins et côtiers pour le harfang (Therrien et al. 2011b, chapitre 2), nous voulions déterminer la contribution du milieu marin au régime alimentaire du harfang et plus spécifiquement durant la période hivernale. Par des reconstructions du régime alimentaire basées sur des analyses d'isotopes stables effectuées sur des plumes récoltées en été, nous avons pu détecter les variations interindividuelles dans les contributions marines. Ces résultats confirment ainsi que certains individus s'alimentent en mer à un moment durant leur cycle annuel. Ils ont aussi permis de conclure que l'utilisation de plumes de harfangs récoltées durant la saison de reproduction était un outil intéressant pour reconstruire le régime alimentaire mais nécessitait un échantillonnage sur plusieurs parties du corps car il a été impossible de cibler un type de plume en particulier pour ces analyses. Ceci pourrait s'expliquer par une phénologie de la mue variable entre les individus ou encore par le fait que seule une faible proportion des plumes sont remplacées durant l'hiver.

## 6.4. Interactions saisonnières et effets reportés

En combinant les analyses isotopiques de plumes et les suivis par télémétrie satellitaire, le chapitre 5 a permis de mettre en évidence un lien entre l'utilisation des milieux marins et côtiers en hiver et la contribution des ressources marines au régime alimentaire des harfangs. Cette approche intégrative constitue une avancée significative dans notre compréhension de certains aspects de l'écologie hivernale (utilisation de l'espace et régime alimentaire) et pourrait faciliter les analyses pour d'autres espèces difficilement accessibles en hiver. Nous n'avons cependant pas observé d'évidences que la variabilité dans l'utilisation du milieu marin pouvait entraîner des effets reportés sur les performances reproductives subséquentes ou sur la condition corporelle. Comme les différences de qualité entre les habitats utilisés par les individus est souvent un facteur menant à des effets reportés sur les performances reproductives chez les oiseaux migrateurs (Norris et al. 2004, Studds and Marra 2005, Inger et al. 2010), il est possible que cette absence d'effets reportés observée ici soit le résultat d'une qualité d'habitat hivernal similaire entre le milieu marin et terrestre pour le harfang, ce qui n'affecterait pas significativement les reproductions subséquentes. Cependant, il n'est pas toujours évident de déterminer la qualité d'un habitat (Johnson 2007) et notre échantillon était relativement petit. Il serait intéressant de continuer cette étude avec un plus grand nombre d'individus pour permettre de confirmer cette absence d'effets reportés.

## 6.5. Limites de l'étude

Bien que les travaux effectués dans cette thèse soient une contribution significative à notre compréhension de l'écologie hivernale des oiseaux migrateurs, plusieurs limitations sont à noter. Tout d'abord, la connaissance de l'abondance et de la distribution des ressources alimentaires d'une espèce à travers le cycle annuel est importante pour comprendre la distribution spatiale d'une population et l'utilisation de l'habitat par les individus (Fretwell and Lucas 1969, Bryant 1979, Brindock and Colwell 2011). Dans le cas présent, peu d'informations quantitatives existent sur les variations annuelles de proies de harfangs. Les bases de données longitudinales de petits mammifères sont rares, particulièrement en dehors de la saison estivale, et nous avons utilisé les seules disponibles en Arctique pour lesquelles les suivis couvraient une période suffisamment longue pour nos analyses (Daring Lake, TNO et Île Bylot, NU). Au même titre, les bases de données multi-annuelles sur l'abondance et la distribution de canards de mer à l'échelle des déplacements de harfangs sont rares ou inexistantes. Il serait très utile d'obtenir des suivis d'abondance longitudinaux de proies marines et terrestres à plus grande échelle durant la période non-reproductive. Deuxièmement, pour une espèce se déplaçant à l'échelle continentale comme le harfang, les données environnementales peuvent aussi être difficiles à extraire. L'épaisseur de neige qui a été associée à chaque localisation de harfang est une interpolation des épaisseurs avoisinantes (dans une grille de 32x32km) et représente donc une estimation grossière. Les variations à plus fine échelle spatiale peuvent ainsi passer inaperçues. Finalement, malgré que nous ayons suivi par satellite le plus grand nombre de harfangs marqués sur leurs aires de reproduction jusqu'à maintenant, le nombre d'oiseaux suivis ici demeure relativement petit pour étudier des patrons à l'échelle populationnelle. Ce nombre a été particulièrement limitant lorsque nous avons tenté d'expliquer les variations interindividuelles dans l'utilisation de l'espace en relation avec des conditions environnementales. De plus, pour une espèce longévive comme le harfang, la durée de suivi était aussi relativement courte. Il est aussi à noter que 30 des 31 émetteurs ont été installés sur des femelles adultes, ce qui n'a pas permis de distinguer l'effet du sexe ou de l'âge sur les patrons migratoires, l'utilisation de l'habitat hivernal ou le régime alimentaire.

## 6.6. Perspectives de recherche

Grâce aux découvertes récentes sur l'utilisation du milieu marin par les harfangs (Therrien et al. 2011b) et à travers les travaux de cette thèse, notre compréhension de l'écologie hivernale du harfang des neiges croît tranquillement. Néanmoins, de nombreuses questions demeurent et mériteraient d'être approfondies.

Tout d’abord, pour permettre de décrire des patrons plus généraux, l’étude des espèces irruptives ou nomades aurait avantage à suivre le plus d’individus possibles, considérant que beaucoup de variabilité inter-individuelle peut exister. À ce titre, malgré que la majorité des mouvements migratoires de harfangs s’effectuent dans un axe nord-sud dans l’est de l’Amérique du Nord, certains semblent adopter des mouvements est-ouest (Fuller et al. 2003). Il semble aussi que les harfangs suivis depuis leurs aires de reproduction en Arctique (cette thèse) et ceux suivis depuis leurs aires d’hivernage au nord des États-Unis (Project SNOWstorm 2017), présentent des patrons migratoires et des aires d’hivernages différents. En effet, on observe que les harfangs équipés d’émetteurs dans le nord-est américain migrent vers leurs aires de reproduction en traversant le Québec ou l’Ontario par le centre, alors que les individus marqués sur leur nid en Arctique semblent migrer vers le sud en évitant les forêts et en suivant plutôt des routes migratoires côtières (côtes de Terre-Neuve, Labrador, Baie d’Hudson). Ces différences pourraient possiblement être expliquées par l’âge des individus marqués car contrairement aux oiseaux marqués en Arctique (tous adultes; cette thèse), les harfangs équipés d’émetteurs dans le nord-est américain sont majoritairement des jeunes immatures (Project SNOWstorm 2017). Ainsi, il semble de plus en plus clair que les patrons de migrations et d’hivernage diffèrent selon l’âge des individus, mais de plus amples recherches sont nécessaires pour comprendre ces différences. Cependant, des similitudes existent aussi entre ces deux groupes de harfangs marqués car tout comme les harfangs hivernant en Arctique, plusieurs individus équipés d’émetteurs dans le nord-est américain ont fait une utilisation importante des milieux aquatiques dulcicoles et côtiers, se nourrissant fort probablement de sauvagine en hiver (voir Smith 1997). Ainsi, dans les deux cas, les zones côtières sont privilégiées. En somme, une méta-analyse de tous les suivis satellitaires disponibles chez le harfang des neiges, en Amérique et ailleurs, serait intéressante et pertinente pour déterminer la variabilité migratoire et hivernale intraspécifique et pourrait permettre d’examiner les différences d’âge (adultes vs juvéniles) et interindividuelles. Un déploiement plus important d’émetteurs satellitaires sur des juvéniles en Arctique pourrait aussi combler un manque dans ces données.

Tel que mentionné précédemment, les harfangs suivis et étudiés dans cette thèse sont majoritairement des femelles adultes (30/31), étant donné la difficulté de capturer des mâles en période de nidification. Nos connaissances sur les patrons migratoires et d’hivernage de cette espèce demeure ainsi limitées principalement à ce seul groupe. Il est intéressant de noter que l'unique mâle suivi durant cette étude a été le seul individu à hiverner sur les côtes du Groenland (chapitre 2), ce qui soulève aussi certaines questions sur les différences qui pourraient exister entre les sexes. Il serait donc primordial d'étendre cette étude aux mâles pour la compréhension globale de l'écologie de l'espèce.

Dans un autre ordre d'idées, il serait intéressant d'étudier en détails les patrons de mue des plumes de corps du harfang et leur variabilité intra- et interindividuelle pour mieux cibler les plumes à échantillonner. Cela pourrait permettre le développement de méthodes d'échantillonnage mieux adaptées qui permettraient de relier les différentes périodes du cycle annuel à l'aide d'analyses peu intrusives et efficaces sur des tissus récoltés durant la saison de reproduction. Pour aller plus loin dans notre compréhension des patrons migratoires et les effets reportés, d'autres types d'analyses d'isotopes stables pourraient être envisagées. Par exemple, les analyses de ratio de deutérium ($^2H/^1H$; δD) peuvent aider à déceler le lieu d'origine d'un tissu prélevé sur un individu sur la base de la variabilité latitudinale connue de ces ratios dans les précipitations (Hobson 1999).

## 6.7. Conservation de l'espèce dans un contexte de changements climatiques globaux

Quoique que le harfang des neiges ne soit pas une espèce considérée à risque par le IUCN (BirdLife International 2016), les experts ne s'entendent pas sur la taille de la population globale (Marthinsen et al. 2009, Potapov and Sale 2012, Holt et al. 2015, BirdLife International 2016). Il n'est donc pas clair si des efforts de conservation de l'espèce seraient requis face aux changements en cours dans l'Arctique. À l'interface des écosystèmes terrestres et marins, le harfang pourrait ainsi subir des impacts sur plusieurs fronts. Ses habitats hivernaux diversifiés couplés à sa grande mobilité pourraient aussi mener à des impacts sur d'autres espèces et d'autres environnements à grande échelle. Il importe donc de mieux comprendre l'écologie de l'espèce pour mieux appréhender les impacts qu'elle subira et qui pourront se répercuter sur les réseaux trophiques dont le harfang occupe le sommet. À l'inverse, ces prédateurs sont aussi exposés à des changements dans l'abondance ou la composition spécifique de leurs proies qui pourraient survenir suite aux changements climatiques (Post et al. 2009, Gauthier et al. 2011, Gilg et al. 2012). D’autres espèces comme le faucon gerfaut (Burnham and Newton 2011) ou le corbeau (Gilchrist and Robertson 2000) font aussi usage des zones de glace en hiver, et les travaux menés dans cette thèse pourraient éventuellement être utiles à la compréhension de l’utilisation de l’habitat ou les patrons migratoires de ces espèces.

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# Annexe S1: Documentation supplémentaire pour le Chapitre 2

**Annexe S1.1.** Complementary information on estimation methods of lemming abundance and snow depth.

### Lemming abundance

Long-term time series of small mammal abundance in the eastern Arctic of North America are very scarce. The only site in this area where lemming abundance was measured annually between 2007-2016 is Bylot Island, NU. At this site, 2 species of small mammals are found: brown lemmings *Lemmus trimucronatus*, the most abundant species, and collared lemmings *Dicrostonyx groendlandicus* (Fauteux et al. 2015b). Summer densities of lemmings were estimated in July on two 11 ha live-trapping grids with 144 traps each performed in July, which allows accurate determination of densities using capture-recapture methods. Winter abundance of lemmings was measured by sampling remnants of winter nests collected on 40 predetermined 500m-transects after snow-melt and estimating their density with distance sampling methods (see Fauteux et al. 2015b for details on the method). The density of winter nests gives a fairly robust estimate of lemming abundance in the following spring (Krebs et al. 2012).

### Snow depth

We obtained snow depth data through the Movebank Env-Data system (Dodge et al. 2013) which provides a set of tools to link animal movement data with information from global environmental datasets. Of the two options available for this variable, we selected the NCEP NARR (NCEP: National Centers for Environmental Prediction; NARR: North American Regional Reanalysis) snow depth dataset because it had the smallest spatial (i.e. 0.3deg = 32km) and temporal resolution (i.e. 3-hr or 8 values per day; NCEP NARR 2016). Units are in meters. The NARR is an extension of the NCEP Global Reanalysis combining actual ground (e.g. land surface, aircraft, ship) and remote (i.e. satellite) measurements along with NOAA climatic monitoring data (Kalnay et al. 1996, Mesinger et al. 2006, NCEP NARR 2016). Snow depth values are interpolated with the inverse distance weighted method in the Env-data system (Li and Heap 2011, Dodge et al. 2013), which estimates the snow depth using the surrounding values in a 32 x 32 km grid, using the inverse of the distance to each surrounding value as a weighting factor. For various analyses, a snow depth was associated with each owl location and averaged over specific time-frames (e.g.

SnowDepthautumn = mean snow depth at all locations of an individual during the autumn season; duration of autumn or winter periods differ for each individual and year; see AnnexeS1.2).

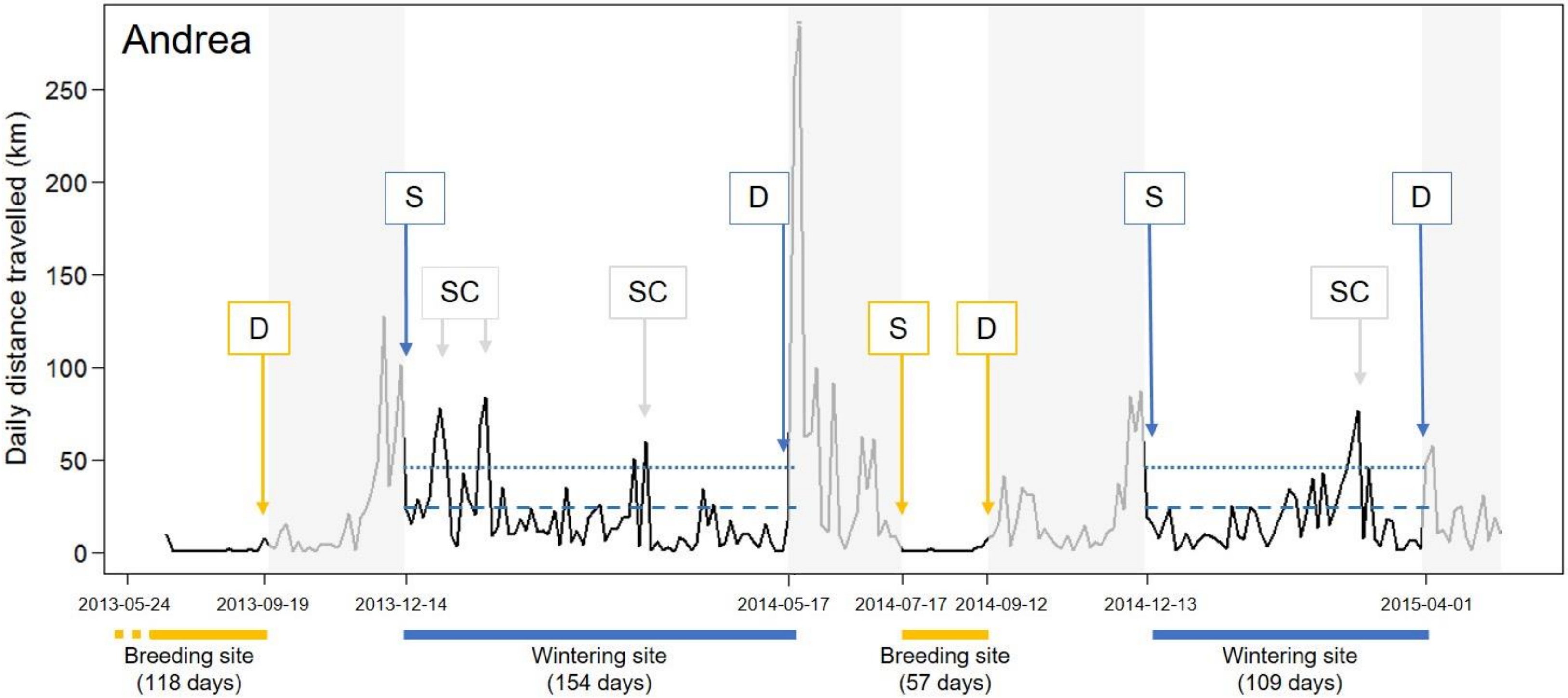
**Annexe S1.2.** Determination of settlement and departure dates on the breeding and wintering sites

Determining settlement and departure dates from a breeding or a wintering site is difficult for a nomadic species like the snow owl (Holt et al. 2015, Therrien et al. 2015). We chose to determine these dates using objective criteria based on spatial movements of individuals whenever possible.

Criteria previously used to infer breeding activity of this species in the eastern Canadian Arctic (Therrien et al. 2012) were used here. Settlement date on a breeding site was the first day in spring after departure from the wintering site when the distance between mean daily locations was < 5 km over suitable breeding habitat (i.e. above the tree line). The 5-km criteria is based on the maximum daily distance (i.e. distance moved between 2 consecutive locations divided by the number of days between those locations) travelled by known successful breeders on their breeding site (Mean ± SD: 1.2 ± 2.2 km; n = 24). Departure date from the breeding site was the first date after settlement when distance between mean daily locations was > 5 km. We further examined the movement map of each individual to ensure that applying these criteria did not yield unrealistic results. In a few cases, distance travelled between consecutive locations could slightly exceed the 5 km criteria but these were ignored because in all cases individuals came back to the central location of their potential breeding site for extended periods.

For the winter period, we first calculated the mean daily distance travelled by each individual across all years from 1 December and 31 March, the period during which owls were most likely to have settled on a wintering site. The settlement date in winter was defined as the first day during the non-breeding period when the distance travelled by an individual between consecutive daily locations was smaller than the mean daily distance travelled in winter across years + 1SD. Inversely, departure date from a wintering area was defined as the last time during the wintering period when the distance travelled between daily locations started to exceed the mean daily distance travelled in winter + 1SD (See Fig. A2 for examples). We again examined the movement map of each individual to ensure that applying these criteria did not yield unrealistic results. Occasionally, distance travelled between daily locations could slightly exceed the mean+1SD criteria for short periods (mean ± SD: 3.0 ± 2.2 days; range: 1 –15 days; n=99) but these were considered shifts in core areas during the winter period rather than genuine migratory movements.

However, in some cases, the previous criteria were not helpful in determining wintering settlement or departure dates (n=15 out of 84 cases). In those situations, we used behavioural criteria and considered the directionality and angles of the individual's trajectory (i.e. frequent changes of direction suggested that the individual switched from migration to search mode within a restricted home range; Therrien et al. 2015) to determine those dates.


Andrea
Daily distance travelled (km)
250
200
150
100
50
0
D
S
SC
SC
D
S
D
S
SC
D
2013-05-24
2013-09-19
2013-12-14
2014-05-17
2014-07-17
2014-09-12
2014-12-13
2015-04-01
Breeding site (118 days)
Wintering site (154 days)
Breeding site (57 days)
Wintering site (109 days)

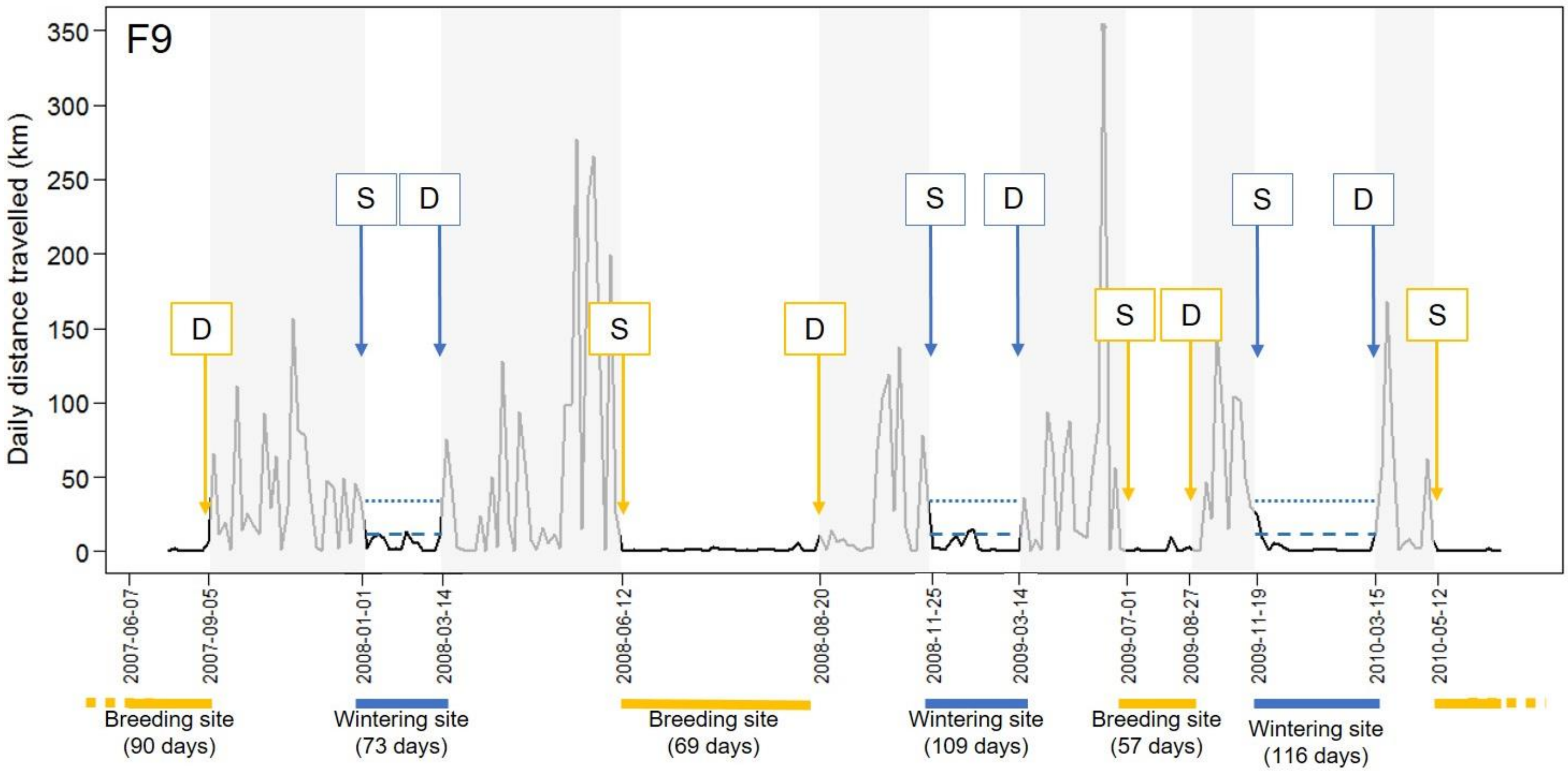


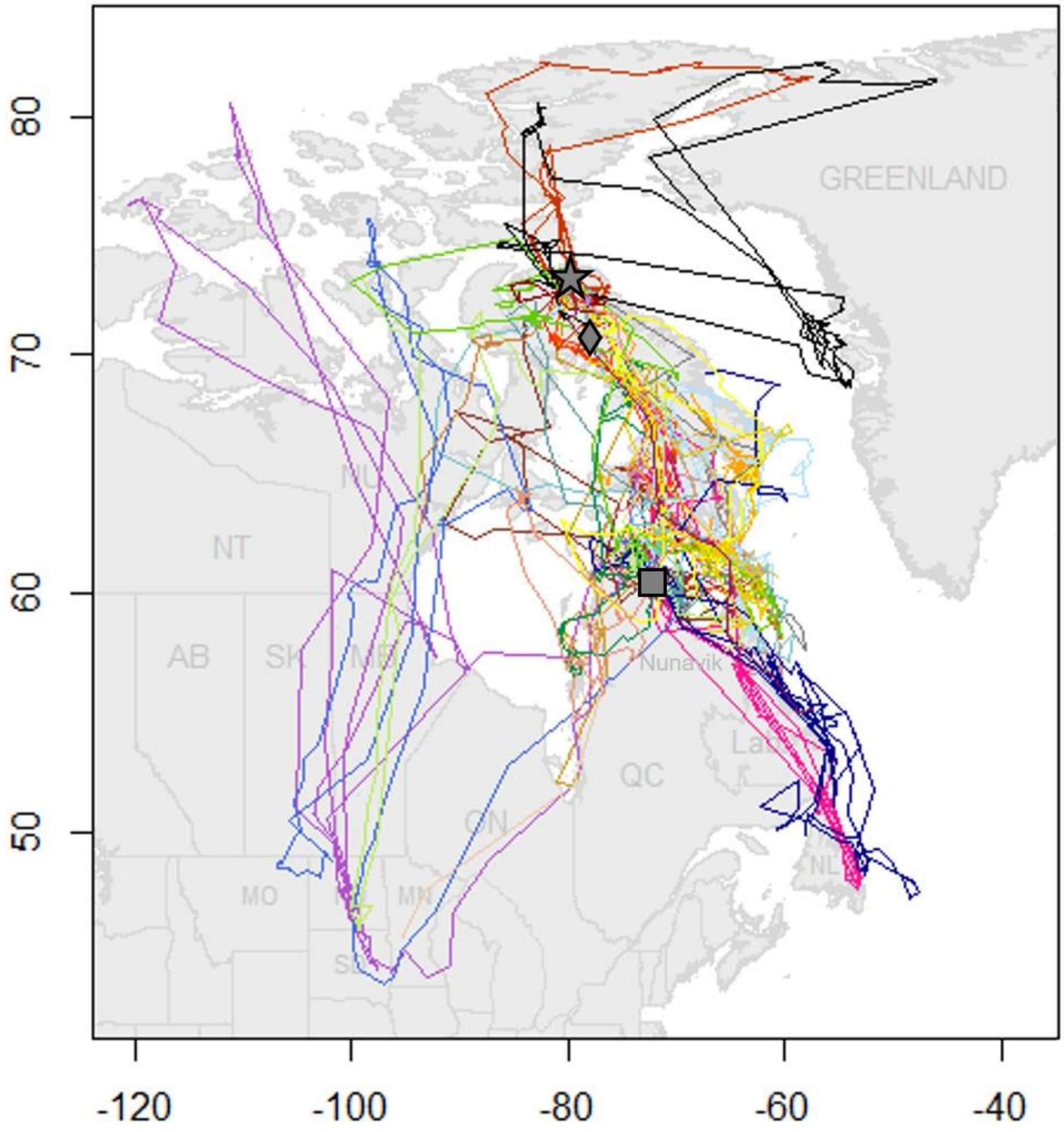
**Figure A2**. Annual daily distance travelled used to define settlement and departure dates of two individuals provided as examples: Andrea (top), a female that wintered in the high Arctic marine environment for two consecutive winters and F9 (bottom), a female that wintered in the American Midwest for 3 consecutive winters. Settlement dates (S), departure dates (D) and shifts in core areas (SC) are illustrated in boxes. Shaded areas represent migratory movements between breeding and wintering periods. Movement dates span from the nest finding of the individual on the breeding grounds to the last location revealed by satellite tracking. Mean daily distances travelled during the wintering period are displayed with their SD (long and short dash, respectively).

**Annexe S1.3**. Tracking information, main wintering environment (Marine or Terrestrial) and latitudinal zones (Arctic or Temperate) used by 28 snowy owls (27 females, 1 male [M10]) between 2007 and 2016 (dash indicates no data due to transmitters that stopped functioning or because individual died).

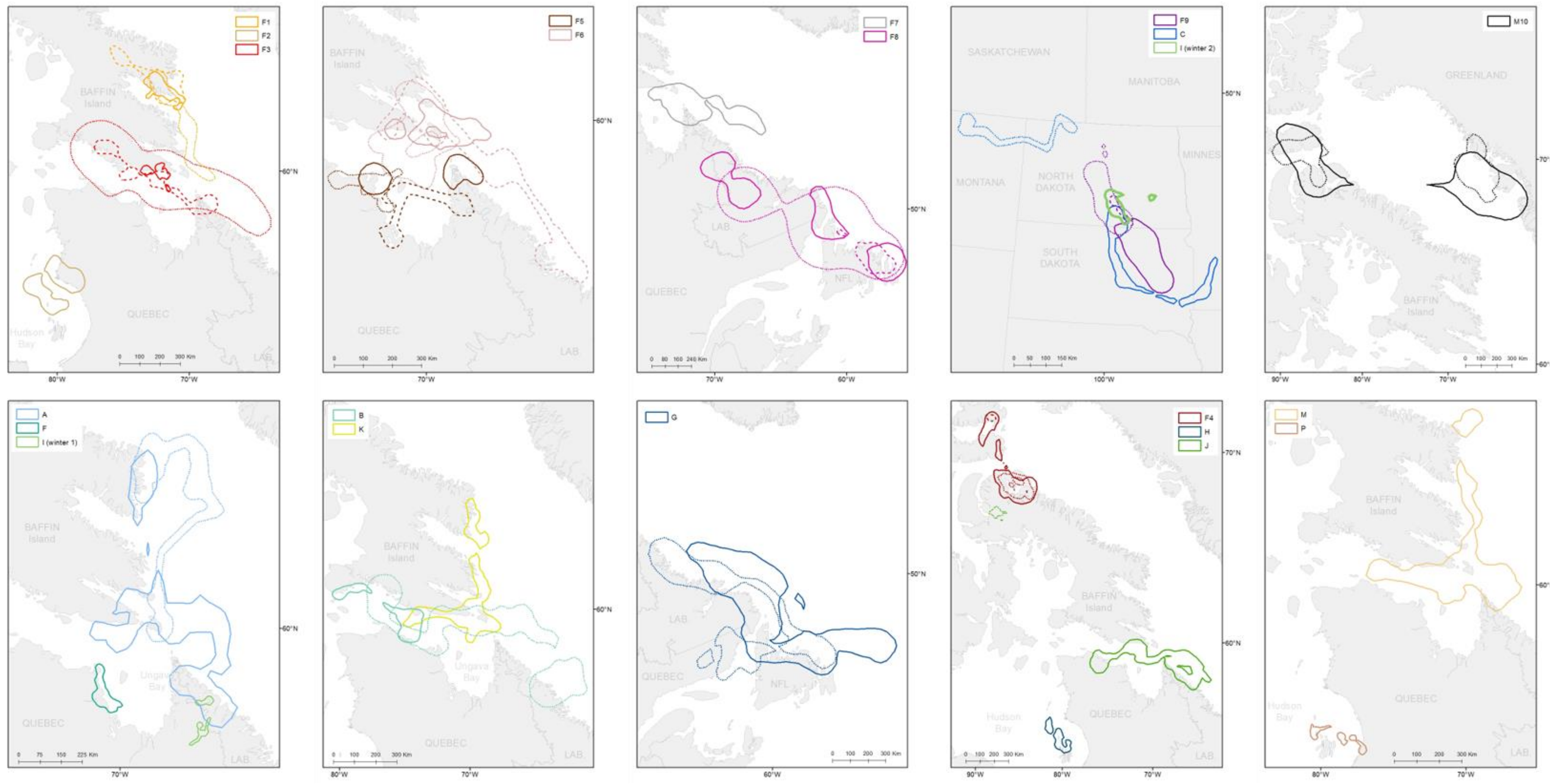
| Id | Marking Year | N days tracked | N daily locations | Winter1 | | Winter2 | | Winter3 | |
|---|---|---|---|---|---|---|---|---|---|
| | | | | Envir. | Lat.Zone | Envir. | Lat.Zone | Envir. | Lat.Zone |
| F1 | 2007 | 1155 | 320 | Terrestrial | Arctic | Terrestrial | Arctic | Terrestrial | Arctic |
| F2 | 2007 | 687 | 157 | Terrestrial | Arctic | - | - | - | - |
| F3 | 2007 | 1267 | 357 | Terrestrial | Arctic | Marine | Arctic | Terrestrial | Arctic |
| F4 | 2007 | 1091 | 315 | Terrestrial | Arctic | Terrestrial | Arctic | Terrestrial | Arctic |
| F5 | 2007 | 1107 | 311 | Terrestrial | Arctic | Terrestrial | Arctic | Terrestrial | Arctic |
| F6 | 2007 | 1135 | 339 | Marine | Arctic | Marine | Arctic | Terrestrial | Arctic |
| F7 | 2007 | 379 | 147 | Marine | Arctic | - | - | - | - |
| F8 | 2007 | 1135 | 331 | Terrestrial | Temperate | Terrestrial | Temperate | Terrestrial | Temperate |
| F9 | 2007 | 1134 | 238 | Terrestrial | Temperate | Terrestrial | Temperate | Terrestrial | Temperate |
| M10 | 2011 | 825 | 292 | Marine | Arctic | Marine | Arctic | - | - |
| A | 2013 | 666 | 237 | Marine | Arctic | Marine | Arctic | - | - |
| B | 2013 | 644 | 206 | Marine | Arctic | Marine | Arctic | - | - |
| C | 2013 | 710 | 254 | Terrestrial | Temperate | Terrestrial | Temperate | - | - |
| D | 2013 | 232 | 75 | - | | - | - | - | - |
| E | 2013 | 148 | 34 | - | | - | - | - | - |
| F | 2013 | 504 | 161 | Terrestrial | Arctic | - | - | - | - |
| G | 2013 | 708 | 245 | Marine | Temperate | Marine | Temperate | - | - |
| H | 2013 | 466 | 153 | Marine | Arctic | - | - | - | - |
| I | 2013 | 704 | 247 | Terrestrial | Arctic | Terrestrial | Temperate | - | - |
| J | 2013 | 714 | 256 | Marine | Arctic | Terrestrial | Arctic | - | - |
| K | 2014 | 541 | 175 | Marine | Arctic | - | - | - | - |
| L | 2014 | 171 | 46 | - | | - | - | - | - |
| M | 2014 | 582 | 197 | Marine | Arctic | - | - | - | - |
| N | 2014 | 49 | 4 | - | | - | - | - | - |
| O | 2014 | 187 | 52 | - | | - | - | - | - |
| P | 2014 | 605 | 207 | Marine | Arctic | - | - | - | - |
| Q | 2014 | 176 | 47 | - | | - | - | - | - |
| R | 2014 | 132 | 32 | - | | - | - | - | - |

Blue: Environment switches between 2 successive winters.
Orange: Latitudinal zone switches between 2 successive winters.

**Annexe S1.4**. Movements of snowy owls tracked by satellite telemetry from 2007 to 2016 in eastern North America (N=28). Also depicted on the graph are the three capture sites: Bylot Island (star), Deception Bay (square) and Mary River (diamond).



**Annexe S1.5.** Overlapping wintering home range contours of all individuals tracked for at least one winter between 2007 and 2016. One to three individuals only are plotted in the same graph to facilitate visual assessment of home range overlaps of the same individuals between years. Full line=1st winter, small dashed line=2nd winter, large dashed line=3rd winter. Wintering environments and latitudinal zones of each individual are listed in Annexe S1.3.



**Annexe S1.6**. Complete statistical results of the relationships between different parameters of winter space and habitat use and all explanatory variables examined: wintering environment (Environment; marine vs terrestrial), wintering latitudinal zone (LatitudinalZone; Arctic vs temperate), snow depth (SnowAutumn; autumn and SnowWinter; winter) and small mammal abundance on Bylot Island (LemmSummer; summer and LemmWinter; winter). Response variables include Distance travelled (km; n=42), Marine environment use (n=36; excludes birds wintering in the Prairies), Settlement and Departure dates (n=42), Length of stay (days; n=42), Home range and Core area size (km$^2$; n=42), Number of core areas (n=42) and extent of home range and core area overlap (%; excluding birds that have switched wintering environment or latitudinal zone; n=16). Bird ID was included in all models as random effect. Latitudinal zone of reference=Arctic. Environment of reference = Marine. Significant relationships are shown in bold.

| Response variables | Explanatory variables | β | Lower CI | Upper CI |
|---|---|---|---|---|
| Distance travelled within wintering area | **Environment** | **-0.788** | **-1.195** | **-0.381** |
| | LatitudinalZone | -0.334 | -0.969 | 0.301 |
| | SnowWinter | 0.004 | -0.017 | 0.025 |
| | LemmWinter | -0.027 | -0.059 | 0.006 |
| | LemmSummer | 0.014 | -0.053 | 0.081 |
| Marine environment use | **SnowWinter** | **-0.089** | **-0.110** | **-0.068** |
| | SnowAutumn | -0.025 | -0.059 | 0.010 |
| | LemmWinter | -0.018 | -0.046 | 0.010 |
| | **LemmSummer**[1] | **0.121** | **0.056** | **0.185** |
| Dates of settlement on wintering ground | **Environment** | **-14.393** | **-28.025** | **-0.761** |
| | LatitudinalZone | 11.745 | -3.849 | 27.339 |
| | **SnowAutumn** | **2.732** | **1.623** | **3.841** |
| | LemmSummer | -0.758 | -3.453 | 1.938 |
| Dates of departure from wintering ground | Environment | -8.733 | -21.922 | 4.456 |
| | **LatitudinalZone** | **-18.812** | **-37.397** | **-0.227** |
| | SnowWinter | 0.195 | -0.363 | 0.752 |
| | LemmWinter | 0.602 | -0.224 | 1.427 |
| Length of stay on wintering site | Environment | 0.070 | -0.821 | 0.961 |
| | LatitudinalZone | -0.907 | -1.859 | 0.045 |
| | SnowWinter | 0.041 | -0.002 | 0.085 |
| | LemmWinter | 0.004 | -0.080 | 0.088 |
| | LemmSummer | 0.053 | -0.102 | 0.208 |
| Wintering home range size | **Environment** | **-1.452** | **-2.229** | **-0.675** |
| | LatitudinalZone | 0.024 | -1.121 | 1.170 |
| | SnowWinter | 0.004 | -0.041 | 0.049 |

| | | | | |
|---|---|---|---|---|
| | **LemmWinter** | **-0.077** | **-0.149** | **-0.005** |
| | LemmSummer | 0.058 | -0.088 | 0.204 |
| Wintering core area size | **Environment** | **-1.698** | **-2.579** | **-0.817** |
| | LatitudinalZone | -0.115 | -1.425 | 1.195 |
| | SnowWinter | 0.001 | -0.048 | 0.051 |
| | **LemmWinter** | **-0.083** | **-0.161** | **-0.005** |
| | LemmSummer | 0.058 | -0.102 | 0.218 |
| Number of core areas in wintering area | **Environment** | **-0.571** | **-0.977** | **-0.165** |
| | LatitudinalZone | -0.426 | -0.881 | 0.029 |
| | SnowWinter | -0.007 | -0.030 | 0.015 |
| | **LemmWinter** | **-0.044** | **-0.082** | **-0.005** |
| | LemmSummer | 0.009 | -0.069 | 0.087 |
| Wintering home range overlap extent | Environment | 0.008 | -0.966 | 0.982 |
| | LatitudinalZone | -0.384 | -1.421 | 0.654 |
| Wintering core area overlap extent | Environment | 0.542 | -0.983 | 2.066 |
| | LatitudinalZone | -0.982 | -2.517 | 0.552 |

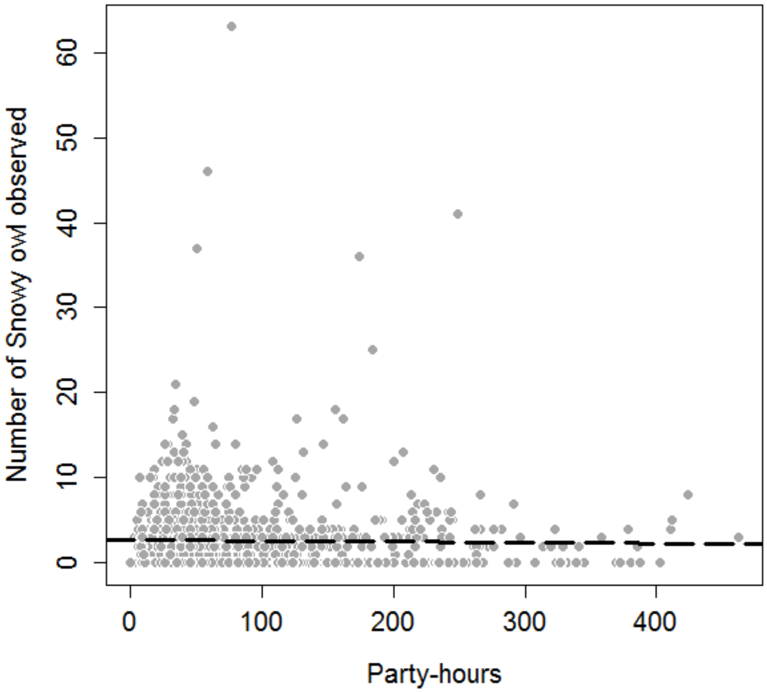
[1] Female J was removed from this model (n=34)

# Annexe S2: Documentation supplémentaire pour le Chapitre 3

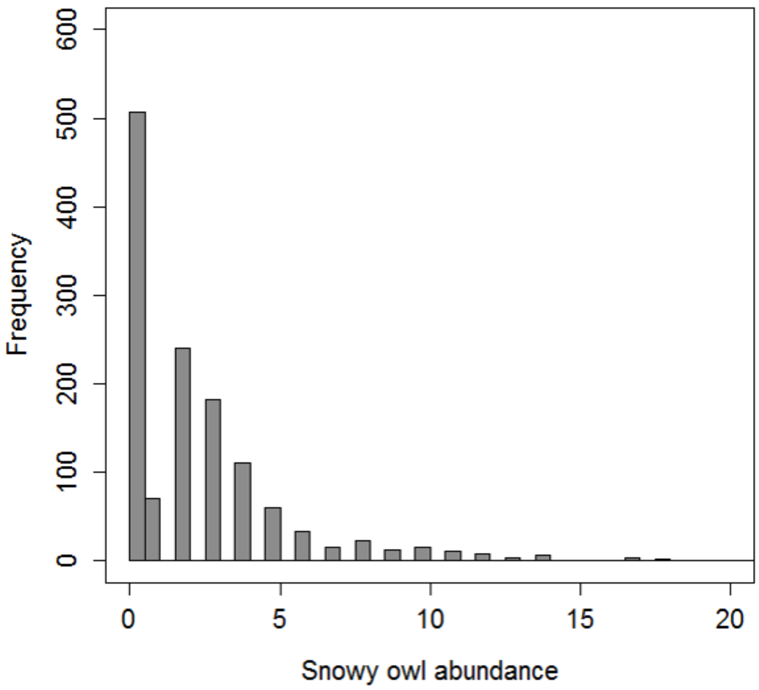
**Annexe S2.1**. Location of the 84 Christmas Bird Count sites (circles) selected in this study. Latitude and longitude are in tenths of degrees and are presented in WGS84. The *Zone* column corresponds to the general location of the site: West (W), Central (C) and East (E) (see Fig. 3.1).

| Circle | Country | Province/State | Zone | Lat. | Long. |
|---|---|---|---|---|---|
| ABCM | Canada | Alberta | C | 53.20 | -112.83 |
| ABDC | Canada | Alberta | C | 53.33 | -113.85 |
| ABED | Canada | Alberta | C | 53.52 | -113.52 |
| ABFS | Canada | Alberta | C | 53.78 | -113.15 |
| ABGP | Canada | Alberta | C | 55.17 | -118.75 |
| ABHC | Canada | Alberta | C | 51.42 | -112.88 |
| ABHR | Canada | Alberta | C | 50.58 | -113.87 |
| ABKM | Canada | Alberta | C | 55.72 | -116.95 |
| ABMH | Canada | Alberta | C | 50.02 | -110.68 |
| ABSA | Canada | Alberta | C | 53.67 | -113.73 |
| ABSP | Canada | Alberta | C | 53.98 | -111.32 |
| ABSR | Canada | Alberta | C | 53.48 | -113.17 |
| ABST | Canada | Alberta | C | 52.32 | -112.63 |
| ABTO | Canada | Alberta | C | 53.42 | -112.68 |
| ABVE | Canada | Alberta | C | 53.35 | -110.85 |
| BCLA | Canada | B.-Columbia | W | 49.05 | -123.05 |
| MACA | USA | Massachussetts | E | 42.60 | -70.72 |
| MACC | USA | Massachussetts | E | 41.72 | -70.00 |
| MAGB | USA | Massachussetts | E | 42.40 | -71.10 |
| MAMA | USA | Massachussetts | E | 42.08 | -70.65 |
| MANA | USA | Massachussetts | E | 41.28 | -70.08 |
| MANE | USA | Massachussetts | E | 42.75 | -70.90 |
| MBBA | Canada | Manitoba | C | 50.25 | -97.32 |
| MBBR | Canada | Manitoba | C | 49.85 | -99.93 |
| MBCR | Canada | Manitoba | C | 49.57 | -99.02 |
| MBDA | Canada | Manitoba | C | 51.15 | -100.05 |
| MBDM | Canada | Manitoba | C | 50.12 | -98.23 |
| MBGS | Canada | Manitoba | C | 49.58 | -99.37 |
| MBME | Canada | Manitoba | C | 49.28 | -100.97 |
| MBOH | Canada | Manitoba | C | 50.12 | -97.08 |
| MBRR | Canada | Manitoba | C | 49.65 | -97.13 |
| MBWI | Canada | Manitoba | C | 49.88 | -97.20 |
| MITU | USA | Michigan | E | 43.62 | -83.57 |
| MNBL | USA | Minnesota | C | 44.82 | -93.22 |
| MNDU | USA | Minnesota | C | 46.85 | -92.03 |
| MNWN | USA | Minnesota | C | 48.20 | -96.77 |
| MTFP | USA | Montana | C | 48.01 | -106.45 |
| NDDL | USA | North Dakota | C | 48.67 | -102.07 |
| NDGF | USA | North Dakota | C | 47.93 | -97.15 |
| NDLL | USA | North Dakota | C | 46.68 | -100.18 |
| NDUS | USA | North Dakota | C | 48.47 | -101.58 |
| NHIS | USA | New Hampshire | E | 43.05 | -70.52 |
| NLCR | Canada | Newfoundland | E | 46.73 | -53.15 |
| NSCS | Canada | Nova Scotia | E | 43.48 | -65.62 |
| NYCA | USA | New York | E | 40.70 | -73.25 |
| ONAI | Canada | Ontario | E | 44.25 | -76.68 |
| ONBL | Canada | Ontario | E | 42.32 | -81.97 |
| ONBW | Canada | Ontario | E | 44.13 | -79.61 |
| ONFL | Canada | Ontario | E | 45.37 | -75.05 |
| ONKC | Canada | Ontario | E | 44.09 | -81.62 |
| ONKG | Canada | Ontario | E | 44.20 | -76.47 |
| ONLP | Canada | Ontario | E | 42.62 | -80.39 |
| ONME | Canada | Ontario | E | 44.53 | -80.57 |
| ONOH | Canada | Ontario | E | 45.42 | -75.70 |
| ONPA | Canada | Ontario | E | 45.33 | -76.33 |
| ONPQ | Canada | Ontario | E | 44.02 | -77.70 |
| ONSR | Canada | Ontario | E | 44.40 | -81.36 |
| ONSS | Canada | Ontario | E | 46.50 | -84.37 |
| ONTB | Canada | Ontario | E | 48.40 | -89.30 |
| ONTO | Canada | Ontario | E | 43.72 | -79.42 |
| QCCJ | Canada | Quebec | E | 48.37 | -71.17 |
| QCCS | Canada | Quebec | E | 47.00 | -70.50 |
| QCHU | Canada | Quebec | E | 45.38 | -74.13 |
| QCLO | Canada | Quebec | E | 45.65 | -73.50 |
| QCMO | Canada | Quebec | E | 45.45 | -73.65 |
| QCPE | Canada | Quebec | E | 48.53 | -64.33 |
| QCQU | Canada | Quebec | E | 46.80 | -71.25 |
| QCST | Canada | Quebec | E | 46.00 | -73.03 |
| SDSL | USA | South Dakota | C | 45.78 | -98.25 |
| SKCC | Canada | Saskatchewan | C | 52.27 | -106.52 |
| SKGD | Canada | Saskatchewan | C | 51.32 | -106.98 |
| SKHA | Canada | Saskatchewan | C | 51.73 | -107.70 |
| SKKU | Canada | Saskatchewan | C | 51.60 | -104.75 |
| SKLM | Canada | Saskatchewan | C | 51.37 | -105.23 |
| SKMO | Canada | Saskatchewan | C | 50.41 | -107.04 |
| SKQD | Canada | Saskatchewan | C | 51.02 | -106.55 |
| SKRE | Canada | Saskatchewan | C | 50.52 | -104.62 |
| SKSC | Canada | Saskatchewan | C | 52.38 | -108.70 |
| SKSW | Canada | Saskatchewan | C | 50.25 | -107.88 |
| WAGH | USA | Washington | W | 46.97 | -124.05 |
| WAML | USA | Washington | W | 47.13 | -119.32 |
| WASB | USA | Washington | W | 48.30 | -122.37 |
| WASD | USA | Washington | W | 48.10 | -123.07 |
| WIDY | USA | Wisconsin | E | 44.60 | -87.78 |

**Annexe S2.2**. Relationship between the number of snowy owls counted annually during the Christmas Bird Count at each site (N = 84) from 1994 to 2011 and the effort of observation reported in party-hours, i.e. the number of observers multiplied by the time spent counting at each site ($p = 0.56$; $r^2 = 0.0003$).



**Annexe S2.3**. Frequency distribution of the annual abundance of snowy owls at each of the 84 sites selected from the Christmas Bird Count data from 1994 to 2011.



**Annexe S2.4.** Details on the structure of ZINB models.

ZINB models come from a mixture of 2 distributions where a logistic regression models the structural zeroes and a negative binomial regression is used for the counts ($y > 0$; Hilbe 2011). The Negative binomial (NB) distribution is characterized by a dispersion parameter $\alpha$ and a mean $\mu$, and its variance is equal to $\mu+\alpha\mu^2$ (Hilbe 2011). Covariates can be added to each part to model the excess of zeroes and/or the count. Zero-inflated models allow modeling of zero counts using both binary and count processes, as opposed to other approaches such as Hurdle models (Sileshi 2008). We nonetheless determined if this type of model was better than more conventional ones. We thus fitted the following additional models: 1) Poisson Generalized Estimating Equation (GEE; Liang and Zeger 1986), 2) Negative Binomial GEE, 3) Poisson mixed model, 4) Zero-Inflated Poisson model and 4) NB mixed model. Based on AIC, the ZINB model clearly performed better than others, and thus confirmed that our data were overdispersed and zero-inflated. All analyses presented in the paper were thus based on the ZINB models.

Analyses of count data represent a challenge as they often depart from normal distributions. The presence of excess zeroes and overdispersion in count data is very common, and these distribution characteristics violate the assumptions of standard statistical tests (Martin et al. 2005, Winkelmann 2008, Okamura et al. 2012). Overdispersion can be caused by excessive variation between counts or by a violation of the assumptions in the shape of the distribution, such as in the case of an excess of zeroes. Failure to accommodate these peculiarities may bias estimations and result in missing statistically significant findings (e.g. Type II error when zero-inflation is ignored) or concluding to statistical significance when there is none (e.g. Type I error if overdispersion is ignored), which would jeopardize the interpretation of ecological effects (Perumean-Chaney et al. 2013).

# Annexe S3: Documentation supplémentaire pour le Chapitre 4

**Annexe S3.1**. Isotopic ratios ($\delta^{13}$C and $\delta^{15}$N values in ‰) of tail feathers of captive snowy owls and of their food (white mice muscles), and diet-tissue discrimination factors of feathers and blood (mean values are presented with SD). Mouse muscle tissues were lipid extracted and feathers were washed in solvent before isotopic analyses.

| | Isotopic ratios | | Diet-tissue discrimination | |
|---|---|---|---|---|
| | $\delta^{13}$C | $\delta^{15}$N | Δ13C | Δ15N |
| White mice muscles (n=5) | -20.41 ± 0.04 | 7.96 ± 0.26 | | |
| Snowy owl feathers | | | | |
| 7700 | -18.68 | 12.00 | | |
| 7729 | -18.56 | 12.40 | | |
| 7751 | -18.30 | 11.91 | | |
| 7751 | -18.59 | 12.00 | | |
| Mean | -18.53 ± 0.16 | 12.08 ± 0.22 | **1.88 ± 0.04** | **4.12 ± 0.26** |
| Snowy owl blood[1] | - | - | **0.3 ± 0.2** | **1.9 ± 0.1** |

[1] From Therrien et al. (2011a)

**Annexe S3.2.** Isotopic ratios ($\delta^{13}$C and $\delta^{15}$N values in ‰) of wild snowy owl feathers and blood, and of potential marine and terrestrial prey of snowy owls. Isotopic ratios have not been corrected with their associated diet-tissue discrimination factors.

| | | Isotopic value | | | Sampling | |
|---|---|---|---|---|---|---|
| | *n* | $\delta^{13}$C | $\delta^{15}$N | Sampling location | year | Source |
| Snowy owl | | | | | | |
| Wing feather (new secondary) | 10 | -23 ± 0.3 | 7.1 ± 1.7 | Deception Bay, QC | 2013 | 1 |
| Wing feather (old secondary) | 10 | -22.8 ± 0.5 | 7.8 ± 2.0 | " | 2013 | 1 |
| Neck feather | 8 | -23.0 ± 0.2 | 7.2 ± 1.4 | " | 2013 | 1 |
| Rump feather | 10 | -23.1 ± 0.5 | 8.1 ± 1.8 | " | 2013 | 1 |
| Flank feather | 10 | -22.6 ± 1.1 | 8.4 ± 2.9 | " | 2013 | 1 |
| Breast feather | 10 | -23.0 ± 0.5 | 7.9 ± 1.6 | " | 2013 | 1 |
| Head feather | 10 | -23.0 ± 0.5 | 8.5 ± 1.9 | " | 2013 | 1 |
| Blood | 8 | -24.8 ± 0.2 | 4.9 ± 0.7 | " | 2013 | 1 |
| Wing feather (new secondary) | 8 | -23.0 ± 0.6 | 8.4 ± 2.4 | Bylot Island, NU | 2014 | 1 |
| Wing feather (old secondary) | 8 | -23.3 ± 0.3 | 6.4 ± 1.4 | " | 2014 | 1 |
| Neck feather | 8 | -23.4 ± 0.4 | 6.7 ± 1.5 | " | 2014 | 1 |
| Rump feather | 8 | -23.6 ± 0.3 | 6.7 ± 1.2 | " | 2014 | 1 |
| Flank feather | 8 | -23.2 ± 1.0 | 6.9 ± 1.9 | " | 2014 | 1 |
| Breast feather | 8 | -23.5 ± 0.5 | 6.5 ± 1.1 | " | 2014 | 1 |
| Head feather | 8 | -23.4 ± 0.5 | 6.8 ± 1.5 | " | 2014 | 1 |
| Blood | 8 | -24.9 ± 0.3 | 5.0 ± 0.9 | " | 2014 | 1 |
| **Mean (Feathers)** | | **-23.1 ± 0.6** | **7.5 ± 1.9** | | | |
| **Mean (Blood)** | | **-24.8 ± 0.3** | **4.9 ± 0.8** | | | |
| Marine sources | | | | | | |
| Common eider | 5 | -19.3 ± 0.3 | 12.3 ± 0.7 | Belcher Islands, NU, Canada | 2012 | 2 |
| Common murre | 5 | -19.9 ± 0.5 | 13.6 ± 0.1 | Twilingate, NFLD, Canada | 2011 | 2 |
| Long-tailed duck | 5 | -19.1 ± 1.0 | 15.5 ± 0.8 | Belcher Islands, NU, Canada | 2000 | 2 |
| Razorbill | 5 | -20.0 ± 0.2 | 13.1 ± 0.3 | NFLD, Canada | 2011-12 | 2 |
| Thick-billed murre | 5 | -19.4 ± 0.7 | 13.8 ± 0.3 | Twilingate, NFLD, Canada | 2011 | 2 |
| **Mean (Marine sources)** | **25** | **-19.5 ± 0.4** | **13.7 ± 1.2** | | | |
| Terrestrial sources | | | | | | |
| *Mammalian* | | | | | | |
| Brown lemming | 30 | -26.5 ± 0.6 | 3.8 ± 1.4 | Bylot Island, NU, Canada | 2007-09 | 3 |
| Collared lemming | 10 | -26.7 ± 1.5 | 2.3 ± 2.5 | Bylot Island, NU, Canada | 2007-09 | 3 |
| Meadow vole | 1 | -26.7 | 4.7 | Deception Bay, QC, Canada | 2013 | 1 |
| Ungava lemming | 2 | -25.8 ± 0.2 | 2.1 ± 1.3 | Deception Bay, QC, Canada | 2013 | 1 |
| *Avian* | | | | | | |
| Rock ptarmigan | 5 | -23.9 ± 0.4 | 2.3 ± 0.5 | Kuujjuaq, QC, Canada | 2014 | 1 |
| **Mean (Terrestrial sources)** | **48** | **-25.9 ± 1.2** | **3.1 ± 1.2** | | | |

[1] Samples collected and analysed in this study

[2] Samples from Environment and Climate Change Canada (ECCC) but analysed in this study

[3] Values obtained from Tarroux et al. (2012) and Gauthier et al. (2015)

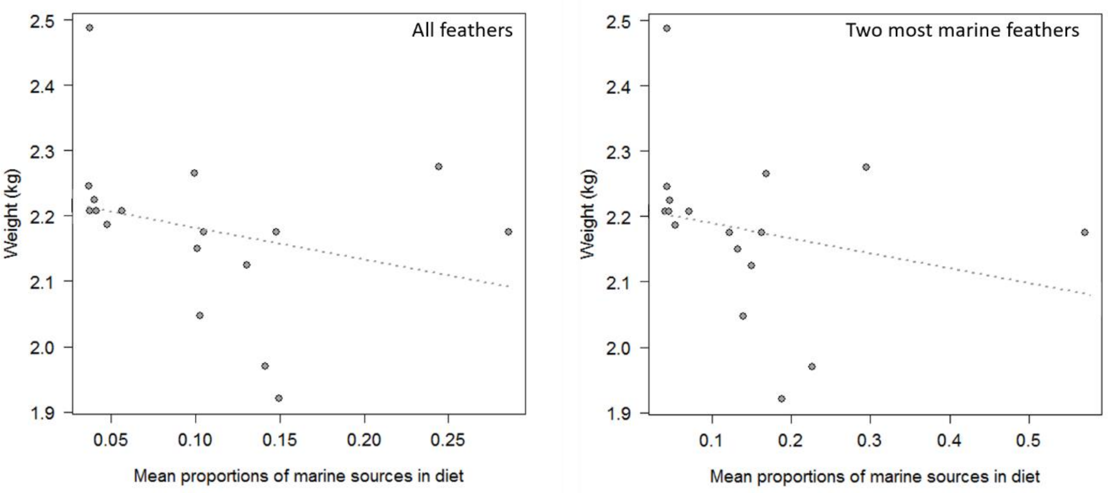
**Annexe S3.3**. Pairwise comparisons of the $\delta^{15}$N isotopic values among various tissues (Feathers: Wn: Wing new, Wu: Wing used, N: Neck, R: Rump, F: Flank, Br: Breast, H: Head; Bl: blood) for each sampling year (post-hoc tests [Differences in LSmeans] shown due to a significant interaction year*tissue; see Table 4.1). Actual values are shown on Fig. 4.3. (*) = 0.05 < p < 0.1, * = 0.01< p < 0.05, ** p < 0.01.

| $\delta^{15}$N 2013 | Feather types | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| | Wn | Wu | N | R | F | Br | H | Blood |
| Wn | -- | -0.68 | -0.15 | -1.01 | -1.31* | -0.77 | -1.32* | -0.06 |
| Wu | | -- | 0.53 | -0.33 | -0.63 | -0.09 | -0.65 | 0.61 |
| N | | | -- | -0.86 | -1.16(*) | -0.62 | 1.17(*) | 0.09 |
| R | | | | -- | -0.30 | 0.24 | -0.32 | 0.95 |
| F | | | | | -- | 0.54 | -0.02 | 1.25(*) |
| Br | | | | | | -- | -0.56 | 0.70 |
| H | | | | | | | -- | 1.26(*) |

| $\delta^{15}$N 2014 | Feather types | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| | Wn | Wu | N | R | F | Br | H | Blood |
| Wn | -- | 2.01** | 1.78* | 1.74* | 1.56* | 1.95** | 1.59* | 1.26(*) |
| Wu | | -- | -0.23 | -0.27 | -0.45 | -0.06 | -0.42 | -0.75 |
| N | | | -- | -0.04 | -0.22 | 0.17 | -0.19 | -0.52 |
| R | | | | -- | -0.18 | 0.21 | -0.15 | -0.48 |
| F | | | | | -- | 0.39 | 0.03 | -0.30 |
| Br | | | | | | -- | -0.36 | -0.69 |
| H | | | | | | | -- | -0.33 |

# Annexe S4: Documentation supplémentaire pour le Chapitre 5

**Annexe S4.1**. Effect of proportion of marine sources in the diet (as a proxy of habitat use/prey use in winter) on the body condition (i.e. mass) of snowy owls (n=17) estimated by linear regression.



**Annexe S4.2.** Proportions of marine sources in the diet of individual snowy owls (ID) inferred from each individual feather. Mean proportion of marine sources for each feather (white circle) are presented along with their 95% (gray line) and 25% (black line) credible intervals.