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RÉPONSES DES PRÉDATEURS AVIAIRES
AUX FLUCTUATIONS D'ABONDANCE DE PROIES DANS
LA TOUNDRA

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Résumé

L'évaluation du rôle joué par les interactions trophiques dans un écosystème est essentielle afin de comprendre sa structure. La prédation pourrait être particulièrement importante dans les réseaux trophiques simples caractérisés par une faible productivité primaire comme la forêt boréale ou la toundra arctique. Nous avons mesuré la pression de prédation imposée par les principales espèces d'oiseaux prédateurs sur les populations de petits mammifères dans la toundra en évaluant précisément leurs réponses numériques, fonctionnelles et totales à l'Île Bylot, Nunavut et à l'Île Herschel, Yukon, Canada. Nous avons ainsi pu démontrer que la pression de prédation imposée par les oiseaux prédateurs est très forte, et qu'elle serait suffisante pour limiter les populations d'une des deux espèces de lemmings pendant la saison estivale. Nous avons ensuite étudié les déplacements annuels du harfang des neiges (*Bubo scandiacus*) afin de mieux évaluer son rôle dans la dynamique spatiale de l'écosystème terrestre arctique. À l'aide de la télémétrie par satellite, nous avons pu déterminer que le harfang effectuait des déplacements exploratoires printaniers importants et démontrait une très grande dispersion reproductive annuelle. De plus, nous avons évalué les taux de survie et de reproduction annuels chez les femelles harfangs et avons démontré que ces oiseaux pouvaient se reproduire à chaque année dans un environnement où la disponibilité des ressources varie considérablement et de façon irrégulière d'une année à l'autre. Finalement, nous avons étudié l'utilisation hivernale de l'espace chez ces oiseaux. Nous avons ainsi pu démontrer les liens étroits qui existent entre écosystèmes puisque le harfang, un prédateur reconnu pour se spécialiser sur des proies terrestres, semble s'alimenter de proies marines pendant une partie importante de son cycle annuel. Globalement, nos résultats indiquent que les oiseaux prédateurs peuvent fortement influencer le fonctionnement du réseau trophique de la toundra. Leur rôle dans l'écosystème terrestre est aussi vraisemblablement modulé par leur mobilité et la présence de subsides allochtones.

Abstract

Evaluation of the role played by predator-prey interactions in an ecosystem is essential to understand its food web structure. Predation has been suggested to be especially important in simple food webs characterized by a low primary productivity such as the boreal forest or the Arctic tundra. We first measured the predation pressure that the main species of predatory birds imposed on small mammal populations of the tundra by assessing precisely their numerical, functional and total responses on Bylot Island, Nunavut and Herschel Island, Yukon, Canada. We were able to show that the predation pressure imposed by predatory birds is very strong, and appears to be sufficient to limit the populations of one of the two species of lemmings during the summer. We then studied the annual movements of snowy owl (*Bubo scandiacus*) to better assess its role in the spatial dynamic of the Arctic terrestrial ecosystem. Using satellite telemetry, we showed that owls do extensive exploratory movements in spring and exhibit very large annual breeding dispersal movements. In addition, we evaluated the annual survival and reproduction rates in breeding female snowy owl and showed that these birds can breed every year in an environment where resource availability can vary considerably and irregularly from year to year. Finally, we investigated winter space use in this species. We were able to demonstrate the close links between ecosystems as snowy owls, well-known to specialize on rodents, seem to feed on marine prey for a significant part of their annual cycle. Globally, our results show that avian predators can greatly influence the tundra food web functioning. Their role is apparently modulated by their mobility and access to allochthonous subsidies.

Avant-Propos

Cette thèse commence par une introduction générale suivie par 5 chapitres rédigés sous la forme d'articles scientifiques et se termine par une conclusion générale. Chacun des chapitres peut être lu indépendamment du reste de la thèse même si l'introduction et la conclusion présentent le fil conducteur reliant l'ensemble des chapitres. Bien que je sois l'auteur principal de tous les chapitres, Gilles Gauthier (directeur de thèse) et Joël Bêty (co-directeur) ont largement contribué à l'élaboration des objectifs, à l'échantillonnage sur le terrain, aux analyses et à la rédaction de tous les manuscrits. Frank Doyle, Don Reid, Charles Krebs et Erkki Korpimäki ont tous participé à la mise en place et/ou aux nombreuses discussions qui ont abouties au chapitre 1 et agissent donc en tant que co-auteurs. De la même manière, Joanie van DeWalle a participé au chapitre 2 par son implication dans l'analyse des données et dans la rédaction. Le chapitre 1 sera soumis pour publication au *Journal of Animal Ecology*. Le chapitre 2 a été soumis pour publication au *Journal of Raptor Research* et est présentement en évaluation. Le chapitre 3 sera soumis pour publication au journal *Animal Behaviour*. Le chapitre 4 est présentement sous presse au *Journal of Wildlife Management*. Enfin, le chapitre 5 a été publié dans la revue *Journal of Avian Biology*.

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À ma famille

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Introduction

Souvent négligée dans le contrôle des réseaux trophiques, la prédation a longtemps été perçue comme étant insignifiante (Errington, 1946). Toutefois, différentes hypothèses ont depuis proposé que la prédation pourrait jouer un rôle majeur dans ce contrôle. En effet, sur une base théorique, Hairston *et al.* (1960) a proposé l'hypothèse selon laquelle les herbivores pouvaient être limités par les prédateurs dans les communautés terrestres. Oksanen (1981) a ensuite repris l'idée pour développer son hypothèse de l'exploitation des écosystèmes, laquelle confère un rôle important aux prédateurs dans certains écosystèmes. En effet, cette hypothèse stipule que chaque niveau trophique agit comme une population qui en exploite une autre et où la prédation peut réguler les herbivores lorsque la productivité du système est suffisante pour supporter ces prédateurs. Enfin, dans leur revue de littérature, Korpimäki & Krebs (1996) ont conclu que beaucoup d'évidences empiriques supportaient l'idée que la prédation jouait un rôle majeur dans la plupart des écosystèmes. Il est maintenant clair que la pression de prédation par les consommateurs de deuxième ordre a le potentiel pour réguler les communautés de vertébrés dans plusieurs écosystèmes (Krebs et al. 1995, Korpimäki & Norrdahl 1998, Ripple *et al.* 2001, Korpimäki *et al.* 2002, Schmitz 2006). Cette force semble particulièrement importante dans les réseaux trophiques simples caractérisés par une faible productivité primaire comme la forêt boréale ou la toundra arctique (Korpimäki & Krebs, 1996). Par contre, l'importance et l'intensité des liens entre les acteurs qui interagissent dans ces écosystèmes demeurent peu connues, tout particulièrement dans la toundra.

Bien que l'écologie de plusieurs espèces arctiques ait été relativement bien étudiée sur une base individuelle (Elmhagen *et al.* 2000, Predavec *et al.* 2001, Bêty *et al.* 2003), les relations trophiques, elles, ont reçu une attention moindre de la part des scientifiques et ce, malgré le fait que ces interactions peuvent être déterminantes dans le fonctionnement et l'équilibre d'un écosystème (Gauthier *et al.* 2004, Ims & Fuglei 2005). Une des raisons majeures de cette sous-représentation dans les études empiriques est la complexité des interactions trophiques et la difficulté à les étudier précisément dans un écosystème donné (Sinclair & Krebs 2001). Il est par contre impératif de bien comprendre les interactions trophiques d'un écosystème afin de mieux anticiper les effets potentiels de changements environnementaux (Korpimäki & Krebs 1996, Schmitz *et al.* 2003, Ims & Fuglei 2005). Cela est particulièrement vrai pour l'écosystème arctique qui verra, selon les prédictions

actuelles, son climat varier le plus au cours des prochaines décennies parmi tous les écosystèmes de la planète (ACIA 2004).

Une des particularités de l'écosystème terrestre arctique est qu'il subit d'importantes variations temporelles dans l'abondance des ressources disponibles aux différents niveaux trophiques (Gauthier *et al.* 2004, Ims & Fuglei 2005). En effet, les petits mammifères (*Lemmus* sp., *Dicrostonyx* sp.) sont des herbivores majeurs et constituent la base de l'alimentation de plusieurs prédateurs (Oksanen *et al.* 1981, Krebs *et al.* 2003, Gauthier *et al.* 2004). Ces rongeurs subissent d'extraordinaires fluctuations d'abondance avec des oscillations de populations irrégulières et de grande amplitude (Elton 1924, Krebs *et al.* 1973, Krebs 2011). L'explication de ce phénomène demeure toujours controversée à ce jour (Turchin *et al.* 2000, Gauthier *et al.* 2009, Oksanen *et al.* 2009, Krebs 2011), mais la prédation pourrait y jouer un rôle central (Korpimäki 1985, Korpimäki & Krebs 1996, Gilg *et al.* 2003, Ims *et al.* 2011).

Deux hypothèses principales visant à expliquer le contrôle du réseau trophique de la toundra s'affrontent présentement. La première avance que le système est contrôlé principalement par les ressources (en anglais « bottom-up »), c'est-à-dire que l'abondance des producteurs primaires (végétaux) influence l'abondance et la reproduction des consommateurs primaires (herbivores) qui, à leur tour, influencent l'abondance et la reproduction des consommateurs secondaires (prédateurs) (Polis & Strong 1996, Polis 1999). À l'opposée, l'hypothèse du contrôle de l'écosystème par les prédateurs (en anglais « top-down ») propose que l'action des consommateurs secondaires, en contrôlant ou du moins en limitant l'abondance des consommateurs primaires dont ils s'alimentent, soulagent les producteurs primaires d'une pression de broutement intense et permet ainsi au système de ne pas s'effondrer par cause de surbroutement (Oksanen *et al.* 1981; Oksanen & Oksanen 2000). Les prédateurs permettraient ainsi de maintenir une densité d'herbivores adéquate pour garder le système en équilibre. Par contre, ces deux hypothèses ne sont pas forcément exclusives et pourraient agir de concert ou en alternance (Sinclair *et al.* 2000, Gauthier *et al.* 2004).

Diverses études empiriques ont étudié les réseaux trophiques dans différents écosystèmes nordiques et en sont venus à des conclusions distinctes. Dans une étude menée au Groenland où le réseau trophique est relativement simple, c'est-à-dire composé d'une faible diversité d'espèces, Gilg *et al.*

(2003, 2006) ont proposé, à la lumière de leurs résultats, que le réseau trophique serait contrôlé par le haut, démontrant un fort impact des prédateurs. Des résultats similaires ont été rapportés sur la côte des Territoires du Nord-Ouest où la prédation semble contrôler les populations de petits mammifères et parfois les maintenir en permanence à de faibles densités (Reid *et al*. 1995, 1997, Wilson *et al*. 1999). À l'opposé, Batzli *et al*. (1980) et Pitelka & Batzli (2007) affirment qu'en Alaska, les différents prédateurs étaient principalement soutenus par les populations d'herbivores qui eux contrôlaient le fonctionnement de l'écosystème, quoique la mortalité des petits mammifères due à la prédation aviaire pouvait atteindre 88% dans certain cas. En Fennoscandia, il semble que les patrons de cyclicité des petits mammifères de la toundra supportent également l'hypothèse d'un contrôle par le bas (Turchin *et al*. 2000), quoique ceci ait été récemment remis en question (Ims *et al*. 2011). Finalement, une étude de grande envergure menée dans un système plus complexe, soit la forêt boréale du Yukon, a suggéré que les deux mécanismes pouvaient opérer dans un même milieu, en alternance (Sinclair *et al*. 2000, Krebs *et al*. 2001). Cette étude, où les différents niveaux trophiques ont été manipulés expérimentalement, démontre ainsi que la compréhension des écosystèmes nordiques n'est pas aussi simple qu'on l'avait imaginé initialement. Il devient donc important d'examiner le fonctionnement de l'écosystème terrestre de l'Arctique canadien, habitat qui représente une part importante du territoire circumpolaire, mais qui a rarement fait l'objet d'études du genre.

Prédateurs de la toundra

Les prédateurs constituent un groupe fonctionnel fort important dans de nombreux écosystèmes de par leur influence sur les consommateurs primaires (McLaren & Peterson 1994, Krebs *et al*. 2003). Dans la toundra arctique, on compte un nombre relativement restreint de mammifères prédateurs qui s'alimentent principalement de petits mammifères, le renard arctique (*Vulpes lagopus*) et l'hermine (*Mustela erminea*) étant les plus communs. Dans certains endroits, on note aussi le loup (*Canis lupus*), le renard roux (*V. vulpes*), le carcajou (*Gulo gulo*) et l'ours brun (*Ursus arctos*) qui s'alimentent principalement de plus grosses proies, contrairement aux autres prédateurs terrestres de la toundra. Les prédateurs aviaires sont pour leur part représentés par une grande diversité d'espèces, répartis selon leur degré de spécialisation alimentaire. Ainsi, des rapaces comme le harfang des neiges (*Bubo scandiacus*) et la buse pattue (*Buteo lagopus*) s'alimentent presque

exclusivement de petits mammifères et leur nidification semble fortement influencée par l'abondance de ces proies. Ils sont considérés comme des prédateurs spécialistes (Parmelee 1992, Bechard & Swem 2002, Wiggins *et al.* 2006). Les labbes à longue queue (*Stercorarius longicaudus*) et parasite (*S. parasiticus*), quant à eux, sont considérés comme des prédateurs plus généralistes puisqu'ils se nourrissent de lemmings mais également de proies alternatives comme des œufs et des jeunes oiseaux en plus d'insectes et autres invertébrés lorsque les petits mammifères sont peu abondants (Wiley & Lee 1998, Wiley & Lee 1999). Le faucon pèlerin (*Falco peregrinus*) est également connu pour s'alimenter de petits mammifères, mais son régime alimentaire est généralement constitué d'oiseaux (White *et al.* 2002). Finalement, d'autres prédateurs comme le goéland bourgmestre (*Larus hyperboreus*) démontrent une très grande plasticité dans leur régime alimentaire et sont considérés comme des généralistes purs (Gilchrist 2001). Bien que tous ces prédateurs se nourrissent au moins en partie de petits mammifères, leur niveau de spécialisation alimentaire suggère qu'ils pourraient démontrer des réponses numériques et fonctionnelles très différentes aux fluctuations d'abondance de petits rongeurs.

Réponses numérique, fonctionnelles et totales

Très peu d'études ont examiné l'impact cumulatif des prédateurs sur les populations de proies dans la toundra arctique mis à part Pitelka *et al.* (1955) et Gilg *et al.* (2006). Cet aspect demeure néanmoins un prérequis essentiel afin d'évaluer le rôle de la prédation dans le contrôle du réseau trophique (Korpimäki & Krebs 1996). Pour évaluer l'impact cumulatif proprement dit, il convient de mesurer les réponses numériques, fonctionnelles et totales des prédateurs.

La réponse numérique d'un prédateur correspond à ses variations d'abondance à un site donné en réponse aux changements dans l'abondance de ses proies principales (Solomon 1949, Holling 1959). La réponse numérique peut être décrite selon qu'elle soit agrégative ou reproductive (Bêty *et al.* 2002). D'abord, la réponse agrégative représente le nombre d'individus adultes présents à un site donné en fonction de l'abondance des proies (Korpimäki & Norrdahl 1989, Hörnfeldt *et al.* 1990, Wilson & Bromley 2001, Gilg *et al.* 2003). Cet élément est étroitement lié à la mobilité des individus, ou à leur potentiel à envahir ou à quitter rapidement un site lors de fluctuations dans l'abondance des proies, phénomène important dans l'écologie des oiseaux de proies (Phelan &

Robertson 1978, Korpimäki & Norrdahl 1989, Korpimäki 1994, Newton 2006). Ainsi, on s'attend à observer, chez les prédateurs de type spécialistes, de fortes réponses numériques agrégatives associées à des mouvements interannuels sur de grandes distances. Plusieurs espèces de rapaces ont démontré des irruptions et des envahissements de milieux devenus soudainement riches en proies dont notamment la chouette épervière (*Surnia ulula*) (Korpimaki 1994), le harfang des neiges (Pitelka *et al.* 1955) et la buse pattue (Reid *et al.* 1997). Ces prédateurs envahiraient donc rapidement les milieux riches en proies et déserteraient les milieux pauvres, entrainant ainsi une faible fidélité aux sites de reproduction d'année en année (Phelan & Robertson 1978, Parmelee 1992, Gilg *et al.* 2003). À l'opposée, chez les prédateurs généralistes, on s'attend à observer de moins grands déplacement interannuels (Galushin 1974) et donc, des réponses numériques agrégatives plus faibles associées à une fidélité plus grande au site de reproduction (Wiley & Lee 1998, Wiley & Lee 1999, Gilchrist 2001). Bien que des déplacements massifs vers des sites riches en proies ont été observées chez des prédateurs spécialistes en forêt boréale (Korpimäki 1985, Korpimäki 1994), aucune étude à ce jour n'a documenté ces comportements chez les prédateurs aviaires arctiques.

La réponse reproductive de ces prédateurs en réponse aux fluctuations d'abondance des proies complète la réponse numérique (Korpimäki & Norrdahl 1989, Hörnfeldt *et al.* 1990, Reid *et al.* 1997, Gilg *et al.* 2003). Chez les prédateurs spécialistes qui démontrent une réponse agrégative très forte aux fluctuations de petits mammifères, on s'attend à observer une réponse reproductive non nulle à un site donné seulement lors des années de forte abondance de petits mammifères. Par contre, même si on s'attend à ce que les prédateurs généralistes démontrent une faible réponse agrégative aux fluctuations d'abondance de petits mammifères, leur succès reproducteur pourrait néanmoins être influencé, entraînant une réponse reproductive plus ou moins forte. En plus d'augmenter la compétition intra et interspécifique (Brommer *et al.* 2002), les faibles densités de petits mammifères pourraient aussi occasionner une augmentation de la prédation intra guilde, principalement chez les espèces généralistes (Polis & Holt 1992, Ratcliffe & Furness 1999, Davis *et al.* 2005).

Une particularité majeure de la réponse numérique est la rapidité avec laquelle les prédateurs sont en mesure de réagir. En effet, plusieurs exemples de fluctuations de populations de prédateurs

démontrent un délai en réponse aux fluctuations dans l'abondance des proies (Elton 1924, McLaren & Peterson 1994, Boutin *et al.* 1995, Gilg *et al.* 2003). Le délai observé peut être inhérent à leur stratégie de reproduction ou à leur capacité d'immigration (Andersson & Erlinge 1977, Hanski *et al.* 1991, Hanski *et al.* 1993, Tornberg *et al.* 2005). Par contre, considérant la grande mobilité des prédateurs aviaires, certains auteurs proposent que ces prédateurs spécialistes agiraient de manière instantanée et pourraient ainsi synchroniser les variations de densité des proies en se déplaçant rapidement selon l'abondance de proies sans démontrer de délai dans leur réponse (Ydenberg 1987, Ims & Steen 1990, Korpimäki & Norrdhal 1991, Korpimäki 1994, Reid *et al.* 1997, Ims & Andreassen 2000, Gilg *et al.* 2003). Puisque les délais des réponses numériques (agrégative et reproductive) des différentes espèces de prédateurs ont été peu étudiés dans l'écosystème arctique, il devient de première importance de les mesurer afin de mieux comprendre le fonctionnement de cet écosystème (Korpimaki & Krebs 1996).

La réponse fonctionnelle, quant à elle, représente le changement du taux de consommation d'une proie donnée par un prédateur en réponse aux fluctuations d'abondance de cette proie (Solomon 1949, Holling 1959). Cette réponse se traduit par des changements de comportements associés à la quête alimentaire (Solomon 1949, Wilson & Bromley 2001, Bêty *et al.* 2002), mais plus spécifiquement par des variations du régime alimentaire lui-même (Phelan & Robertson 1978, Korpimäki & Norrdahl 1989, Gilg *et al.* 2003) en fonction des variations de proies disponibles dans un milieu donné. Ainsi, on s'attend à observer peu de variation dans le régime alimentaire des prédateurs spécialistes puisque ces derniers ne font pas varier énormément les proportions des différentes proies qu'ils consomment (Reid *et al.* 1997). Au contraire, le régime alimentaire des prédateurs généralistes devrait varier en fonction de l'abondance des différentes proies (Reid *et al.* 1997). Néanmoins, tous ces prédateurs (spécialistes ou généralistes) peuvent démontrer une variation dans le taux de consommation quotidien de proies entraînant ainsi une réponse fonctionnelle forte. La quantification du taux de consommation des différentes proies par les prédateurs aviaires de l'écosystème arctique ont rarement fait l'objet d'étude spécifique (mis à part de Gilg *et al.* 2003, Gilg *et al.* 2006), mais s'avère nécessaire, notamment pour le calcul de l'impact total de la prédation.

En effet, en intégrant les réponses numériques et fonctionnelles des différents prédateurs, on peut estimer la réponse totale de ce groupe fonctionnel sur le niveau trophique inférieur et ainsi

expliquer une partie du fonctionnement de l'écosystème (Holling 1959). Si le taux de prédation quotidien exercé par les prédateurs est plus grand que le taux de croissance intrinsèque des proies, l'effectif des populations de proies diminuera, et inversement (Begon *et al*. 1996). En calculant la fraction de la population de petits mammifères qui est consommée quotidiennement, il devient possible d'évaluer le rôle des prédateurs aviaires dans l'écosystème terrestre arctique (Batzli *et al*. 1980, Gilg *et al*. 2006).

Objectifs de la thèse

Mon projet s'insère dans la continuité d'études similaires qui ont été menées en Alaska de 1955 à 1974 (Batzli *et al*. 1980, Pitelka & Batzli 2007) et au Groenland de 1988 à 2002 (Gilg *et al*. 2003, Gilg *et al*. 2006) où les communautés de vertébrés sont relativement semblables, offrant ainsi des points de comparaisons pertinents. Toutefois, mon projet s'intéresse à des communautés de vertébrés de l'Arctique canadien légèrement plus diversifiées qu'au Groenland (i.e. avec plus d'espèces de prédateurs) mais moins qu'en Alaska, ce qui offre un gradient pertinent pour les comparaisons. De plus, les populations de petits mammifères de l'écosystème terrestre canadien démontrent des densités (<0,1 à 12 individus/ha; Gruyer 2010, Blackburn 1998) du même ordre de grandeur qu'au Groenland (<0,1 à 11 individus/ha; Gilg *et al*. 2003), mais ont la particularité d'être représentées par deux espèces de lemmings comparativement à une seule au Groenland. En revanche, on trouve les mêmes espèces de petits mammifères en Alaska, mais les valeurs de densités qui y sont reportés sont nettement supérieures (<0,1 à 225 individus/ha; Batzli *et al*. 1980) à celles mesurées au Canada et au Groenland. Compte tenu de l'abondance des prédateurs aviaires dans l'écosystème arctique et du peu d'information sur leur rôle exact en tant que prédateurs dans cet écosystème, mon projet étudie donc ce groupe de prédateurs en particulier.

Mon étude vise principalement à (1) mesurer les changements locaux dans l'abondance et le succès reproducteur des prédateurs aviaires selon les variations annuelles dans l'abondance de petits mammifères (réponse numérique), (2) déterminer la proportion des différentes proies dans le régime alimentaire et le taux de consommation journalier de proie de ces prédateurs en fonction de l'abondance des proies disponibles (réponse fonctionnelle), (3) mesurer la réponse totale (intégration des réponses numériques et fonctionnelles) de ces prédateurs et la comparer au taux de

croissance intrinsèque des populations de petits mammifères. De plus, ce projet vise à (4) mesurer l'amplitude des mouvements du harfang des neiges, un des prédateurs clés, durant plusieurs années consécutives afin de voir si leur mobilité peut contribuer à synchroniser les fluctuations d'abondance de petits mammifères à une échelle régionale, à (5) déterminer le rôle de l'abondance locale de petits mammifères dans la sélection du site de nidification de ces prédateurs et à (6) évaluer si le harfang des neiges démontre des comportements reproducteurs année après année dans des sites distincts. Ultimement, ces résultats contribueront à mieux comprendre l'impact des prédateurs aviaires sur les fluctuations d'abondance de petits mammifères et leur rôle dans le contrôle du réseau trophique arctique.

Organisation de la thèse

Le premier chapitre évalue spécifiquement les réponses numériques, fonctionnelles et totales des oiseaux prédateurs à deux sites de l'arctique Canadien. En se basant sur l'hypothèse du contrôle par le haut ("*top-down hypothesis*" en anglais), j'ai évalué jusqu'à quel point la pression de prédation exercée par les oiseaux pouvait limiter les populations de petits mammifères.

Le deuxième chapitre est intimement lié au premier car j'y compare l'efficacité de méthodes utilisées pour évaluer le régime alimentaire et mesurer le taux de consommation quotidien de proies par le harfang des neiges. En effet, différentes méthodes sont couramment utilisées pour évaluer ces paramètres, mais aucune évaluation de leur efficacité relative n'avait à ce jour été effectuée.

Le troisième chapitre évalue les mouvements annuels à grande échelle du harfang des neiges à l'aide d'émetteurs satellites. En se basant sur les implications de ce comportement dans la dynamique de l'écosystème et les relations prédateurs-proies, le suivi individuel nous a permis de démontrer empiriquement l'étendue des mouvements, l'échelle d'exploration printanière ainsi que la distance moyenne de dispersion reproductive sur plusieurs années consécutives.

Le quatrième chapitre est lié au troisième alors que j'y évalue les taux de reproduction et de survie des harfangs marqués à l'aide d'émetteurs satellites. En effet, le suivi individuel combiné à des visites sur le terrain ont permis d'évaluer pour la première fois ces traits biodémographiques chez des harfangs des neiges sauvages.

Finalement, le cinquième et dernier chapitre utilise les déplacements hivernaux des harfangs des neiges suivis à l'aide d'émetteurs satellites afin de faire une ouverture sur les liens qui existent entre écosystèmes. Peu étudiés, les échanges de nutriments entre écosystèmes (aussi appelés subsides allochtones) semblent soutenir une partie de la population de prédateurs du milieu terrestre arctique pendant l'hiver, période où la disponibilité des ressources alimentaires en milieu terrestre est plus faible. Puisque ces mêmes prédateurs exercent une forte pression de prédation en milieu terrestre l'été venu, ce chapitre illustre l'importance que peuvent avoir les échanges entre écosystèmes sur le fonctionnement du réseau trophique de la toundra.

Chapitre 1

Predation pressure imposed by avian predators suggests regulation of tundra small mammal populations

Résumé

L'évaluation des interactions trophiques dans un écosystème est essentielle à la compréhension de son fonctionnement. Il a été suggéré que la prédation pouvait être particulièrement importante dans les réseaux trophiques simples et les écosystèmes démontrant une faible productivité primaire comme la toundra. Une forte densité et diversité d'oiseaux prédateurs, tant spécialistes comme le harfang des neiges (*Bubo scandiacus*) et la buse pattue (*Buteo lagopus*), que plus généralistes comme le labbe à longue queue (*Stercorarius longicaudus*), habitent la toundra arctique. Nous avons évalué la pression de prédation imposée par les oiseaux prédateurs pendant la saison estivale en mesurant leurs réponses numérique (variations en nombre d'oiseaux nicheurs et de succès reproducteur) et fonctionnelle (variations dans le régime alimentaire et le taux de consommation quotidien) en fonction des variations d'abondance des proies principales, le lemming variable (*Dicrostonyx, groenlandicus*) et le lemming brun (*Lemmus trimucronatus*). Nous avons mesuré ces réponses à deux sites situés dans l'arctique canadien entre 2004 et 2010. Les prédateurs spécialistes ainsi que le labbe à longue queue ont démontré de fortes réponses numériques aux variations de densités des lemmings. La proportion de lemmings variables dans le régime alimentaire des trois principaux prédateurs (harfang des neiges, buse pattue et labbe à longue queue) était forte à faible abondance de lemmings, mais a diminué avec l'augmentation des densités de lemmings. Les taux de consommation quotidiens ont également varié en réponse aux variations de densités de lemmings bruns, alors que ces mêmes taux sont demeurés constants pour le lemming variable. La consommation totale de lemmings variables par les trois principaux prédateurs, et principalement par le labbe à longue queue, est demeurée très forte peu importe la densité de proies, alors qu'elle a atteint un niveau élevé seulement à très forte abondance de lemmings bruns. Les oiseaux prédateurs ont consommé une forte proportion des populations de lemmings variables, ce qui suggère une régulation par la prédation agissant sur cette espèce. Cette possible limitation n'était pas aussi présente chez le lemming brun. En démontrant des réponses instantanées, les oiseaux prédateurs semblent créer un effet tampon contribuant à la limitation de certaines populations de lemmings.

Abstract

Assessing the strength of top-down forces in an ecosystem is essential to understand food web functioning. Predation has been hypothesised to be especially important in simple food webs and less productive ecosystems such as the arctic tundra. A very dense and diverse suite of predatory birds, from diet specialists, such as the snowy owl (*Bubo scandiacus*) and the rough-legged hawk (*Buteo lagopus*), to more diet generalists, such as the long-tailed jaeger (*Stercorarius longicaudus*), inhabits the arctic tundra and we anticipate that they may have a strong impact on small mammal herbivores during the snow-free period. We evaluated predation pressure by avian predators as their combined numerical (variation in breeding numbers and reproductive success) and functional (variation in diet and daily consumption rates) responses to the variation in collared (*Dicrostonyx groenlandicus*) and brown lemming (*Lemmus trimucronatus*) densities at two study sites in the Canadian Arctic during the 2004 – 2010 period. Lemming specialists as well as the long-tailed jaeger exhibited strong numerical responses to variations in lemming density. The proportion of collared lemmings in the diet of the three main predators (snowy owl, rough-legged hawk and long-tailed jaeger) was high at low lemming density but decreased as lemming density increased. Daily consumption rates also varied in relation to changes in brown lemming density, although those rates remained stable in relation to collared lemming density. Total consumption of collared lemmings by the main avian predators remained high at all density whereas it only reached high levels at very high density of brown lemmings. Taken together, avian predators consumed a large fraction of collared lemming populations, suggesting a predation-driven control on that species. This possible limitation was less apparent in brown lemmings. By exhibiting responses with no time-lag, those predators likely provide a dampening force contributing to the limitation of some lemming populations.

Introduction

Predation pressure by second order consumers has the potential to regulate vertebrate communities in several ecosystems (Krebs et al. 1995, Korpimäki and Norrdahl 1998, Ripple et al. 2001, Korpimäki et al. 2002, Schmitz 2006). This force has been hypothesised to be especially important in simple food webs characterized by a low primary productivity such as the boreal forest or the arctic tundra (Korpimäki and Krebs 1996, Strong 1992). Assessing the relative strength of top-down vs bottom-up (i.e. resources) forces in an ecosystem is essential to understand the food web functioning and to predict impacts of anticipated environmental changes.

In the tundra, small mammals such as lemmings (*Dicrostonyx* and *Lemmus* spp.) are often the dominant herbivores (Krebs et al. 2003). Those herbivores show tremendous variations in numbers from year to year and exhibit population cycles in most circumpolar regions (Elton 1924, Stenseth 1999, Predavec et al. 2001, Gilg 2002). Proximal causes of those fluctuations remain controversial (e.g. Gauthier et al. 2009, Oksanen et al. 2009, Krebs 2011) although in several systems high predation rates have been documented, especially during the summer (Reid et al. 1995, Korpimäki and Krebs 1996, Wilson et al. 1999, Hanski et al. 2001, Gilg et al. 2003, Korpimäki et al. 2004, Ims et al. 2011). Very few studies, however, have quantified the response of arctic predators to fluctuations in small mammal abundance and their cumulative impact on prey populations (but see Pitelka et al. 1955, Gilg et al. 2006), an essential prerequisite to evaluate the role of predation in the control of food webs (Korpimäki and Krebs 1996).

In the tundra, birds present an astonishing diversity of small-mammal predators compared to mammals, ranging from dietary specialists (such as the snowy owl *Bubo scandiacus* and rough-legged hawk *Buteo lagopus*) through semi-generalists (such as the long-tailed jaeger *Stercorarius longicaudus* and peregrine falcon *Falco peregrinus*) and generalists (such as the parasitic jaeger *S. parasiticus* and glaucous gull *Larus hyperboreus*). Diet has been previously described individually for those predators in different regions of the Arctic (reviewed in Birds of North America accounts; glaucous gull: Gilchrist 2001, long-tailed jaeger: Wiley and Lee 1998, parasitic jaeger: Wiley and Lee 1999, peregrine falcon: White et al. 2002, rough-legged hawk: Bechard and Swem 2002, snowy owl: Parmelee 1992) and showed that the primary prey for most of them are small mammals.

However, there has been very few simultaneous assessment of their breeding numbers, diet and consumption rates when these predators occur in sympatry during contrasting years of lemming abundance.

The response of snowy owls and long-tailed jaegers to varying abundance of lemmings has been studied in northern Greenland by Gilg et al. (2003, 2006). They found that density-dependent predation by these two species stabilised the cyclic dynamic of lemmings. However, the food web at this site is simpler than at most other tundra sites. Indeed, whereas only one species of lemming and two species of avian predators breed in Greenland, much of the circumpolar tundra is inhabited by at least two species of small mammals and four or more competing species of avian predators. Therefore, competition for scarce resources among these multiple predators could be high in the relatively unproductive tundra ecosystem. As suggested by Reid et al. (1995) and Wilson et al. (1999), we anticipated that avian predators could have a significant impact on small mammal numbers and thus on the food web functioning.

Our aim was to assess the predation pressure of sympatric avian predators by simultaneously determining variations in numbers (numerical response) and in diet and consumption rates (functional response) to varying lemming density. Arctic avian predators are predominantly migrants and predation on lemmings mostly occurs when snow cover is absent (typically from early June to early October). These predators are highly mobile and have the potential to track small mammal outbreaks over large geographic areas (Korpimäki and Norrdahl 1991, Norrdahl and Korpimäki 1996). We thus hypothesized that (1) specialist avian predators of the tundra would exhibit strong numerical responses without any time lag to local variations in lemming abundance; (2) consumption rate of lemmings by avian predators would vary in response to variations in lemming abundance but to a greater extent in generalists than in specialists and (3) the combined predation pressure by avian predators would be sufficient to regulate the summer growth of lemming populations during the snow-free period. Here we present a detailed evaluation of the numerical, functional and total responses of avian predators at two North American tundra sites in order to provide further insights into the trophic control of arctic terrestrial food webs.

Methods

Study areas

The primary study site was located on Bylot Island (Nunavut, 73° N, 80° W) and field work occurred during summers 2004 to 2010. A secondary study site was located on Herschel Island (Yukon, 70° N, 139° W) where field work occurred during summers 2007 to 2009. The studied area covered approximately 100 km^2 on Bylot Island and 50 km^2 on Herschel Island. Both study sites were dominated by rolling hills and low elevation plateaus interspersed by streams and rivers that created numerous valleys ranging in size from narrow gullies to wide and relatively flat valley bottoms. Mesic tundra (dominated by forbs and a few prostrate shrubs and graminoids) was most common in the hilly landscape whereas flat areas had a mosaic of mesic and wet tundra (the latter habitat being dominated by graminoid plants growing through a ground moss cover; see Gauthier et al. 2011 and Reid et al. 2012). Primary production of vascular plants averages 50 g/m^2/yr on Bylot (Valéry et al. 2010) and 130 g/m^2/yr on Herschel (S. Gilbert, unpublished data). This landscape offered prime habitat for several nesting predatory birds and their prey.

Brown (*L. trimucronatus*) and collared (*D. groenlandicus*) lemmings have a widespread distribution across most of the Canadian tundra and are major herbivores on both Bylot and Herschel Islands. At Herschel Island the tundra vole (*Microtus oeconomus*) was also captured in two of three years, but always in much lower numbers than lemmings. Both study sites have similar communities of breeding predatory birds and are dominated by the snowy owl, the rough-legged hawk, the long-tailed jaeger and the peregrine falcon. Breeding short-eared owls (*Asio flammeus*) have been observed at both sites although their numbers were extremely low. On Bylot, breeding glaucous gulls and parasitic jaegers are also present. No nesting raven (*Corvus corax*) or gyrfalcon (*F. rusticolus*) was found during the study. Other major predators present on both sites include the arctic fox (*Vulpes lagopus*) and the ermine (*Mustela erminea*). On Herschel, the red fox (*V. vulpes*), the grizzly bear (*Ursus arctos*), the wolverine (*Gulo gulo*) and the least weasel (*M. nivalis*) are also encountered on occasions. Herschel Island has muskox (*Ovibos moschatus*) and caribou (*Rangifer tarandus*) populations whereas these ungulates are absent from Bylot Island. By contrast, Bylot Island has a large breeding snow goose (*Chen caerulescens*) colony, situated roughly 30 km to the south of the study area, while Herschel Island has few nesting geese. Potential alternative prey species such as passerines (*Calcarius* and *Plectrophenax* spp.), shorebird species (*Charadrii* spp.),

ptarmigan (*Lagopus* sp.), ducks (*Somateria* and *Clangula* spp.) as well as many arthropods taxa (such as *Arachnidae, Tipulidae, Muscidae*) are present at both sites.

Small mammal density

We measured small mammal density throughout the snow-free period each year by live-trapping them on two trapping grids spaced by at least 2 km at each site (11 ha each on Bylot, 9 ha each on Herschel). Trapping grids were set up in areas representative of the typical habitat found at each study site. On Bylot, one grid was located in hill side dominated by mesic tundra and one grid in a valley bottom dominated by wet habitat. On Herschel, both grids were located in upland tundra. Each trapping grid had 128-144 Longworth live traps that were opened over a 3 or 4 consecutive days at each trapping period, and checked at 4-12 h intervals. We conducted three (sometimes four) trapping sessions each summer (early June, mid-July and late August or September). We determined the sex and mass (g) and we individually marked (with PIT tags on Bylot Island, ear tags at Herschel) and released all animals (see Gruyer et al. 2010 and Krebs et al. 2011 for details). We estimated densities of each species at each trapping session using mark-recapture techniques with the Program DENSITY 4 (Efford et al. 2004, Efford 2009). When the number of captured individuals was too low for analysis in DENSITY (i.e. < 4 individuals), we used the minimum number known to be alive and divided this number by the effective trapping area (see Krebs et al. 2011). We averaged densities of each species between the two grids for each corresponding trapping session in order to have a global measure of density at both study sites.

Avian predators

Numerical responses

We systematically searched for nests of predatory birds during June and early July at both study sites. Over hilly terrain, we followed ridges and scanned the surrounding landscape from vantage points. Nests of most avian predators are conspicuous and typically located on elevated mounds. Moreover, nesting predators often reveal their presence from a relatively long distance through alarm calls and behavioural displays. For species with less conspicuous nests that prefer lowland habitats such as long-tailed jaegers, we systematically covered such habitats in each study area by walking parallel transects 250 m apart. Although we cannot assess the nest detection probability, we

are confident that it was very high (>95%) in this open landscape. However, any possible bias related to detection probability would result in an underestimation of nest density and hence, predation pressure. For lowland nesting species, the search area was restricted to 30 km^2 on Bylot Island and ranged from 22 to 49 km^2 on Herschel Island depending of years. Except for snowy owls in summer 2007 on Herschel Island, we seldom encountered non-breeding, resident adults of any species at our study sites. The number of nests of each species was divided by the area searched annually to obtain nesting density. We assessed the numerical responses of avian predators by plotting their annual nesting densities separately against the density of lemming (both species combined) measured at snow melt in June. At both study sites, we assessed fledgling numbers by revisiting nests at regular intervals. We considered chicks able to sustain flight as fledglings.

Functional responses

The proportion of collared lemming species in the diet of snowy owls, rough-legged hawks and long-tailed jaegers was measured by pellet analyses (Errington 1930, Lewis et al. 2004) collected throughout the breeding season annually on Bylot and Herschel Islands. At each visit to a nest, we collected all pellets found in its surrounding (< 20 m). Pellets were later analyzed in the laboratory to identify ingested prey using hair, bones and feather remains. We determined the minimal number of prey ingested by counting the number of jaws and skulls found in pellets. On Bylot Island, we collected and analysed 1668, 28 and 147 pellets from snowy owls, rough-legged hawks and long-tailed jaegers respectively. On Herschel Island, we collected and analysed 90, 147 and 11 pellets from the same species respectively. We plotted the annual percentage of collared lemmings in the diet of the three main predators in relation to the density of both lemming species on the study area and we compared it to the percentage of collared lemmings in the overall lemming population (both species combined).

We used direct observations to assess the number of prey consumed daily by the three major avian predators from 2007 to 2010 on Bylot Island. We set up blinds about 150 m from focal nests and we conducted behavioural observations during 3 to 8 hr bouts using a spotting scope. Observations covered the 24-hr period to account for any possible circadian variation in predator activity due to the 24-hr daylight during the summer. We conducted observation from the mid-incubation (20 June) through the chick-rearing period (until 15 August). We spend a total of 50, 50 and 80 hr of direct

visual observations on snowy owls, rough-legged hawks and long-tailed jaegers respectively. We also set automatic-triggered cameras at about 5 m from a sample of nests to monitor food delivery over periods of 2 to 7 days. We programmed the motion-sensitive cameras to take pictures every time a movement was detected and under fixed intervals (ranging from 1 to 20 sec). Cameras worked well for snowy owls (see Chapter 2) and rough-legged hawks but not for jaegers because the chicks leave the nest 1 or 2 days after hatching and cannot be followed by a fixed camera. We recorded a total of 3876 and 314 hr of observations with cameras on snowy owl and rough-legged hawk nests respectively.

We assessed the functional response of those three avian predators by plotting their mean daily consumption rates (DCR: lemming individuals consumed per day) in relation to mean daily lemming density on the study area. The lemming density needed for each DCR estimate was calculated by assuming a linear change in density between the two closest trapping sessions. We assessed consumption rates on a nest rather than an individual basis. Since the two techniques (direct observations and cameras) were directed towards the nest, they cannot assess prey consumed away from the nest by adults. This was especially true for snowy owls and rough-legged hawks which nest in territories with topographical features that prevent observers from monitoring provisioning adults away from the nest. In those cases, the consumption that we measured at the nest applies only to the incubating/brooding adult and the growing chicks. We assigned the same consumption level recorded during incubation to the other adult. Any possible bias resulting from this estimation would tend to underestimate consumption rates because the energetic needs of an incubating adult is likely lower than that of a foraging one. Long-tailed jaegers, on the other hand, nest in flatter landscape and were seldom foraging out of view during observations. We are therefore confident that we recorded almost all feeding events, whether close to the nest or further away in the territory.

Total responses

The total response or predation rate (the number of lemmings eaten /day*km^2) was obtained by multiplying the numerical (number of nests per km^2) and functional (number of lemming consumed daily per nest) curves of individual predators and relating the result to the density (individuals/km^2) of each lemming species. Since we did not have empirical consumption rate data on Herschel

Island, we assessed those values by dividing the number of lemmings (all species combined) consumed daily in relation to lemming density on Bylot Island (Annexe 1) according to the proportion of each lemming species in the diet measured on Herschel Island. As sensitivity analysis, we varied the consumption rates measured on Bylot Island by 10% to assess if a change in consumption rate could change the overall picture on Herschel Island. We compared the estimated daily predation rates to the maximum daily potential growth rates of lemming populations assuming that they suffer no mortality and that each adult female produces seven offspring per month with a sex ratio of 1:1. Given that young females become mature at about one month old, those parameters, reviewed in Stenseth and Ims (1993), confer to lemming populations a maximum potential growth rate of 2.44% per day (finite rate of increase for one year: $r = 8.88$, assuming continuous breeding year round). Using maximum values ever recorded yielded population growth rates that probably rarely occur in the wild. Indeed, other studies either used longer generation time or lower litter sizes in their calculation of maximum daily potential growth rates, thereby yielding lower values (brown lemmings: 1.97%, Batzli et al. 1980; collared lemmings: 2.27%, Gilg 2002).

Statistical analyses

We used sigmoid functions to fit the numerical responses (breeding densities expressed as BD and number of fledglings produced per km^2 expressed as NFP) as provided by Gilg et al. (2006):

$$\text{BD (or NFP)} = a\, N^2 / (b^2 + N^2)$$

where a is the asymptotic density of adults, b is lemming density at the inflexion point of the curve and N is lemming density per km^2 at snow melt. We then fitted the same equations with the lemming density measured at year t-1 to test if a time-lag of one year would better fit the data. We compared breeding densities of all avian predators among the two sites using t-tests. We assessed the variation of the proportion of collared lemmings in the diet of the three main predators in relation to the variation of each lemming species density using linear multiple regressions. Since collared and brown lemming densities were strongly correlated ($r = 0.98$, $p < 0.01$), we used actual collared lemming density values and the residuals of the relationship between brown and collared lemming density (i.e. actual density minus that predicted by the relationship) to avoid autocorrelation. For the functional response, given that the main avian predators are absent from the site at low prey density, type III curves did not provide a better fit than the simpler type II curves.

We thus present functional response curves (daily consumption rates, expressed as DCR) fitted with the type II equation (i.e. the simplest model) provided by Gilg et al. (2006):

$$DCR = c\,N' / (d + N')$$

where c is the asymptotic value of the curve, N' is lemming density per km^2 and d is the half-saturation constant (the N' value when $DCR = c/2$). We estimated all parameters in both equations (i.e. a, b, c and d) by fitting curves where the least-square residuals were minimized iteratively. We performed analyses with the "*nlin*" procedure in SAS release 9.2 (SAS Institute Inc. 2008). Results are presented as mean ± SE unless otherwise stated.

Results

Numerical responses

On Bylot Island, we monitored 30, 21, 98, 64, 3 and 3 nests of snowy owls, rough-legged hawks, long-tailed jaegers, glaucous gulls, peregrine falcons and parasitic jaegers, respectively, over the 7 years of the study. On Bylot Island, the breeding density of some predators changed considerably in response to variation in lemming density at time t but not all of them (Figure 1). Strong numerical responses were observed in lemming specialists such as the snowy owl ($F_{2,5} = 41.2$, $p < 0.01$) and the rough-legged hawk ($F_{2,2} = 18.4$, $p = 0.05$). However, long-tailed jaeger also showed a strong numerical response to variations in lemming density ($F_{2,5} = 34.5$, $p < 0.01$) and reached the highest densities among all avian predator species (0.9 nests/km^2). Adding a time lag of one year to the response to lemming density provided a much poorer fit for all the relations described above (all $F < 0.6$, all $p > 0.63$). The other avian predators exhibited no detectable response to an increase in lemming density at time t and t-1 (all $F < 3.6$, all $p > 0.20$, Figure 1).

On Herschel Island, we monitored 6, 17, 11, 0, 14 and 0 nests of snowy owls, rough-legged hawks, long-tailed jaegers, glaucous gulls, peregrine falcons and parasitic jaegers, respectively, over the 3 years of the study. The lower range of lemming density recorded and the shorter length of the study prevented us from detecting any relations between lemming density and breeding numbers of avian predators at this site. Overall, breeding density of rough-legged hawks ($t = -3.5$, df $= 5$ $p = 0.02$), and peregrine falcons ($t = -13.3$, df $= 4$, $p < 0.01$) were higher on Herschel than on Bylot Island, whereas long-tailed jaegers ($t = 3.1$, df $= 8$, $p = 0.02$), parasitic jaegers and glaucous gulls (n = 0 on

Herschel in the latter cases) were more numerous on Bylot. Snowy owls had similar breeding densities at the two sites ($t = -0.6$, df $= 8$, $p = 0.57$).

With an increase in lemming density on Bylot Island, the number of fledglings produced by km^2 increased sharply in snowy owls ($F_{2,5} = 38.4$, $p < 0.01$), rough-legged hawks ($F_{2,2} = 13.7$, $p = 0.07$), long-tailed jaegers ($F_{2,5} = 186.6$, $p < 0.01$) and glaucous gulls ($F_{2,2} = 62.0$, $p = 0.02$), but remained constant in peregrine falcons and parasitic jaegers (all $F < 1$, all $p > 0.58$, Figure 2). Overall, for species exhibiting the strongest responses in breeding numbers (snowy owl, rough-legged hawk and long-tailed jaeger), the number of young fledged per nest at the highest lemming density was 3.0 ± 0.3 (n $= 18$), 3.0 ± 0.7 (n $= 5$) and 1.0 ± 0.1 (n $= 71$), respectively. On Herschel Island, again the low range of lemming density recorded during the three years of the study prevented us from detecting any relations between lemming density and the number of fledglings per km^2. Compared to Bylot Island, the number of fledglings per km^2 on Herschel was higher in peregrine falcons ($t = -3.3$, $p = 0.03$) but similar in snowy owls ($t = 0.7$, $p = 0.49$), rough-legged hawks ($t = -1.2$, $p = 0.27$) and long-tailed jaegers ($t = 0.5$, $p = 0.61$). At the highest lemming density, snowy owls, rough-legged hawks and long-tailed jaegers produced 0.7 ± 0.3, 3.9 ± 0.4 and 1.6 ± 0.2 fledglings per nest respectively.

Functional responses

The proportion of collared lemming in the diet of snowy owls varied with density of both lemming species on Bylot Island ($F_{2,39} = 5.5$, $p < 0.01$) and similar tendencies were found in rough-legged hawks ($F_{2,9} = 2.2$, $p = 0.18$) and long-tailed jaegers ($F_{2,29} = 2.3$, $p = 0.12$, Figure 3). Given the large difference in lemming density (and most probably availability) between the two species in years of peak abundance (brown lemmings averaged 7 times the density of collared lemmings), the proportion of collared lemmings in the diet decreased sharply in those years. Nonetheless, the proportion of collared lemmings in the diet of all three predators remained higher than its proportion in the overall lemming population at all times except for the long-tailed jaeger at very low collared lemming density (Figure 3). At low lemming density, collared represented 82, 61 and 83% of the diet of snowy owls, rough-legged hawks and long-tailed jaeger respectively whereas at high lemming density, those proportions fell to 24, 13 and 8%.

On Bylot Island, the three main avian predators did not show any variation in their daily consumption rates in relation to collared lemming density, which changed relatively little among years of measurements (all $F > 6.2$, $p > 0.08$). Average daily consumption of collared lemming individuals by a breeding pair was 6.9 ± 0.6 (n = 14) for snowy owl, 2.8 ± 0.3 (n = 6) for rough-legged hawk and 2.1 ± 0.8 (n = 8) for long-tailed jaeger (Figure 4). Daily consumption rate of brown lemmings by snowy owls, however, was typical of a true specialist as a sharp type II response was observed ($F_{2,12} = 28.5$, $p < 0.01$, Figure 4). Snowy owl breeding pairs started consuming brown lemmings when density reached 300 ind/km^2 (as they were absent from the system at lower density; see Fig. 1) and their consumption quickly rose to 28.5 individuals/pair/day when density reached 1150 ind/km^2. Daily consumption rate of brown lemmings by rough-legged hawk breeding pairs increased more gradually with prey density and reached 10.8 individuals/pair/day when brown lemming density equalled 1125 ind/km^2 ($F_{2,4} = 12.9$, $p < 0.02$, Figure 4). Daily consumption rate by long-tailed jaeger breeding pairs also showed a sharp type II response as they started consuming brown lemmings when density was 250 ind/km^2 and their consumption reached 12.1 individuals/pair/day at 1230 ind/km^2 ($F_{2,6} = 7.3$, $p < 0.03$, Figure 4).

Total responses

On Bylot Island, total consumption of collared lemmings by the three main avian predators gradually increased as their density increased and tended to stabilize around 3.1 individuals consumed daily per km^2 above 100 ind/km^2 (Figure 5). Total consumption of brown lemming was negligible until density reached a threshold around 300 ind/km^2 and then increased very rapidly to level off around 15.7 individuals consumed daily per km^2 above 900 ind/km^2 (Figure 5). It is noteworthy that the long-tailed jaeger showed the highest consumption rate per km^2 of all avian predators for both lemming species (consumption was 0.8, 0.4 and 1.9 lemmings/km^2 at 150 collared lemmings per km^2 and 3.0, 1.5 and 10.7 lemmings per km^2 at 1000 brown lemmings/km^2 for the snowy owl, rough-legged hawk and long-tailed jaeger, respectively). This is mainly due to the higher breeding densities of jaegers compared to the two other species.

All three avian predators consumed a high proportion of the summer lemming populations on Bylot Island. Their combined daily predation rate exceeded the maximum daily potential growth rates of collared lemming populations over a wide range of recorded densities, suggesting a control of that

species by predation (Figure 6). The pattern was very different for brown lemmings, which suffered a negligible predation rate at low density. However, above 300 ind/km^2, the daily predation rate increased sharply to reach the maximum daily potential growth rate at intermediate densities (ca 450 ind/km^2), before quickly falling below this level as density continued to increase (Figure 6). On Herschel Island, total consumption by avian predators was always below the maximum daily potential growth rate of lemmings.

Discussion

As we expected, lemming specialists (snowy owl and rough-legged hawk) responded to local variations in lemming density by exhibiting strong numerical responses without any time lag. However, even though the long-tailed jaeger is often considered a generalist species (Wiley and Lee 1998), it behaved like a diet specialist and also showed strong and immediate numerical responses. In contrast with our prediction, consumption rates by the three main predator species remained constant in relation to collared lemming density, but showed strong and similar variations in relation to brown lemming density. Nevertheless, measured predation pressure by the dominant avian predators, snowy owls, rough-legged hawks and especially long-tailed jaegers, suggests that it has the potential to regulate collared lemming populations at low density during the snow-free period on Bylot Island. Such observation is in accordance with previous studies conducted in the central Canadian Arctic where the collared lemming was apparently continuously maintained at low density by predators (Reid et al. 1995, 1997). The situation differed for the brown lemming as predation rate remained very weak at low density and, despite a sharp increase between 275 and 500 lemmings/km^2, predation rate was below brown lemming maximum potential growth rate over most of the range of densities encountered during the snow-free period. Therefore, we conclude that avian predation may be sufficient to stop the growth of at least one of the two lemming species during the snow-free period, a situation similar to the one previously reported for voles in the boreal forest (Korpimäki 1985, Korpimäki and Norrdahl 1989, 1991, Ims and Andreassen 2000).

Even though up to six avian predators may occur at our study sites, our analysis focused primarily on the three most abundant species. Peregrine falcons, glaucous gulls and parasitic jaegers are all known to prey upon lemmings to some extent during the breeding season (Pitelka et al. 1955,

Gilchrist 2001, White et al. 2002), but none of them showed a numerical response to lemming densities and their densities were low, except for the glaucous gull. Therefore, we doubt that failure to include these species in our estimation of the overall predation rate would have changed much our conclusions. Nonetheless, the lemmings consumed by these predators should be additive to those taken by the three dominant species, which therefore render our evaluation of the impact of avian predators on lemming populations conservative.

Overall, the collared lemming suffered a much higher predation rate than the brown. Indeed, even though the proportion of collared lemmings in the diet of the three main avian predators decreased when brown lemming abundance increased on Bylot Island, the collared was always consumed in a greater proportion than their relative availability in the overall lemming population, suggesting a preferential predation towards this species. Those differential predation rates may be a key factor explaining the divergent population dynamic observed in these two species when they occur in sympatry (Gruyer et al. 2010, Krebs et al. 2011). Indeed, on Bylot Island, the collared lemming seldom reaches densities higher than 170 ind/km^2 in contrast to Greenland where the collared is the only lemming species present and where densities can be as high as 1000 ind/km^2 in a peak year (Gilg et al. 2002, 2003). Our results suggest that the two lemming species are influencing each other population, either through direct competition (Morris 2000), or perhaps more likely indirectly via apparent competition due to shared predators (Holt 1977), with the brown lemming acting as an alternative prey species significantly consumed only when reaching >200 ind/km^2. By attracting large densities of avian predators during its population outbreaks, this species would contribute to further depress collared lemmings and keep their populations at relatively low densities.

Our results should, however, be taken with care before extrapolating to the whole circumpolar tundra as many differences among sites may affect predator-prey dynamics. Indeed, the results from our Western Canadian Arctic study site of Herschel Island did not provide support for a strong effect of avian predators on any lemming species at this location since predation rate did not exceed their estimated maximum potential growth rate. The most notable difference in the avian predator community among these two sites was the lower breeding density of long-tailed jaegers on Hershel Island, the species that contributed the most predation on Bylot Island. On the other hand, rough-legged hawks and peregrine falcons were more numerous on Herschel than on Bylot Island. In

addition, mammalian predators were more diverse and possibly more abundant on Herschel than on Bylot Island (Reid et al. 2011). Although the direct effect of mammalian predation on lemmings was not taken into account at either site, a denser and more diverse suite of mammalian predator species on Herschel Island could have indirect effects on predation rate by birds, for example by increasing competition among predators. Furthermore, the presence of alternative prey species (such as the goose colony on Bylot Island) could allow predator populations to subsist at higher density then would be otherwise possible, therefore increasing their impact on lemming populations (Gauthier et al. 2011, Giroux et al. 2012). Finally, a slight difference in primary production, like the one observed between our two sites, may increase cover and thus enhance the availability of predator refuges, thereby lessening the impact of avian predators on small mammals.

Our conclusions are limited to the range of lemming density encountered during the study period. A question that remains unanswered is whether collared lemmings could escape from regulation at low density by avian predators and become limited by other density-dependent factors like food resources, as suggested by Turchin et al. (2000), or inherited stress (Boonstra and Hochachka 1997, Inchausti and Ginzburg 2009). For instance, the numerical aggregative responses recorded for the main avian predators eventually levels out, as evidenced by the asymptotic curves observed in most species, possibly due to territoriality. Because lemming reproduction starts under the snow and predation by birds is likely to be very weak when the snow cover is present, it is conceivable that lemmings could reach densities at snow-melt that are already beyond the range over which regulation by avian predators could occur (Ims et al. 2011). Therefore, an accurate assessment of factors influencing lemming population growth rate during the long winter period (October to May) are needed before we can reach definitive conclusions on the role of predation in the regulation of lemming population dynamic (see also Legagneux et al. 2012). On the other hand, it is possible that avian predators could still increase their numerical reproductive responses and hence their predation pressure if resource levels were higher. Indeed, over the range of lemming density recorded during the study period, the three main avian predators apparently did not reach their maximum reproductive capacity and the average fledgling numbers per nest that we recorded during years of high lemming abundance were lower than the maximum potential clutch sizes reported for those species (Parmelee 1992, Bechard and Swem 2002, Wiley and Lee 1998).

In conclusion, a combination of factors may contribute to the high rates of predation by birds on lemmings during the snow-free period. First, the open landscape and scant cover characteristic of the tundra environment may provide few refuges for small mammals during the snow free period, thereby increasing their vulnerability to predation (Ims and Andreassen 2000). Second, the diverse suite of predators present on the tundra and their associated diverse hunting behaviours may further increase the vulnerability of lemmings. Finally, subsidies acquired from adjacent ecosystems (Henden et al. 2010, Therrien et al. 2011, Gauthier et al. 2011) may help to maintain the populations of some predators at higher levels than autochthonous resources would allow in this relatively low productivity environment. The combined predation pressure exerted without delay by birds of prey is apparently sufficient to regulate populations of collared lemmings at low levels during the snow-free period, but not for brown lemmings. This study adds to the growing evidence that mobile avian predators, in combination to resident mammalian predators, may play a key role in controlling the population dynamic of tundra small mammals (Reid et al. 1997, Gilg et al. 2003, Ims et al. 2011, Legagneux et al. 2012).
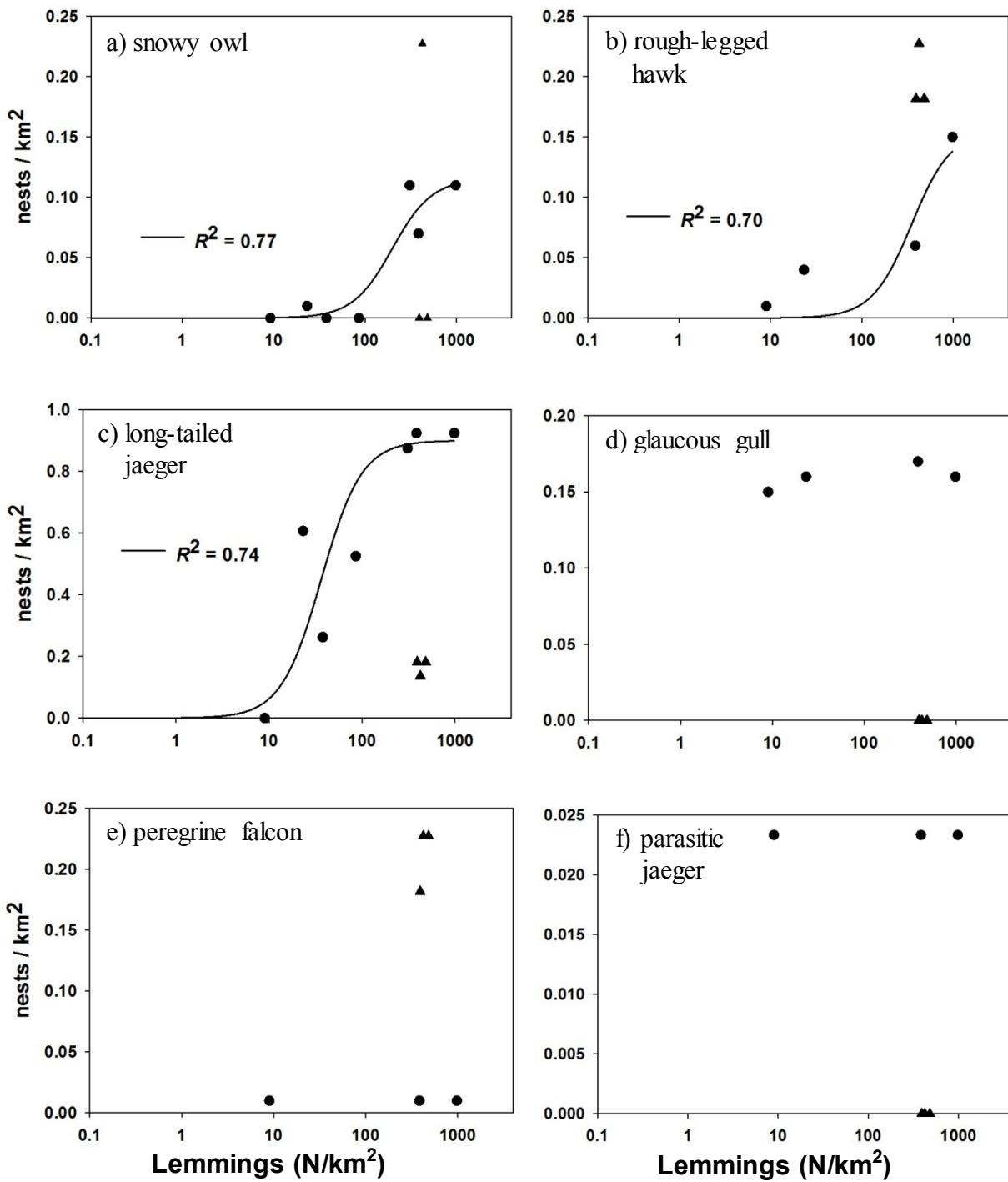
Figure 1. Breeding density of avian predators in relation to lemming density (both species combined) at snow melt on Bylot (circles, 2004 – 2010) and Herschel (triangles, 2007 – 2009) Islands, Canada. Sigmoïd curves were fitted with the Bylot Island data.
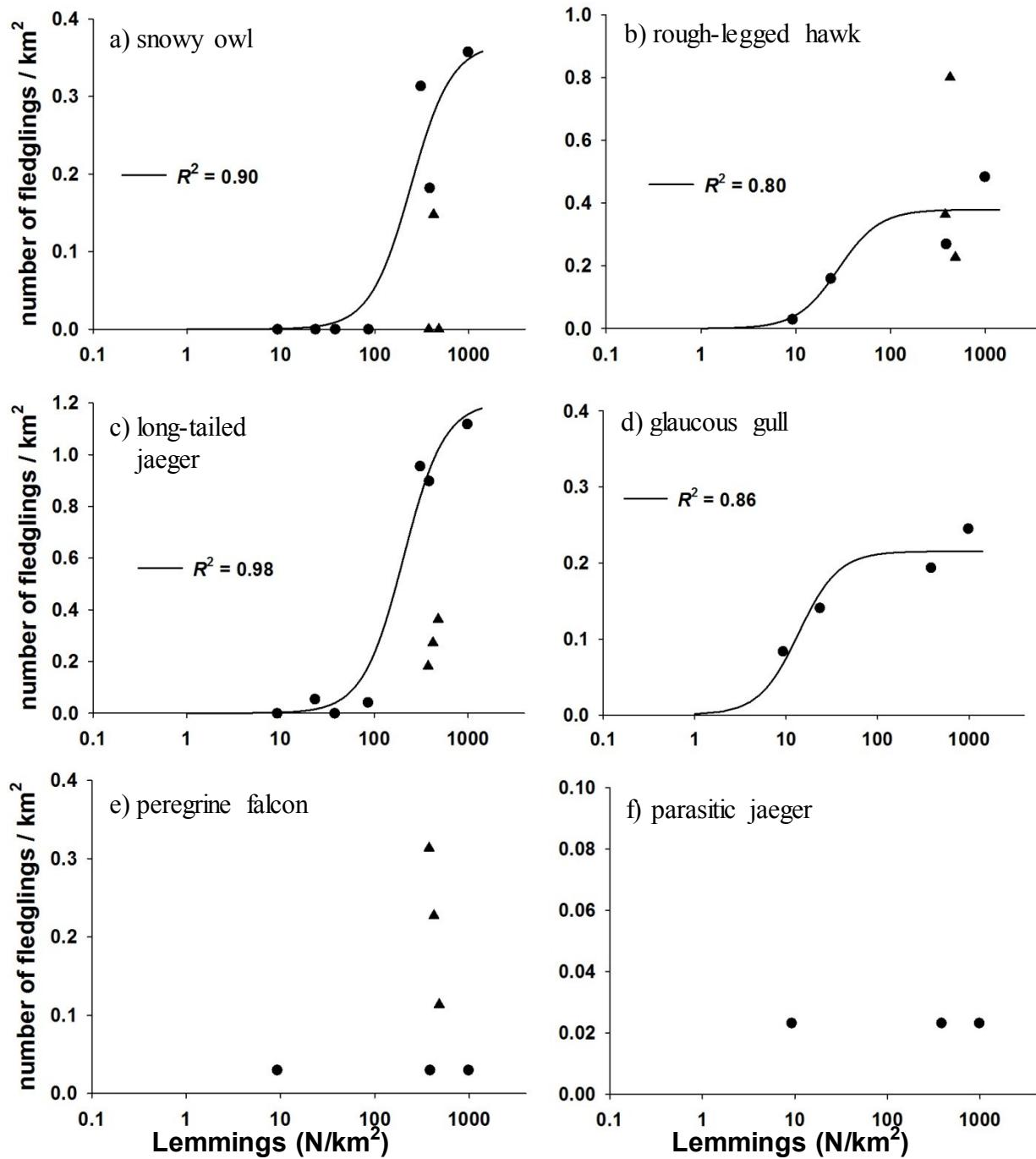
Figure 2. Reproductive success (number of fledglings produced) of avian predators in relation to lemming density (both species combined) at snow melt on Bylot (circles, 2004 – 2010) and Herschel (triangles, 2007 – 2009) Islands, Canada. Sigmoid curves were fitted with the Bylot Island data.
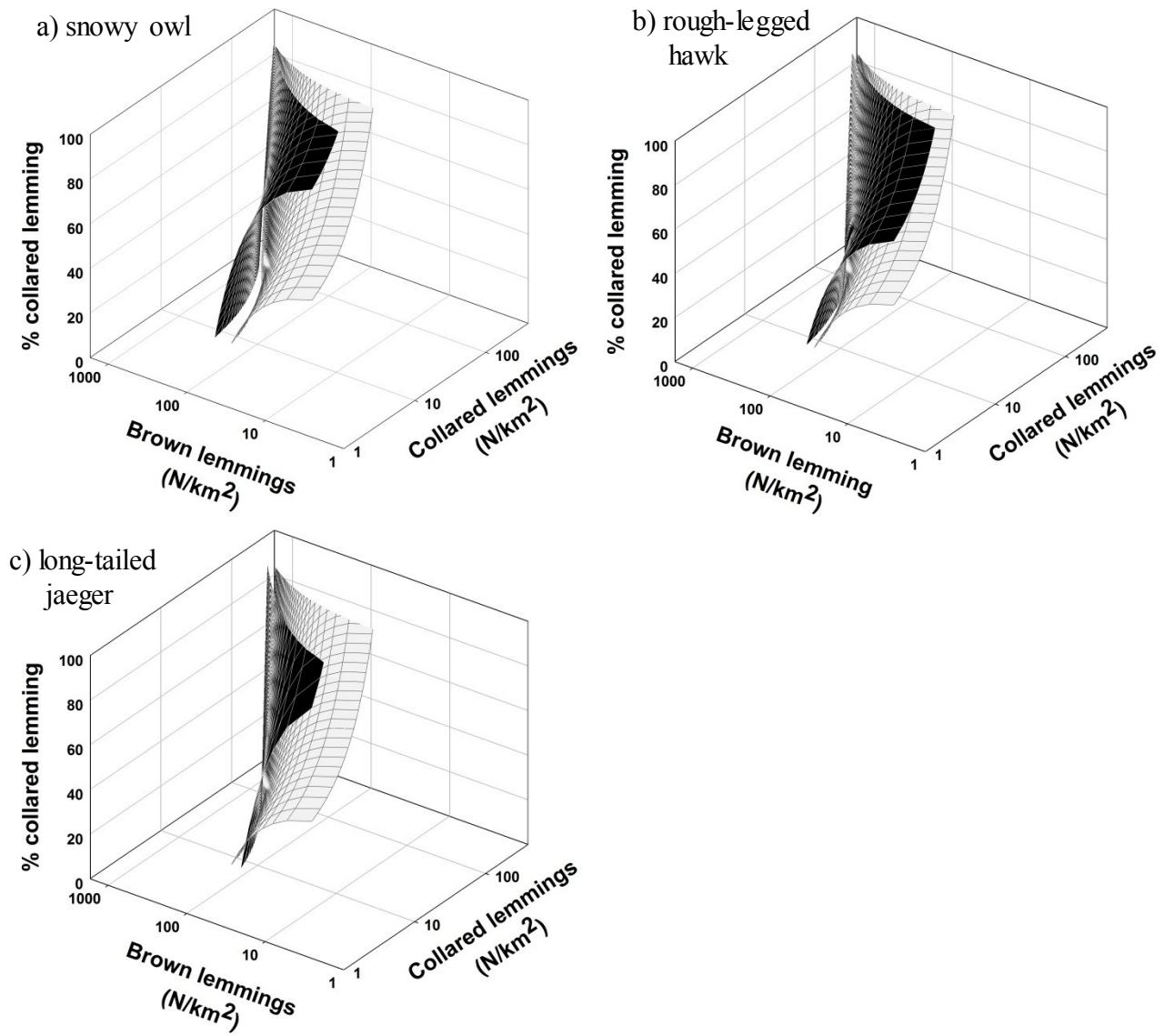
Figure 3. Proportion of collared lemmings in the diet of the main avian predators in relation to the density of both lemming species on Bylot Island, Canada (2004 – 2010). Dark planes represent the proportion of collared lemmings in the diet and the white planes represent the proportion of collared lemmings in the overall lemming population.
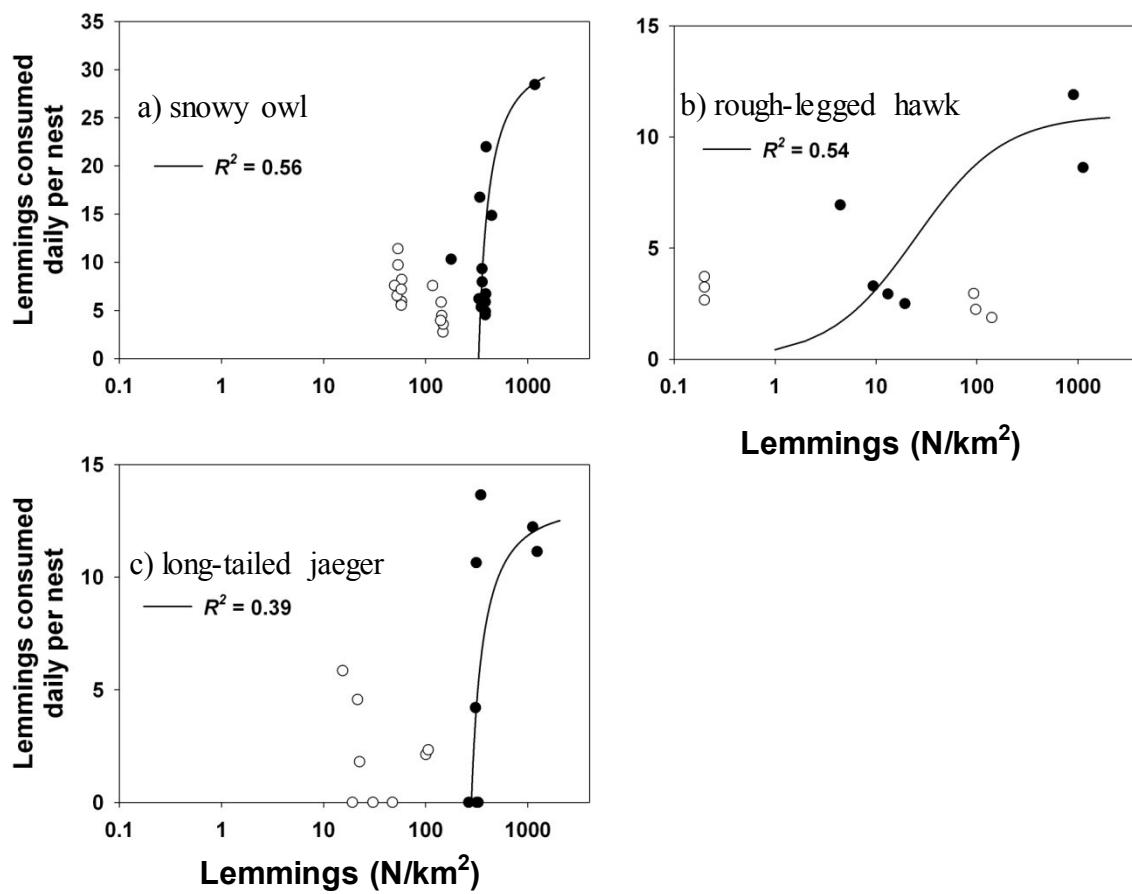
Figure 4. Daily consumption rate by breeding pairs of the main avian predators in relation to daily lemming density on Bylot Island, Canada, 2007 – 2010. White circles represent collared lemmings while black circles and solid line represent brown lemmings.
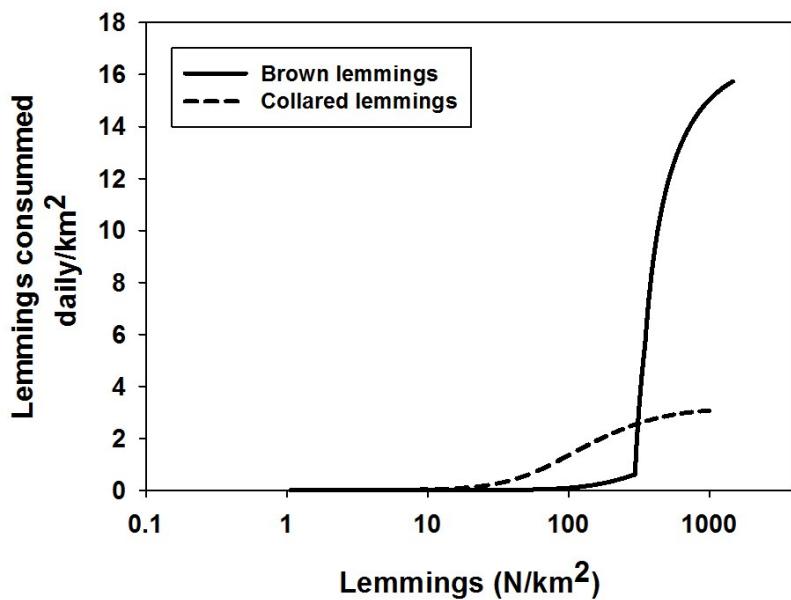
Figure 5. Total lemming consumption by the three main avian predators in relation to the density of lemmings (both species combined) on Bylot Island, Canada (2004 – 2010).
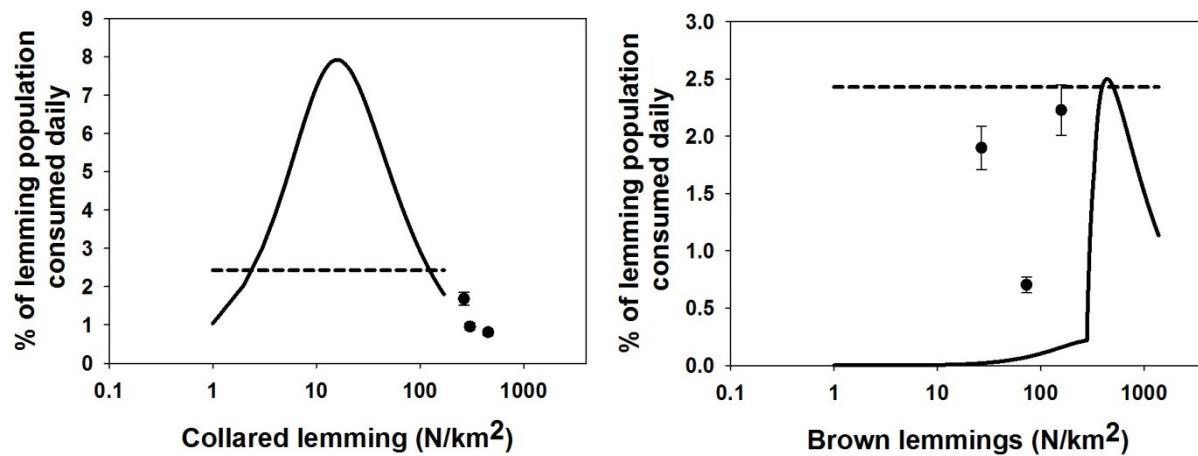
Figure 6. Daily predation rate (% of the lemming population consumed) by avian predators in relation to the density of each lemming species at snow melt on Bylot (solid line, 2004 – 2010) and Herschel (2007 – 2009) Islands. Error bars on Herschel data points represent the variation measured with the 10% sensitivity analysis on consumption rates. Horizontal dashed lines represent estimated maximum daily potential growth rate of lemmings (see methods).

Chapitre 2

Determination of diet and consumption rate in breeding snowy owls: a comparison of three methods

Résumé

Afin d'évaluer le rôle des prédateurs dans le contrôle des populations de proies, une évaluation précise de leur régime alimentaire et de leur taux de consommation de proie quotidien est requise. Nous avons comparé la performance de 3 méthodes (analyses de boulettes de régurgitation, observations visuelles directes et observations visuelles à l'aide de caméras) afin de déterminer le régime alimentaire et le taux de consommation de proies quotidien par le harfang des neiges en période de reproduction. Pendant les étés 2008 et 2010, nous avons utilisé ces 3 méthodes à 11 nids de harfangs des neiges sur l'Île Bylot, Nunavut, Canada. Toutes les méthodes ont confirmé que les lemmings constituaient la proie principale des harfangs nicheurs (de 93 à 99%). Par contre, moins de 15% des proies rapportées au nid ont pu être identifiées à l'espèce par les observations visuelles directes ou à l'aide de caméras alors que les analyses de boulettes de régurgitation ont permis d'identifier pratiquement toutes les proies trouvées (>99%). Les observations visuelles directes et à l'aide de caméras ont estimé des taux de consommation journaliers similaires, mais la variance des résultats était réduite avec la méthode des caméras. L'analyse des boulettes de régurgitation sous-estime le taux de consommation journalier et ce biais augmente tout au long de la période de reproduction (20 jours après la ponte, la sous-estimation est d'environ 43% et augmente à 81%, 80 jours après la ponte). Nous recommandons donc l'utilisation des boulettes de régurgitation afin d'évaluer précisément le régime alimentaire et la diversité des proies consommées, mais l'utilisation de caméras pour l'évaluation précise du taux de consommation journalier chez le harfang des neiges en période de reproduction.

Abstract

Assessing the role of predators in the control of prey populations requires accurate determination of their diet and consumption rates. We compared the performance of three different methods (pellets analysis, direct visual observations and automated cameras at nests) to determine the diet and the daily consumption rate (DCR) of prey by breeding Snowy Owls. During summer 2008 and 2010, we applied these three methods at 11 Snowy Owl nests monitored on Bylot Island, Nunavut, Canada. All methods confirmed that lemmings were by far the dominant prey item of breeding owls (93 to 99%). However, <15% of the delivered prey were identified to the species level by direct observations or cameras while pellet analyses successfully identified virtually all prey items (>99%). Direct visual observations and automated cameras revealed similar DCR values but the variance was reduced with the latter method. Pellet analyses underestimated DCR, and this bias increased over the breeding cycle (from an underestimation of 43%, 20 days after nest initiation, to 81% after 80 days compared to direct observations). We therefore recommend the use of pellet analyses for an accurate assessment of diet composition and prey diversity but the use of cameras to obtain both accurate and precise DCR estimates in breeding Snowy Owls.

Introduction

Top predators can play a key role in several food webs. For instance, in some boreal ecosystems, birds of prey can control the population fluctuations of their prey (Korpimäki 1985; Korpimäki and Norrdahl 1991; Norrdahl and Korpimäki 1996; Thirgood et al. 2000). In the arctic tundra ecosystem, the Snowy Owl (*Bubo scandiacus*) is one of the most important avian predators. During the summer, they have been reported to feed almost exclusively on lemmings (*Dycrostonyx* and *Lemmus* sp.; Watson 1957; Gilg et al. 2006; Hakala et al. 2006), which are major herbivores of the tundra. Factors controlling the large fluctuations in lemming populations in many parts of the Arctic are still controversial (Turchin et al. 2000; Oksanen et al. 2008; Gauthier et al. 2009; Krebs 2011) although it has been suggested that predators, including Snowy Owls, can play a role (Gilg et al. 2003; 2006; Gauthier et al. 2004). Assessing the impact of predators on their prey requires a detailed knowledge of their functional response, i.e. the change in predation rate in relation to variation in prey abundance (Solomon 1949; Holling 1965; Gilg et al. 2006). To determine this relationship, precise estimates of diet composition and daily consumption rate (hereafter DCR: number of prey taken per day) are essential.

In raptors, the analysis of discarded pellets of undigested material has long been used to study their diet (Errington 1930, Lewis et al. 2004) because they are easy to collect and they allow prey determination at the species level. The use of pellets has also been proposed to estimate DCR (Reid et al. 1997), but this approach has shortcomings. First, pellets are often discarded elsewhere than in the adjacent nesting area, where they are typically collected during the breeding season, making the collection of all discarded material almost impossible. Second, the low stomach pH of many raptors can result in the digestion of a surprisingly high proportion of ingested bones (Duke et al. 1975). Those two elements should cause an underestimation of DCR when using pellet analyses alone. Moreover, the rate of pellet casting is variable among individual birds and species, and varies with meal size (Duke et al. 1976), preventing the use of conversion factors to assess DCR in field situations.

Direct visual observations of prey delivery at or near the nest is an alternative method to assess diet and DCR in the field (Gilg et al. 2003, 2006). Although DCR estimates should be less biased with this method than with pellet analyses, direct observations are time consuming, therefore

limiting the sample size a researcher can obtain. To circumvent this problem, Reif and Tornberg (2006) proposed the use of video or photo cameras at nests to measure prey delivery rates. Pictures or video recordings constitute objective material, which can be analyzed by different persons (Lewis et al. 2004, Reif and Tornberg 2006). However, this method is still limited by the field of view of the camera, potentially leading to underestimations if the unit is not correctly installed and if some prey are delivered outside the field of view (Lewis et al. 2004).

Our aim was to compare three methods to assess diet and DCR of breeding Snowy Owls in the field: direct visual observations, automated cameras and pellet analyses. We hypothesized that although all three methods should yield similar proportion of food items in the diet, the proportion of identified prey items should be higher with pellet analyses than with the other two methods. We also hypothesized that DCR estimates should be higher with direct observations than with the other two methods, even when correcting pellet analyses with bone digestion coefficient factors derived from the literature.

Methods

The study took place on Bylot Island, Nunavut; 73° N, 80° W, from June to August 2008 and 2010 (see Gauthier et al. 2011 for a description of the study area). In the Canadian Arctic, Snowy Owls mainly prey upon two species of rodents, Collared (*D. groenlandicus*) and Brown (*L. trimucronatus*) lemmings (Sutton and Parmelee 1956, Watson 1957). Both species are present at our study site. Other potential prey available on Bylot Island include passerines, such as Snow Bunting (*Plectrophenax nivalis*) and Lapland Longspur (*Calcarius lapponicus*), Snow Goose (*Chen caerulescens*), Rock Ptarmigan (*Lagopus muta*), shorebirds (*Charadrii* sp.), Arctic Hare (*Lepus arcticus*), Ermine (*Mustela erminea*) and Arctic Fox (*Vulpes lagopus*).

Each year, we systematically searched the entire study area (~100km^2) by helicopter and by foot for Snowy Owl nests. In 2008, we monitored eight nests on a weekly basis (mean of 7.5 visits per nests) and in 2010, three nests at 7 to 14-day intervals (mean of 4.3 visits per nests). Nests were found during incubation. We inferred the nest initiation date (laying of the first egg) assuming that eggs were laid every other day, that the incubation period lasts 32 days and starts upon laying of the first egg (Parmelee 1992).

Our observations covered the second half of the incubation period and most of the chick-rearing period. We set up blinds at approximately 250m from nests and we conducted direct observations using a spotting scope. Focal observations bouts lasted 3 to 8 hrs and covered the full 24-hr daylight period. All prey delivery events by either parent (mostly males) were noted and the prey item identified in the beak of the bird.

We installed automatic, motion-triggered cameras (Reconyx, Silent Image PM35T25) at 3 to 5m from the same nests. We programmed cameras to take a series of five black and white pictures (in <2 sec) each time a movement was detected. Furthermore, in order to minimize the risk of missing prey delivery events (in case the motion-detector did not trigger), we also initially set the cameras to take a single picture every 20 sec. We later (July 2008) reduced the time lapse recording to 5 sec after noting that males were often staying for very short periods of time (mean = 10 sec) when delivering a prey. In the laboratory, we examined all pictures taken in the field to count prey delivery events and to identify prey items, pooling pictures taken using the motion sensitive trigger and time lapse method. The 20-sec time lapse allowed us to count the number of prey delivered but we sometimes had to infer it by noting new prey item at the nest or in the incubating female's beak. With the 5 sec time lapse, all visits by the male were recorded on the pictures. In 2010, special effort was made to conduct simultaneous visual observations from a blind while using a camera at the same nest in order to assess the reliability of the methods. Since cameras account only for prey delivered at the nest, we restrained our direct visual observations to the female and chicks in order to make the comparison. Table 1 summarizes the sample sizes obtained with each method.

At each visit in 2008, we collected all pellets found in the surrounding of the nest (<20m). Pellets were later analyzed in the laboratory to identify ingested prey using hair, bones and feather remains. We determined the minimal number of prey ingested based on the number of jaws and skulls found. We classified all prey items found in pellets or observed (from blinds or on pictures) as precisely as possible in the following categories: Collared Lemming, Brown Lemming, lemming sp., gosling, Lapland Longspur, Snow Bunting, shorebird, Ermine, Arctic Fox, Arctic Hare, unknown bird and unknown prey. To assess daily consumption rates from pellet analyses, we divided the minimal number of prey found in all pellets by the number of days between visits to the nest. In captive Snowy Owls fed with laboratory mice, the percentage of bones found in

pellets has been estimated at 49% of the ingested bones (Duke et al. 1975). We used this value to account for bone digestion and thus divided the number of prey found in pellets by 0.49 to estimate DCR. The DCR compared in the present study refers to the total consumption by the female and chicks.

Statistical analysis

We compared the proportion of prey items successfully identified to the species level and the proportion of lemmings in the diet obtained with the three methods using ANOVAs on square root transformed data. We compared DCR among the three methods according to the following procedure. Because DCR remains relatively stable until hatching but then increases as chicks grow to finally reach a plateau later in the season, the relation follows a logistic curve. We therefore transformed the original DCR data according to the following equation (Sit and Poulin-Costello 1994),

$$DCR' = -\log((a/DCR)-1) \qquad \text{eqn.1}$$

where a is the asymptotic value of the curve determined as the maximum DCR value recorded (40). This transformation allowed us to analyze DCR' with a generalized linear mixed model (GLMM) for repeated measures on our sample of nests, which was set as a random factor (because we had multiple observations per nest). In our comparison of DCR' among the 3 methods, we added days since nest initiation and the number of fledglings per nest as covariates. Coefficients obtained with the generalized linear mixed model were back-transformed into DCR values according to equation 2,

$$DCR = a/(1+e^{(-b-cX)}) \qquad \text{eqn.2}$$

where b is the intercept and c is the slope of the equation. We performed all analyses using SAS release 9.2 (SAS Institute Inc. 2008).

Results

Pellet analysis identified to the species level a much higher percentage of prey consumed than the two other methods ($F_{2,20} = 28.1$, $p < 0.001$; Table 2). Nonetheless, all three methods identified lemmings sp. as the main prey taken by owls, although their proportion in the diet differed slightly but significantly among methods ($F_{2,20} = 4.07$, $p = 0.04$; Table 2). Pellets identified a greater

diversity of prey than the other methods, but these additional prey species contributed little to the overall diet.

DCR measured simultaneously with direct visual observations and with cameras during 24 hr of observations at three nests provided exactly the same values (13 lemmings and one gosling consumed). Similarly, analysis of the whole dataset indicated no difference in DCR between these two methods (Table 3). However, the DCR estimated from pellet analyses was lower than with the two other methods, and this difference increased over time (significant interaction day*method for pellet analysis; Table 3, Fig. 1). At 20 days following nest initiation, DCR estimated by pellet analysis was 1.75 times (43%) lower than the value estimated by the other two methods but at 80 days, the underestimation had increased to 5.27 times (81%, Fig. 1). As expected, DCR increased over time but was not affected by the number of fledglings per nest (Table 3), probably because it did not vary much among the monitored nests (mean $\pm$ SD = 2.6 $\pm$ 1.1).

Discussion

Our results confirmed our first hypothesis since pellet analysis performed much better than visual observations or cameras in identifying prey items at the species level. Our low resolution, black and white pictures may have contributed to the very low proportion of lemmings identified to the species level but considering the poor performance of direct visual observations as well, it is doubtful that higher resolution pictures could have performed much better. However, at a coarser level, all three methods agreed that lemmings (pooled species) were by far the dominant prey of breeding owls, despite slight differences among methods. This confirms what has been reported elsewhere for this species (Parmelee 1992, Gilg et al. 2006). Pellets are known to bias diet proportions towards vertebrate prey and small prey ingested whole (Redpath et al. 2001, Simmons et al. 1991). However, Snowy Owls do not feed on invertebrates and our observations coupled with reports from the literature confirm that larger vertebrates such as ducks or hares are rarely targeted as prey on the breeding grounds (Parmelee 1992), which should minimize biases. Even when such prey are consumed, owls should still ingest bones, hairs or feathers parts, which will end up in pellet, as shown by the Arctic Fox jaws found in our pellets. Given that they are relatively easy to collect and that large sample size over the complete reproduction period can be obtained, we suggest that pellet analyses should be the preferred method to determine diet composition and/or prey diversity of large breeding avian predators like the Snowy Owl.

Our study provides the first comparison of methods to assess the daily consumption rate of a raptor in the wild. Our results partially supported our second hypothesis since pellet analyses underestimated DCR compared to visual observations. However, cameras performed equally well compared to the latter method. Although all methods may potentially underestimate DCR, it has been generally accepted that direct visual observations are likely to provide the less biased estimations (Redpath et al. 2001). It is thus reassuring to find that cameras performed equally well. Lewis et al. (2004) also concluded that video-recording was the best method to quantitatively assess prey deliveries in the Goshawk (*Accipiter gentilis*) although they could not compare their value to direct visual observations. Moreover, the DCR values of incubating females measured with cameras during the incubation period in our study (first 32 days, mean = 5.6 lemmings per day) are similar to the food requirements measured on adult female Snowy Owls in captivity (4 to 6.7 lemmings per day; Gessaman 1972) and in the wild (Gilg et al. 2006).

Our analysis indicates that the use of pellet analyses to assess DCR is questionable. Pellets are often discarded away from the immediate vicinity of the nest, even in incubating females (Lewis et al. 2004). The collection of pellets at the nest thus often leads to an underestimation of DCR, as observed in the present study. This underestimation increases over time probably because females spent an increasing amount of time away from the nest as they start hunting later on, and some chicks, which will also cast pellets, may wander off the nest as they get older. It has also been reported that heads or other portions of prey can be discarded prior to ingestion, therefore leading to an underestimation when inferring the number of prey taken from pellets (Hakala et al. 2006). Finally, even though we corrected for bone digestion based of the values reported by Duke et al. (1975) in captive Snowy Owls, we do not know if these factors are applicable to field situations. If a higher proportion of bones is digested in wild owls, this would also lead to an underestimation of DCR.

Direct visual observations, though accurate, are time consuming, thus limiting the size of data sets one can obtain. The inherently low sample sizes increases the variance of DCR estimates and thus reduces their precision. In contrast, automatic cameras not only provide reliable and accurate estimations of DCR, as we showed, but can also yield large sample sizes (e.g. see number of data points in Fig. 1) with the added benefit of increased precision. This efficiency could explain the increasing popularity of the method with avian predators in field situations (see Cutler and Swann

1999, Reif and Tornberg 2006). We therefore conclude, along with Redpath et al. (2001), that pellet analyses is the most accurate method to assess diet of breeding raptors at the species level but that cameras is the most reliable and cost-effective method to determine DCR.

Table 1. Samples sizes (mean ± SD) used to compare diet and daily consumption rate of breeding Snowy Owls during summer 2008 and 2010 on Bylot Island, Nunavut, Canada.

Parameter	2008	2010	Total[a]
Nests monitored	8	3	11
Pellets collected per nest	76 ± 20	0	610
Number of days covered by pellet analyses	75 ± 13	0	600
Nests observed from a blind	4	3	7
Hours of observation from a blind per nest	6.5 ± 6.4	8 ± 3.5	50
Nests observed with camera	8	3	11
Hours of observation with camera per nest	460 ± 118	65 ± 32	3,876
Pictures taken per nest	85,753 ± 25,283	47,040 ± 23,279	827,144

[a] summation across all nests

Table 2. Diet determined from direct visual observations, automated cameras and pellet analyses of breeding Snowy Owls during summer 2008 on Bylot Island, Nunavut, Canada.

	Observations	Cameras	Pellets
Number of prey detected	27	1,153	2,653
Diversity of prey species encountered	4^a	5^b	9^c
% of prey identified to the species level	15	1	> 99
% of prey identified to the order level	74	67	> 99
% of identified prey as lemmings	93	99	96

[a] Brown Lemming, Collared Lemming, Lapland Longspur and gosling

[b] same as previous plus Ermine

[c] same as previous plus Arctic Fox, Snow Bunting, Arctic Hare and shorebird sp

[d] % of prey identified as lemming sp among total prey delivered

Table 3. Results from the generalized linear mixed model used to compare the daily consumption rate (DCR: number of prey taken per day) among three methods (direct visual observations, automated cameras and pellet analyses) of breeding Snowy Owls during summer 2008 on Bylot Island, Nunavut, Canada.

Parameters		β	SE	df	t	p
Intercept		-1.733	0.177	1,7	-9.80	< 0.001
Day[a]		0.028	0.004	1,8	6.13	< 0.001
Method	Observations	0.429	1.291	1,8	0.33	0.75
	Pellets	0.527	0.278	1,8	1.89	0.10
	Cameras	-	-	-	-	-
Day*method	Observations	-0.009	0.018	1,8	-0.50	0.63
	Pellets	-0.019	0.006	1,8	-3.44	< 0.01
	Cameras	-	-	-	-	-
Number of fledglings		0.011	0.051	1,8	0.23	0.82

[a] number of days since nest initiation
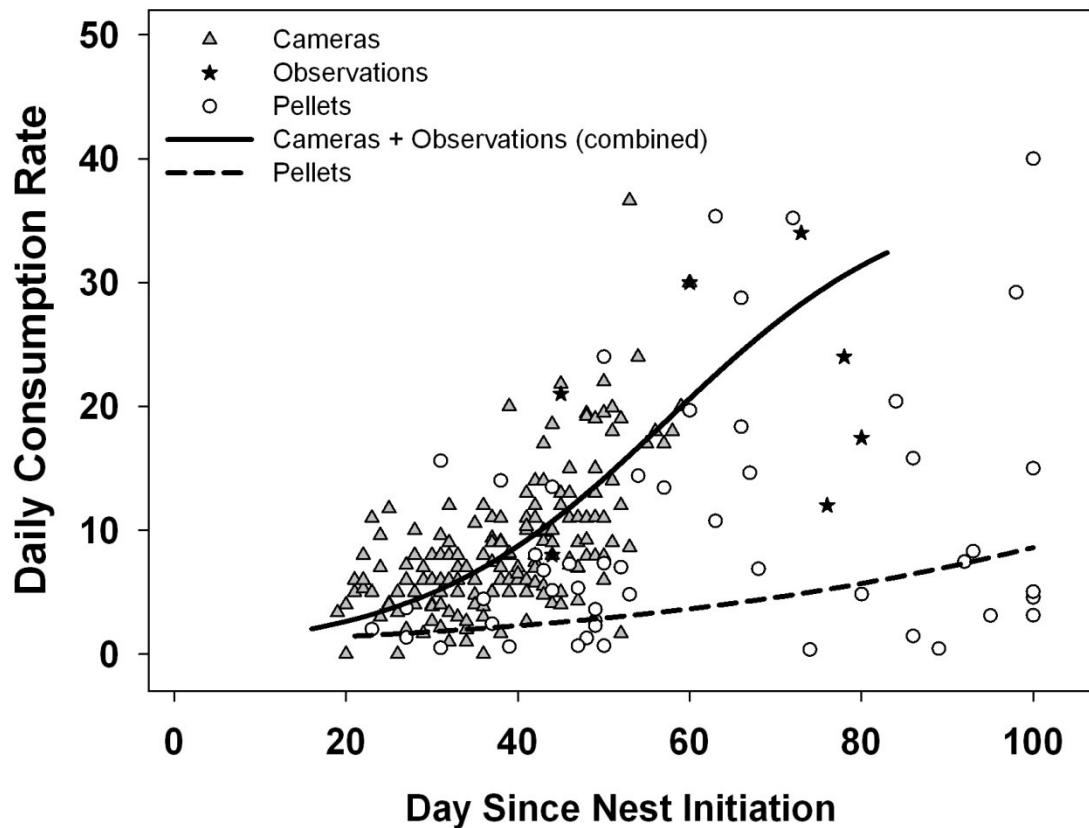
Figure 1. Daily consumption rate (DCR: number of prey taken per day) of nesting Snowy Owls during the breeding period obtained from direct visual observations, automated cameras and pellet analyses during summer 2008 on Bylot Island, Nunavut, Canada. The solid line combines direct visual observations and automated cameras (no difference found; see Table 3) and the dashed line represents pellet analyses.

Chapitre 3

Irruptive movements and breeding dispersal of snowy owls: a specialised predator exploiting a pulsed resource

Résumé

La mobilité et les déplacements irruptifs ont été proposés comme mécanismes pouvant permettre à certaines espèces ayant un régime alimentaire spécialisé d'habiter et de se reproduire dans des environnements démontrant une imprévisibilité dans l'abondance des ressources, comme la toundra arctique. Le harfang des neiges, l'un des principaux prédateurs aviaires de la toundra, est reconnu pour s'alimenter presqu'exclusivement de lemmings pendant la saison de reproduction. Ces petits mammifères sont aussi connus pour leurs extraordinaires variations spatiales et temporelles d'abondance. Nous avons étudié les mouvements pré-reproductifs printaniers (de mars à juin) et la dispersion de reproduction annuelle des harfangs des neiges en marquant, avec des émetteurs satellites, 12 femelles reproductrices sur l'île Bylot dans l'Arctique canadien. Nous avons aussi mesuré l'abondance des lemmings à certains sites utilisés par les oiseaux marqués. Les harfangs, suivis jusqu'à 3 années consécutives, ont démontré des mouvements exploratoires pendant un à deux mois de mars à juin et se sont déplacés durant cette période sur une distance moyenne d'environ 1200 à 1900 km à chaque année. Les harfangs ont effectués ces mouvements exploratoires sur une échelle moyenne de 218 km de rayon. La durée des mouvements exploratoires, la distance parcourue et la date à laquelle les oiseaux se sont établis étaient plus élevées l'année où les densités de lemmings étaient au plus faible dans l'est de l'arctique canadien. Néanmoins, les oiseaux marqués se sont établis dans des zones où l'abondance locale de lemmings était relativement forte. La distance de dispersion reproductive entre des années consécutives était de 725 km en moyenne, variant de 18 à 2224 km. La grande mobilité observée chez les femelles harfangs leur a permis de maintenir leurs activités de reproduction à chaque année dans un écosystème où l'abondance de proies semble hautement imprévisible. Compte tenu des forts taux de consommation quotidiens mesurés chez ce prédateur nomade, nous suggérons que le harfang des neiges pourrait avoir un impact majeur sur les populations de lemmings de la toundra à l'échelle régionale.

Abstract

Mobility and irruptive movements have been proposed as mechanisms that could allow some diet specialists to inhabit and breed in environments with highly unpredictable resources, like the arctic tundra. The snowy owl, one of the main avian predators of the tundra, is known to specialize on lemmings during the breeding season. These small mammals are also well known for their tremendous spatial and temporal variations in abundance. We examined the spring (pre-breeding, from March to June) movements and breeding dispersal of snowy owls by marking 12 breeding females on Bylot Island in the Canadian Arctic and tracking them for up to 3 years with satellite transmitters. We also ascertain lemming abundance at some of the sites used by the marked owls. Tracked owls displayed exploratory movements for a period of 1 to 2 months from March to June and travelled over distances ranging from 1200 to 1900 km each year during that time. The scale of these exploratory movements occurred over a radius of 218 km on average. The duration of exploratory movements and distance travelled were longest, and the settlement date in spring was latest in the year where density of lemmings was lowest. Nonetheless, snowy owls settled in areas where local lemming abundance was relatively high. Individual breeding dispersal distance between consecutive years averaged 725 km (range 18 to 2224). Overall, the high mobility of female snowy owl allowed them to behave as irruptive migrants and to sustain their reproductive activities during consecutive years in a highly unpredictable ecosystem. Given the high consumption rates of this predator, we suggest that the snowy owl can have a major impact on lemming populations of the tundra at the regional scale.

Introduction

Predators living in seasonal and heterogeneous environments rely on resources that vary spatially and temporally in availability. Pulsed resources represent an extreme case because they typically become super abundant for a very short, and often unpredictable period of time (Ostfeld and Keesing 2000). Examples include the blooming of plankton in ephemeral ponds, the massive and periodic emergence of some insects and mast fruiting by several trees. In all these cases, resources can be plentiful in a given year but virtually non-existent in others (Ostfeld and Keesing 2000). Consumers have developed several strategies to cope with variable or pulsed food sources. In presence of highly variable resources, some species broaden their diet in order to maximize energy gain (e.g. Terraube and Arroyo 2011) while others rely on hoarded resources (e.g. Careau et al. 2008) or reduce metabolic (or reproductive) activities until the next resource pulse (Stearns 1992).

Consumers are not expected to specialize on ephemeral food supply. Instead, diet generalists are more likely to exploit pulsed resources because they can switch to alternative food sources during periods of low availability of the former (Ostfeld and Keesing 2000). However, high mobility and irruptive movements have been proposed as mechanisms that could allow some diet specialists to inhabit and breed in environments with highly unpredictable resources despite the inherent uncertainties and associated costs of locomotion (Newton 2006). Irruptive migration due to large-scale movements of individuals in response to variation in local food supplies will thus result in large fluctuations in local numbers of a given species. Individuals exhibiting such behavior often breed in widely spaced localities in different years (Newton 2006). While the effects of pulsed resources on consumers are obvious, predators exhibiting irruptive movements can also have an impact on lower trophic levels, for instance by reducing seed survival and plant recruitment (Janzen 1971) or decreasing population growth of small mammals (Korpimäki 1985, Korpimäki and Norrdahl 1991, Korpimäki 1994, Norrdahl and Korpimäki 1996).

The Arctic tundra is a highly seasonal environment well-known for the high-amplitude, multi-annual variations in population densities of small mammals such as lemmings (*Lemmus* and *Dicrostonyx* sp., Elton 1924, Krebs 2011). Those cyclic fluctuations affect local breeding densities and reproductive success of several avian and mammalian predators, which exhibit strong

numerical responses (Pitelka et al. 1955, Reid et al. 1997, Wiklund et al. 1998, Gauthier et al. 2004, Gilg et al. 2006, chapter 1). Although high lemming abundance can occur synchronously over relatively large areas (Angerbjörn et al. 2001, Krebs et al. 2002), numerous biotic and abiotic factors can affect the periodicity and amplitude of these outbreaks, rendering them rather unpredictable on a year to year basis (Myrberget 1973, Ims et al. 2011).

The snowy owl, one of the main avian predators of the tundra, is known to specialize on lemmings during the breeding season (reviewed by Parmelee 1992). This species can exhibit large variations in breeding numbers, ranging from 0 to 17 nests/100 km^2, in relation to changes in local lemming abundance (Gauthier et al. 2004, Gilg et al. 2006, chapter 1). These local fluctuations in numbers are most likely due to movements of individuals because years with high breeding numbers are typically preceded by years of total absence of individuals in a given area (Gauthier et al. 2004). The limited information coming from ring recoveries and satellite tracking of a small number of birds has revealed the high mobility of this species (Oeming et al. 1958, Fuller et al. 2003), which is often presented as the classic example of a nomadic species (Greenwood and Harvey 1982, Parmelee 1992, Newton 2006). However, the paucity of information on their movements and their determinants hinders considerably our understanding of their role in the tundra food web structure and functioning (Korpimäki and Krebs 1996).

In this paper, we examined the spring (pre-breeding) movements and breeding dispersal of female snowy owls. We specifically examined the influence of spatial and temporal variability in food resource (lemmings) availability on those movements and we assessed the scale of exploratory movements using first-passage time analysis (Fauchald and Tveraa 2003). We hypothesized that (1) snowy owls should exhibit extensive, large-scale exploratory movements during spring as they search for areas of high lemming abundance, (2) a high abundance of lemmings is an essential condition to allow settlement of snowy owls in a specific area for breeding, and (3) breeding dispersal of owls occur at the continental scale because lemming population cycles tend to be synchronized regionally. To achieve these objectives, we tracked the movements of 9 radio-marked snowy owls for up to 3 years and ascertain lemming availability at some of the sites used by the owls annually.

Methods

Field activities primarily occurred on the southern portion of Bylot Island, Nunavut, Canada (73°N, 80°W), over a 400 km^2 area of Arctic tundra. The landscape is made of gently rolling hills and river valleys and is a prime breeding habitat for snowy owls and lemmings (Gauthier et al. 2004). Every year, we assessed the density of snowy owl nests in a core study area of 100 km^2 through systematic searches. From 27 June to 11 July 2007, we captured 12 adult female snowy owls on their nest using a bow-net trap. All of these birds were captured outside our core study area because none nested in that area that year (except one that abandoned during egg-laying; see results). We marked owls with 30-g satellite transmitters (Microwave Telemetry Inc., MD, USA; PTT-100) attached with back-pack harnesses (Steenhof et al. 2006) made of Teflon ribbon (see chapter 4 for details). Transmitters were programmed to transmit continuously for an average of 5 hr and then turned off for an average of 125 hr from marking to the end of the following winter (February 2008). During the first spring and summer period (March to July 2008), transmitters were programmed to transmit for 5 hr and then turned off for 49 hr. Finally, cycles of 4 hr of transmission and 142 hr off were programmed for the remaining battery life of the transmitters. We received locations of marked owls on a regular basis via the Argos system (Collecte Localisation Satellites 2011). Each location was assigned to a class (0, 1, 2, 3, A, B, or Z) according to its estimated precision. The estimated accuracy of location classes 0, 1, 2, and 3 followed a normal distribution with a standard deviation of >1,000 m, <1,000 m, <350 m, and <150 m, respectively. Location classes A, B, and Z were considered to be of poorer accuracy by the system and we therefore only used locations with an accuracy class ≥1 for all analyses. We also removed from the analyses all locations resulting in unrealistic speed values (>100 km/h for more than 10 km). Overall, locations of class 1, 2 and 3 represented 50%, 34% and 16% of the whole data set used for the analyses, respectively.

Two species of lemmings, the brown (*L. trimucronatus*) and collared (*D. groenlandicus*) lemming, are present on Bylot Island and both have a widespread distribution across North American tundra. From 2004 to 2010, we measured lemming density with live-trapping on two trapping grids (11 ha each) spaced by 2 km. Grids were set up in areas representative of the main habitats found at the study site, one in wet meadow and one in mesic tundra. Each trapping grid had 144 Longworth live traps placed at 30-m interval in a Cartesian plan and were opened for three or four consecutive

days at each trapping period. Traps were baited with apples and checked at 12 hr intervals. We conducted three trapping sessions each summer (mid-June, mid-July and mid-August). All captured animals were identified to species level, individually marked with PIT tags and released following capture (see Gruyer et al. 2010 for details). The trapping grids were located at the center of our 100 km^2 core study area.

In 2008, we visited by helicopter distant sites (n = 8) where satellite-tracked owls had settled. One site selected by a female could not be visited because it was located in the western Canadian Arctic (>1,200 km away from Bylot Island). We assessed lemming abundance using snap traps at two sites on Baffin Island where the marked owls had settled, Mary River (71.3°N, 79.4°W) and Dewar (69.1°N, 70.8°W), 200 and 560 km south of Bylot Island, respectively. At each site, we set 240 traps distributed on 80 stations along two transects 100 m apart. We set three traps within 2-m of each station and each station were spaced by 15 m. Trapping lasted 48 hr at Mary River (6-8 July) and 24 h (8-9 July) at Dewar.

Statistical analyses

We calculated the average location of each marked owl using all locations received during each 5-hr transmission window; thereafter, we refer to those as individual locations. Spring movements were those occurring between the areas where birds had settled for winter and where they eventually settled for the summer. We defined individual departure date from wintering sites when movements were greater than 5 km between the date of the current location and the date of the previous location (departure date was the midway point between those two dates, Ganusevich et al. 2004). Since some birds did not settle at all during winter, we defined their spring departure date as the midway point between the date when movements were not oriented and when they became oriented towards potential breeding grounds (i.e. directional movement) after 1 March. Since most of the tracked birds wintered either on the sea-ice or at low latitudes (below the tree line; Therrien et al. 2011), potential breeding grounds refer to the arctic tundra. Settlement of individuals on a potential breeding site occurred when movements between the date of the current location and the date of the previous location was less than 5 km (settlement date was the midway point between these two dates; Ganusevich et al. 2004, chapter 4). We separated spring

movements in two parts: directional and exploratory movements. We defined the transition from directional to exploratory movements as the first time when individuals exhibited a turn angle of 45° or more during three successive locations (Annexe 2). We calculated the duration, the total distance travelled and the net linear movement for both behaviors (directional or exploratory movements).

We assessed the scale of exploratory movements using first-passage time analysis (FPT, Fauchald and Tveraa 2003). FPT is based on calculating the time taken by an animal to cross a circle of a given radius. It is a measure of how much time an animal uses the area included in that circle. Calculations of FPT are repeated along the path of the animal by moving the circle at distance d and for circles of various radii r (i.e. spatial scale). We performed this calculation every second kilometer travelled (i.e. $d = 2$ km) during exploratory movements, for values of r ranging from 5 to 1000 km. The relative variance $S(r)$ in FPT is then calculated for the whole path, given by var[log($t(r)$)], where $t(r)$ is the FPT for circles of radius r, and is log-transformed to make the variance $S(r)$ independent of the magnitude of the mean FPT (Fauchald & Tveraa 2003). Maxima in the plot of $S(r)$ in relation to r indicate the presence of search behavior (i.e. an increase in turning rate and a decrease in speed) and indicate the scale, r, at which the animal is performing this search (Fauchald & Tveraa 2003). When a path exhibited more than one maximum (resulting from search behavior at various scales), we selected the largest one because we were interested in large-scale exploratory behavior rather than fine-scale searching. Moreover, previous FPT analysis on travel paths of birds showed that search at very small scale (0–20 km) cannot be separated from resting period given the inherent imprecision of Argos locations (Pinaud and Weimerskirch 2007). We thus plotted $S(r)$ in relation to r for values ranging from 20 to 1000 km.

We calculated the annual breeding dispersal distance of individuals as the distance between the center of their summer home range once they had settled (or their nest site when known) in year i and $i+1$ (see chapter 4 for details on how summer home range was determined). We compared the duration, total distance travelled, date of settlement and scale of exploration during exploratory movements among years using ANOVAs with posteriori Tukey tests and individual's ID as a random factor. We estimated densities (individuals/ha) of live-trapped lemmings at each trapping session using mark-recapture techniques with the program DENSITY 4 (Efford et al. 2004, Efford

2009). All parameter settings in DENSITY were similar to those used by Krebs et al. (2011). We averaged densities of each species between the two grids for each year in order to have a global measure of density on the study area. We performed spatial analyses with ArcGIS 9.2 software (ESRI Inc., Redlands, CA, USA) and statistical analyses with R 2.10.1 software. All animal manipulations were conducted in accordance with the animal care committee of Université Laval (CPAUL permit #84921).

Results

We successfully tracked 9 of the 12 marked adult female snowy owls during one year and 7 of them for 3 years. Departure dates from the wintering site were variable among individuals. Birds departed from their wintering ground in mid-March in two years but later in the other year (mean ± SD; 17 March ± 0 d, n = 2 in 2009, 19 March ± 5 d, n= 6 in 2010 and 1 April ± 8 d, n = 6 in 2008). Settlement dates on the breeding ground were also variable among individuals and years. Birds settled in early May in 2008 (9 May, SD = 20 d) and 2010 (2 May, SD = 8 d) but later in 2009 (26 May, SD = 25 d; $F_{2,22} = 2.9$, $p = 0.04$).

Many birds did not show any directional movements in early spring but rather exhibited exploratory movements as soon as they moved from their wintering site (Table 1). Birds that showed strong directional migratory movements in early spring (e.g. birds F7, F8 and F9 in 2008 and 2009) were generally those that wintered the furthest south (Table 1, Fig. 1). Tracked owls exhibited a broad range of exploratory behavior in spring as distance travelled and duration were highly variable among birds and years (Table 1, Fig. 1). On average, birds exhibited exploratory movements between 1 and 2 months in spring, which was at least 4 times longer than the time spent in directional movements (Table 1). The duration of the spring exploration period was longer in 2009 (66 d) than in 2008 (36 d) and 2010 (47 d; $F_{2,22} = 5.7$, $p = 0.01$). The total distance travelled each year during these exploratory movements ranged from 1200 to 1900 km on average, which was about twice the linear distance travelled during this period (Table 1). Total distance travelled tended to be higher in 2009 compared to 2008 and 2010 (Table 1; $F_{2,22} = 2.5$, $p = 0.07$).

Analysis of FPT allowed us to determine the scale of exploratory movements, though not in all cases. Indeed, for some birds in some years we did not find any peak in $S(r)$ apart from the one occurring at a very small, local spatial scale (i.e. ~20 km). This was especially the case in 2009 for several birds, e.g. birds F1, F3, F4, F5 and F8 (Annexe 3). Based on the individuals for which we detected a searching area, the scale (i.e. radius) of the search area in spring ranged on average from 214 to 224 km, depending of the year (Table 2). The scale of spring exploration did not differ among years ($F_{2,14} = 0.03$, $p = 0.97$).

Except in 2007 when only one nest, which failed during laying, was found in the systematically searched area of 100 km^2, snowy owls only settled to breed on our core study area when lemming numbers were over 3.8 ind/ha (or 2.3 ind/100 trap-nights, Gauthier et al. 2004). In those years, density of nesting snowy owls reached 11 ± 2 nests/100 km^2 (Fig. 2). Similarly, lemming abundance was high in the two areas where snowy owls settled in 2008 and where lemmings could be trapped (Mary River: 4.0 ind/100 trap-nights, Dewar: 2.3 ind/100 trap-nights).

After breeding on Bylot Island in 2007, marked birds settled in far apart areas during the three subsequent breeding periods, except for one bird that came back to breed on Bylot Island in 2010, 1.1 km from where it nested in 2007. Most birds settled on Baffin Island in 2008 and 2009 but one settled in northern Greenland and one on Prince Patrick and Borden Islands in the western Canadian Arctic (Fig. 3). In 2010, most birds settled further south, in northern Quebec, thereby showing an almost complete lack of site fidelity. Based on their summer movements, we were able to infer that these birds bred in all years, which was confirmed by visits on the ground for all birds but one in 2008 (chapter 4). Individual breeding dispersal distance between consecutive years ranged from 18 to 2224 km and averaged 725 km over the 3 years (Table 2), which represents the longest confirmed mean breeding dispersal ever recorded for a bird species.

Discussion

The movements of female snowy owls recorded by satellite-tracking for up to three consecutive years generally supported our three hypotheses. First, owls showed prolonged (1-2 months) exploratory movements over a broad scale (radius of 218 km) as they search for potential breeding

sites in spring and these movements were generally tortuous in accordance with the observed spatial unpredictability of small mammal outbreaks (Myrberget 1973, Ims et al. 2011). Moreover, movements lasted longer, tended to be lengthier and led to a later settlement date in the year where summer abundance of lemmings was lowest on Bylot Island. Considering the scale of spatial synchrony in lemming cycles (see below), we presume that the situation encountered on Bylot Island in 2009 was representative of the Eastern Canadian Arctic, as confirmed in 2008. Second, owls settled in our main study area almost exclusively when lemming abundance was high, as observed in other tundra areas (Pitelka et al. 1955, Wiklund and Stigh 1986, Wiklund et al. 1998, Gilg et al. 2003, 2006). Moreover, trapping conducted at two sites in 2008 confirmed that owls had moved to areas of high lemming abundance to settle that year. Third, the scale at which annual breeding dispersal occurred was very large, approaching the continental scale (>700 km on average). This value provides an order of magnitude of the average linear distance that owls need to move annually to find suitable areas to breed. Interestingly, this value seems to correspond to the scale of spatial synchrony of lemming population cycles reported in previous studies (phase synchrony in lemming populations up to distances ranging from 500 to 1000 km but asynchronous phases in populations separated by ≥1000 km; Erlinge et al. 1999, Angerbjörn et al. 2001, Predavec et al. 2001, Krebs et al. 2002).

Despite those results, some issues regarding the mechanisms involved in the settling decision of snowy owls remain unanswered. Indeed, in 2007, lemming density was low in our core study area and one owl was found nesting. However, a few snowy owls still bred on Bylot Island outside of our core study area that year (but had a low breeding success; see Chapter 4) and we marked 12 of them. Local lemming density in those areas remains unknown, but was likely relatively low. It is possible that the decision to settle and initiate a nest might not depend solely on absolute local lemming density, but also on the relative lemming density in the surrounding regions. Thus, relatively low lemming densities may occasionally attract owls if prey densities are even lower in the general surrounding areas. Moreover, none of the owl marked in 2007 on Bylot Island came back one year after marking even though lemming density was high and numerous snowy owl nested there. In that year, however, lemming abundance was high over a large portion of the eastern Canadian arctic and individuals may have encountered numerous suitable nesting locations during their spring exploratory movements.

The unpredictability of resources seems to be the major factor promoting irruptive migration as similar behaviors have been reported in other birds feeding primarily on temporally and spatially unpredictable resources such as coniferous seed (e.g. crossbills *Loxia curvirostra*; Newton 2006). However, the great-horned owl (*Bubo virginianus*), a strigidae of similar size than the snowy owl but inhabiting the boreal forests, exhibits very few annual movements even if its main prey, snowshoe hares (*Lepus americanus*), vary considerably in abundance from one year to another (Rohner 1996). Its capacity to turn to alternative prey present in the system (Rohner 1995) and the long-term benefits of remaining on their territory likely outweigh the potential gains of moving.

As a behavioral strategy, irruptive migration has many potential drawbacks. Indeed, such large-scale movements bear inherent locomotor energy expenses and costs such as uncertainty, hazards and the risk of "moving for nothing". Furthermore, by moving extensively from one year to the next, individual birds loose detailed knowledge and familiarity with a given area, which has been identified as a prime advantage of breeding site fidelity in many species (Hinde 1956, Gavin and Bollinger 1988). In the short-term, all of those could hinder resource acquisition and ultimately reproductive output and survival, which would not promote the evolution of such behavior. However, the costs associated with irruptive migration seem to be compensated by its potential benefits since it is used by some specialist species living in seasonal environments such as the snowy owl (Newton 2006). Indeed, being a diet specialist can increase foraging efficiency and compensate some of the previously described disadvantages (Terraube et al. 2011). Moreover, the potential access to plentiful resources and the possibility to sustain reproductive activities every year, despite a strong reliance on an unpredictable food supply, likely outweigh the costs of irruptive migration for female snowy owls. Ultimately, the use of a common theoretical framework incorporating the main costs (locomotor expenses, uncertainty, and loss of familiarity) and benefits (foraging efficiency, sustained reproductive activity) would help understanding the optimal strategy for bird species or populations facing various environmental conditions.

Several adaptations may have contributed to the success of the snowy owl as an irruptive migrant. First, the relatively low wind-loading characteristic of strigidae should allow snowy owls to reduce the costs of locomotion compared to birds with higher wing-loading (Poole 1938, Johnson

1997). This also means that it can accumulate energy reserves without impairing its flight capability and then fast for several days if needed. Second, its "sit and wait" hunting strategy should reduce foraging costs compared to actively foraging predators. Third, large body size and especially powerful talons allow snowy owls to feed opportunistically on a large variety of prey if lemmings are scarce in a given region (reviewed in Parmelee 1992, see also Therrien et al. 2011). Fourth, adult birds face limited threats from other predators of the tundra, at least when not incubating, thus reducing the risks associated with exploration in unfamiliar areas. Fifth, previous knowledge of potentially competing neighbors in its breeding area may be of limited importance because snowy owls can efficiently defend a large breeding territory from any species competing for similar resources in the tundra (Parmelee 1992). Finally, snowy owls can raise large clutches (from 6 to 10 chicks) when resources are abundant (Parmelee 1992, chapter 4) and thus the reproductive benefits of finding an area with a high density of lemmings is relatively high.

At the ecosystem level, it has been suggested that irruptive predators could affect prey populations if they exhibit strong aggregative responses with no time-lag to an increase in prey abundance (Janzen 1971, Korpimäki 1985, Korpimäki and Norrdahl 1991). Avian predators inhabiting the tundra such as the snowy owl can consume large quantities of lemmings, with consumption rates sometimes exceeding the maximum growth rate of lemming populations, thereby potentially limiting their growth in a top-down manner (Gilg et al. 2003, 2006, chapter 1). Such a phenomenon has been documented in the boreal grasslands of Finland where an assemblage of owl species can regulate rodent populations (Korpimäki 1985, Korpimäki and Norrdahl 1989, 1991). Our study provides evidence that snowy owl is a predator that can act in this manner in the tundra as it can explore large expanses of the tundra every spring to find areas of high lemming abundance and settle in those areas to breed without any time-lag, even if this entails net linear movement of up to 1000 km or more between consecutive years. Such large-scale irruptive movements combined with their high consumption rates could in turn promote synchronization among fluctuating small mammal populations over wide regions (Ims and Andreasson 2000, Krebs et al. 2002). Predation by this irruptive migrant could therefore have a dampening effect on the amplitude of lemming population cycles over a broad continental scale and suggests that the snowy owl could play a major role in the tundra food web structure and functioning.

Table 1. Duration, total distance travelled and net linear movement during directional (D) and exploratory (E) pre-breeding movements of nine adult female snowy owls marked with satellite transmitters on Bylot Island, NU, Canada in 2007 and tracked for up to 3 years.

	Duration (days)						Total distance travelled (km)						Net linear movement (km)					
	2008		2009		2010		2008		2009		2010		2008		2009		2010	
ID	D	E	D	E	D	E	D	E	D	E	D	E	D	E	D	E	D	E
F1	0	54	0	44	0	45	na	705	na	1440	na	1070	na	235	na	710	na	790
F2	0	39	-[a]	-	-[a]	-	na	2325	-[a]	-	-[a]	-	na	1240	-[a]	-	-[a]	-
F3	18	33	36	66	0	36	390	1095	1440	300	na	615	340	780	1370	140	na	350
F4	0	59	0	69	0	72	na	915	na	1410	na	1050	na	210	na	1015	na	415
F5	6	31	0	108	15	21	390	670	na	3820	480	415	390	40	na	630	475	320
F6	6	4	0	59	0	47	182	210	na	1375	na	1035	182	180	na	585	na	240
F7	16	36	-[a]	-	-[a]	-	1000	745	-[a]	-	-[a]	-	980	460	-[a]	-	-[a]	-
F8	16	26	24	62	0	56	1720	1710	1230	1565	na	2160	1720	620	1220	1100	na	1345
F9	22	41	42	51	9	49	1810	3340	1740	3690	470	2220	1520	2220	1700	1970	460	1985
Mean	9.3	35.9	14.6	65.6	3.4	46.6	915	1302	1470	1943	475	1224	855	665	1430	879	468	778
SD	8.7	16.0	18.9	20.6	6.1	15.9	713	989	256	1309	7	705	654	691	246	575	11	657

[a] Transmission stopped before the breeding season

Table 2. Scale of spring exploratory movements and breeding dispersal distance between consecutive years of nine adult female snowy owls marked with satellite transmitters on Bylot Island, NU, Canada in 2007 and tracked for up to 3 years.

ID	Scale of spring exploratory movements (km)			Breeding dispersal distance (km)		
	2008	2009	2010	2007-2008	2008-2009	2009-2010
F1	130	-[a]	340	861	528	375
F2	755	-[b]	-[b]	471	-[b]	-[b]
F3	-[a]	-[a]	55	262	18	1225
F4	125	-[a]	310	235	1272	1069
F5	110	-[a]	-[a]	975	202	665
F6	155	115	150	985	87	909
F7	55	-[b]	-[b]	539	-[b]	-[b]
F8	-[a]	-[a]	275	1041	175	993
F9	170	315	215	1228	332	2224
Mean	214	215	224	733	373	1066
SD	241	141	107	363	430	582

[a] Searching area not detected

[b] Transmission stopped before the breeding season
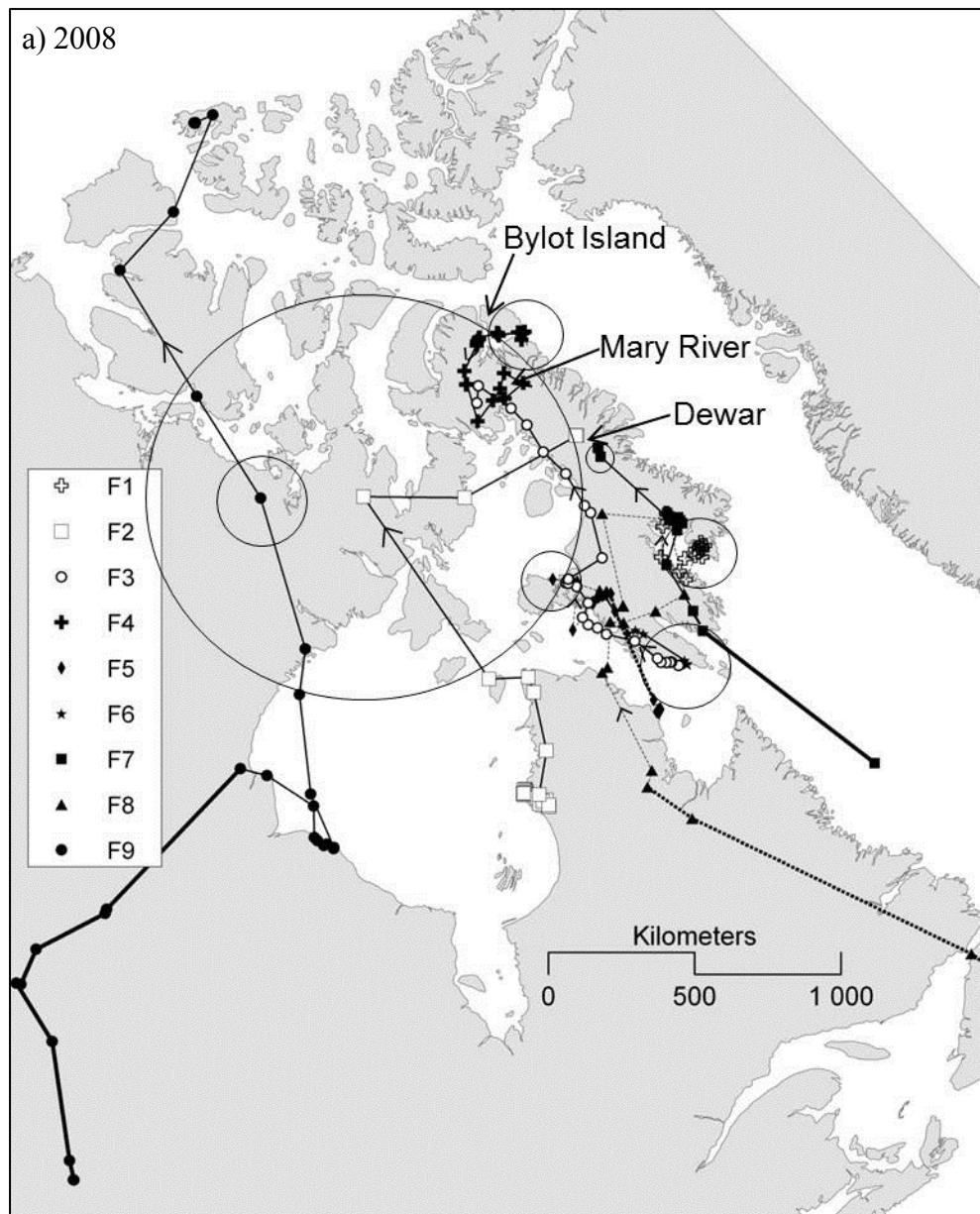
Figure 1. Spring exploratory movements of adult female snowy owls tracked with satellite transmitters in northern Canada from 10 March to 10 June over three years. The bold lines represent directional movements when applicable whereas the thin lines represent exploratory movements. Circles (centered on a specific location) represent the scale of spring exploratory movements for a given bird.

b) 2009

c) 2010
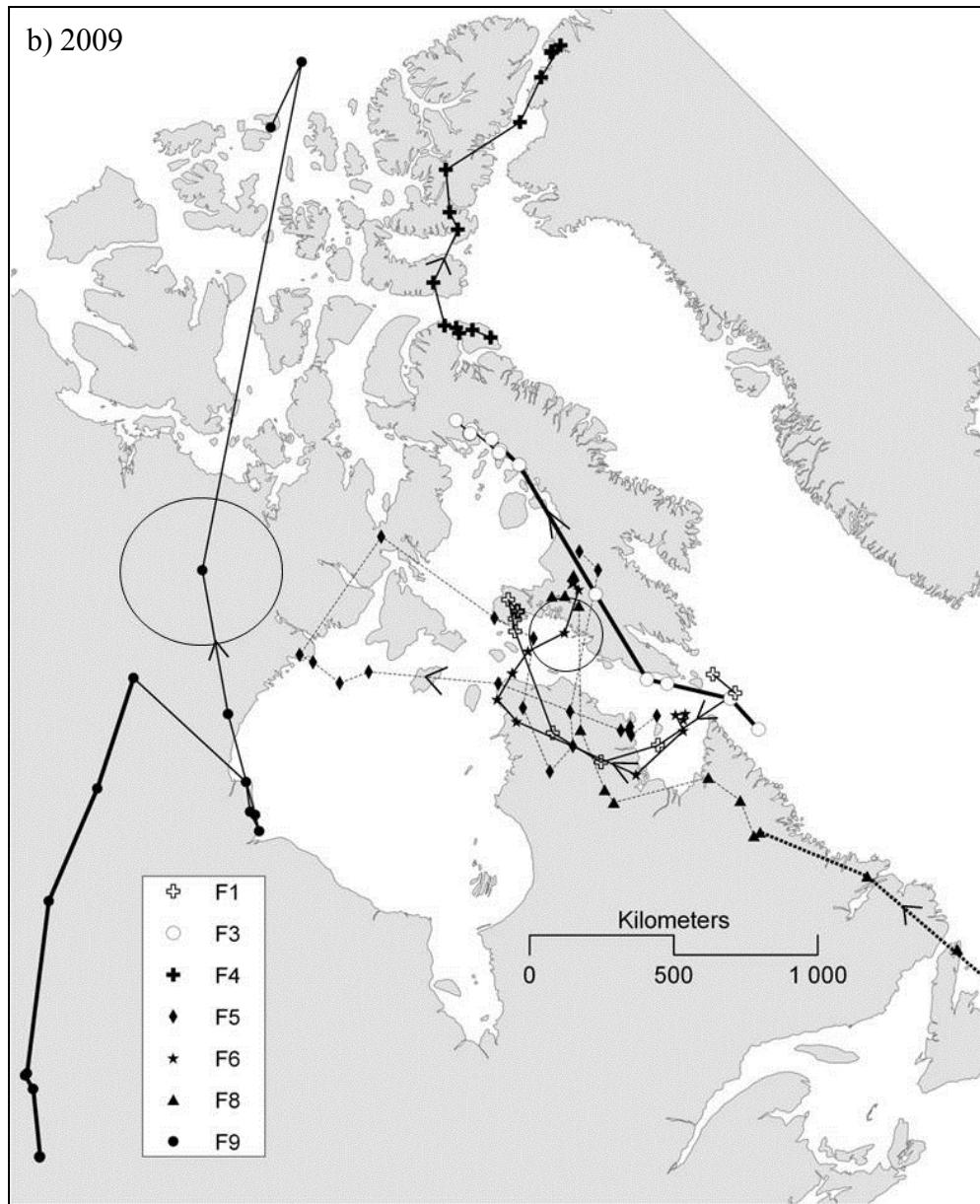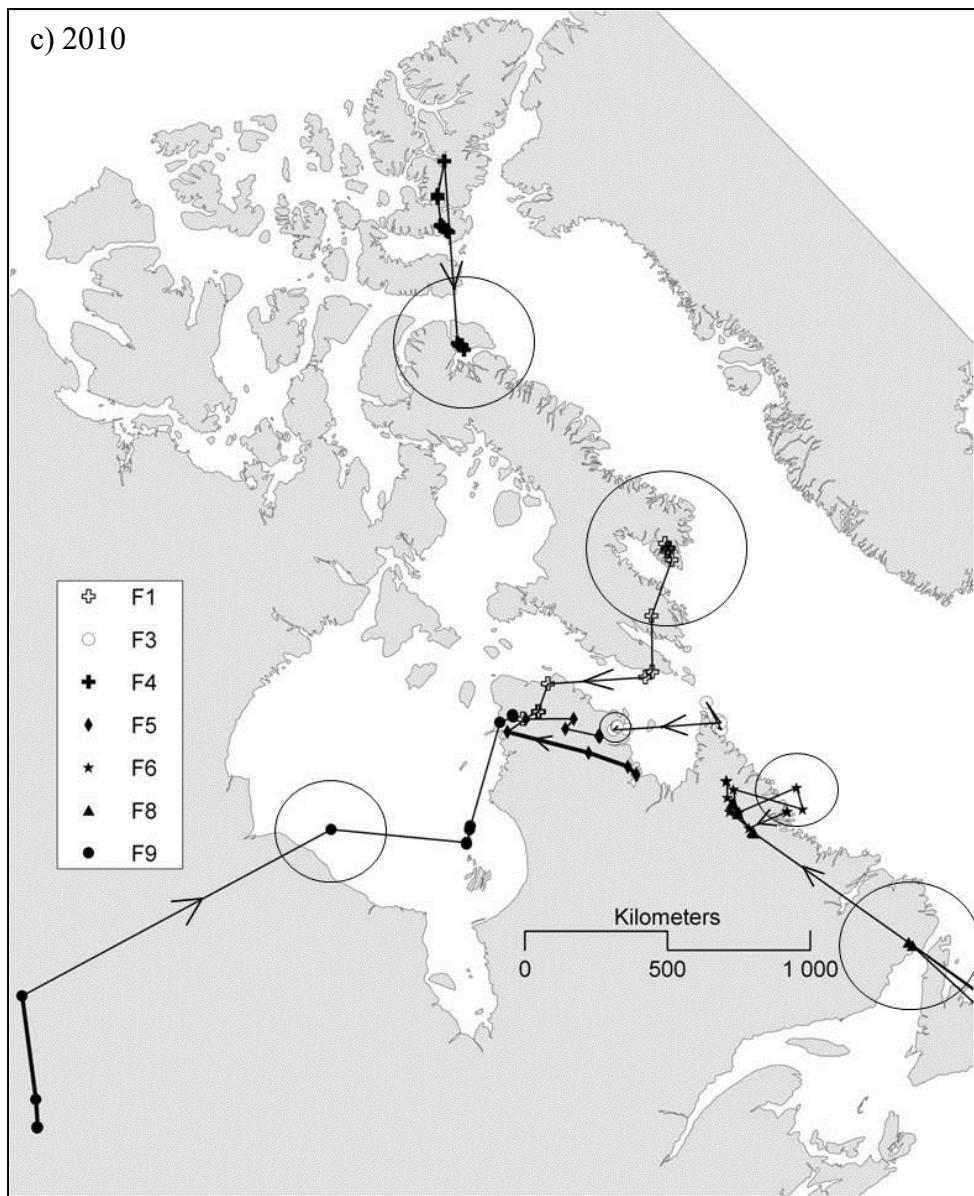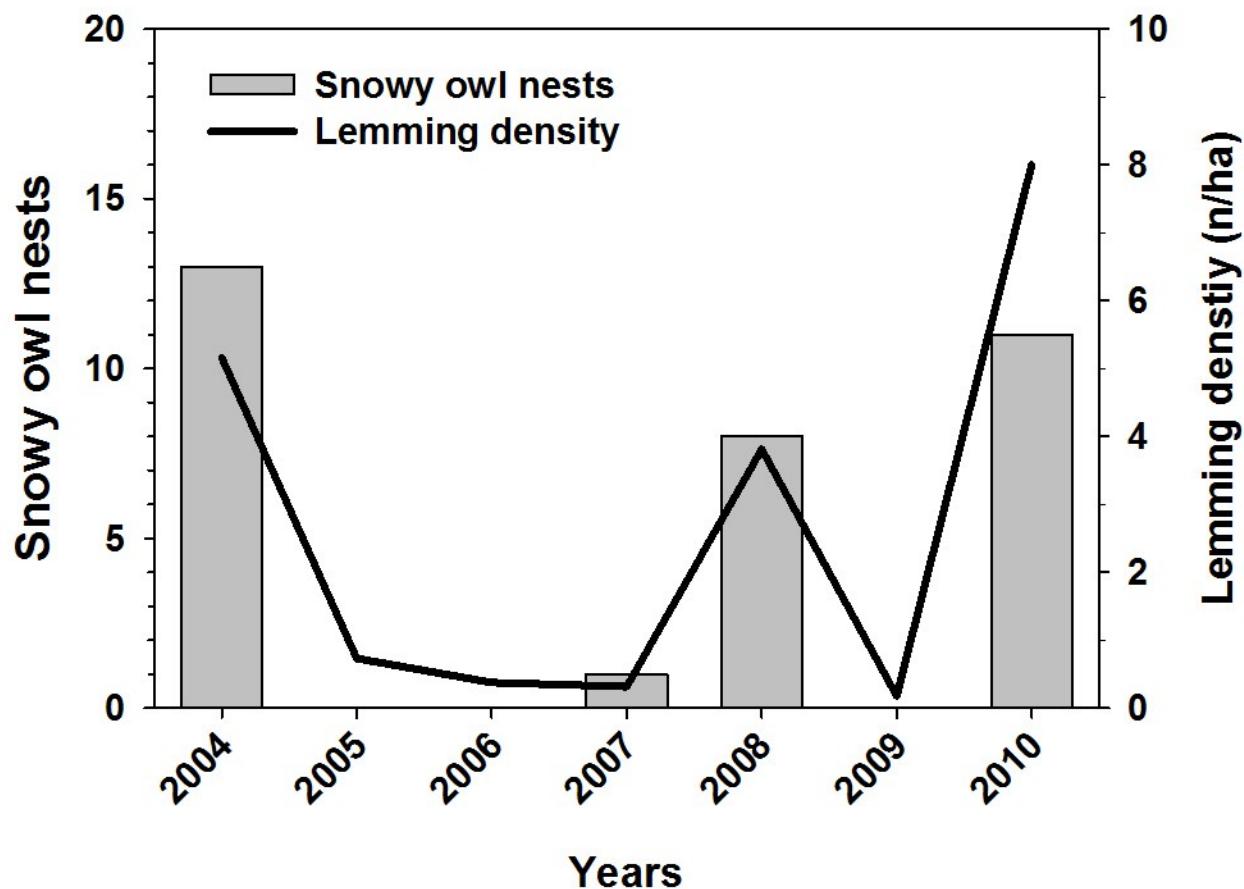
Figure 2. Lemming density measured annually with live-trapping at snow-melt (n/ha) and number of snowy owl nests monitored in the 100 km^2 systematically searched area on Bylot Island, Nunavut, Canada from 2004 to 2010.
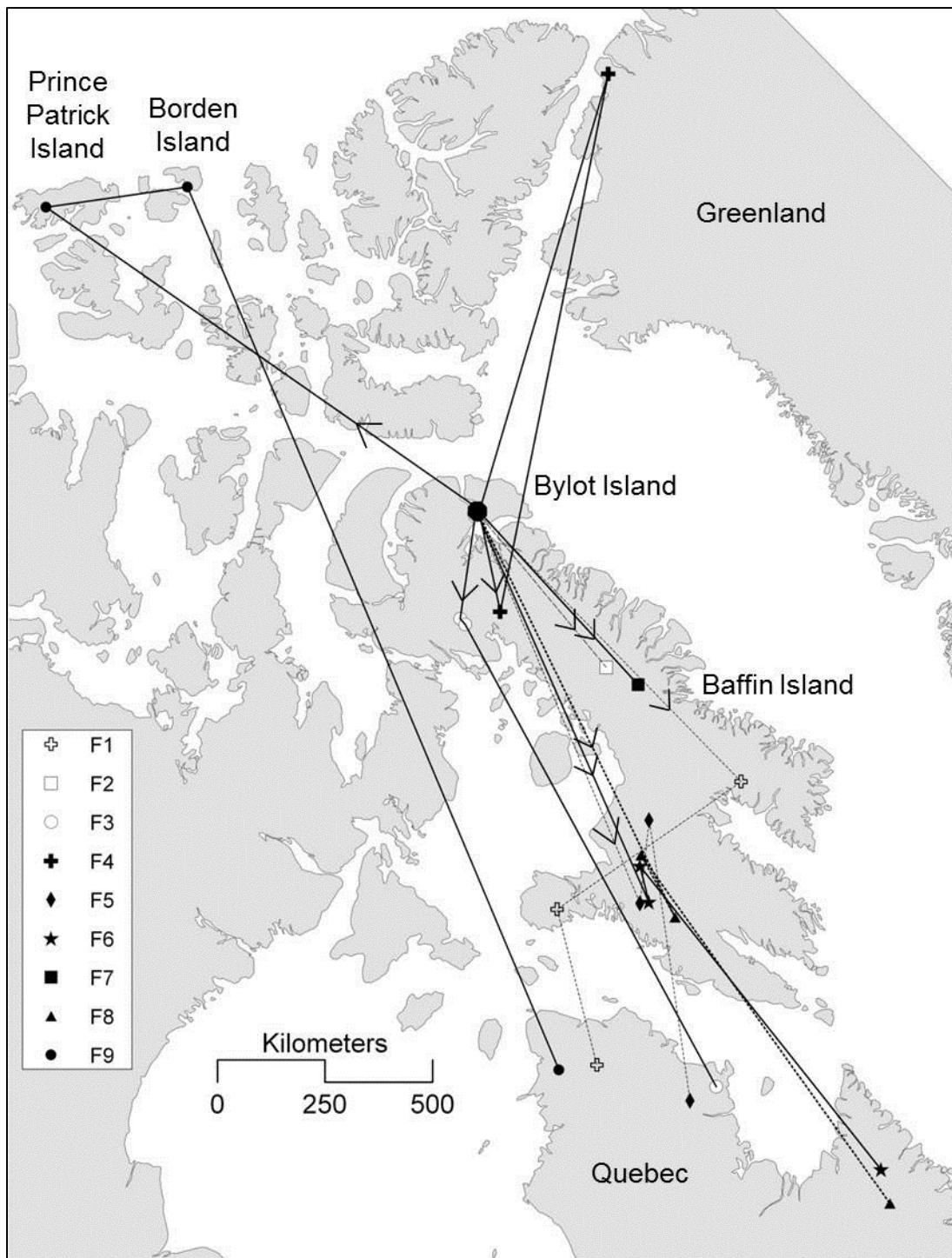
Figure 3. Breeding site locations of nine adult female snowy owls originally marked on Bylot Island (large dot) and tracked with satellite transmitters over four consecutive breeding seasons (2007 – 2010) in northern Canada. Sites are chronologically displayed and linked by a line for each individual.

Chapitre 4

Survival and reproduction of adult snowy owls tracked by satellite

Résumé

La télémétrie par satellite permet d'obtenir des informations précieuses sur l'écologie spatiale des animaux, en particulier pour les espèces habitant des régions isolées comme l'Arctique. Toutefois, la prudence est toujours de mise lors de la sélection de la taille des émetteurs et de la technique d'attachement en raison des impacts négatifs potentiels de l'appareil lui-même sur les individus. Nous avons déterminé les taux de survie et de reproduction de femelles harfangs des neiges (*Bubo scandiacus*) adultes suivies à l'aide d'émetteurs satellites afin d'évaluer leurs effets défavorables potentiels. À l'été 2007, nous avons capturé 12 femelles adultes sur leur nid dans l'Arctique canadien, et les avons marqués individuellement à l'aide d'émetteurs satellites pesant 30 g afin de suivre leurs déplacements pendant 3 ans. Tous les oiseaux marqués ont repris leurs activités normales peu de temps après les manipulations (<60 minutes) et aucun oiseau n'a abandonné son nid. Au cours de la période d'étude de 3 ans, nous avons confirmé le décès de 2 oiseaux et 2 émetteurs ont cessé de bouger, indiquant un taux de survie annuel se situant entre 85,2 ± 7,0 et 92,3 ± 5,7%. Par ailleurs, les patrons de mouvement estivaux, combinés dans plusieurs cas à des confirmations sur le terrain, suggèrent que tous les oiseaux suivis ont initié un nid chaque année après le marquage. Enfin, pour tous les individus, la date et la taille de ponte n'ont pas changé suite au marquage. Dans l'ensemble, nos données indiquent que les traits biodémographiques des femelles harfangs des neiges adultes n'ont pas été affectés par les émetteurs.

Abstract

Satellite telemetry can provide valuable information on spatial ecology of animals, especially in species inhabiting remote areas such as the Arctic. However, caution is always needed when selecting transmitter size and attachment methods because of the potential negative impact of the device itself on individuals. We determined survival and reproductive performance of adult female snowy owls (*Bubo scandiacus*) tracked by satellite to evaluate potential adverse effects of transmitters. In summer 2007, we captured 12 adult females on their nest in the Canadian Arctic, marked them with 30-g harness-mounted transmitters, and tracked their movement for up to 3 years. All marked birds resumed normal activities shortly (<60 min) after release and none deserted their nest. We had 2 known deaths and 2 transmitters that stopped moving over 3 years, yielding an annual survival rate between 85.2 ± 7.0 and $92.3 \pm 5.7\%$. Moreover, summer movement patterns, combined with ground checks in several cases, suggested that all successfully tracked birds initiated a nest every year after marking. Finally, laying date and clutch size of individuals did not differ before and after marking. Overall, our data indicate that life history traits of adult female snowy owls were not affected by satellite transmitters.

Introduction

Satellite telemetry greatly enhances our ability to study free-ranging wildlife and increases our understanding of the spatial ecology of animals (Fuller et al. 2005). This technique is especially useful for the study of highly mobile species such as birds and it can provide crucial information on movement and dispersion parameters, migration routes and chronology, demography, home range, and habitat use. Satellite telemetry is thus probably the most powerful tool available to obtain crucial ecological information that would be extremely difficult to document otherwise. However, potential adverse effects of those devices on the behavior and life history traits of studied organisms remain an ethical and scientific concern. Indeed, because species management and conservation are among the ultimate goals of most scientific studies involving the tracking of wild animals, detrimental effects on the studied organisms while gaining knowledge would be disturbing. Moreover, if transmitters adversely affect some life history traits, then researchers must take those into account before inferring to the whole population any scientific result obtained with the technique.

Although transmitters are now commercially available in highly compact sizes and aerodynamic shapes, fitting animals with such devices can still have negative consequences on them, and this is particularly true in flying organisms such as birds (reviewed by Barron et al. 2010). Negative effects of transmitters on birds can occur over short- (days) and long-term (months or years) time scales. Short-term effects, mostly due to handling stress and habituation to the device, can result in altered behaviors (Demers et al. 2003, Chipman et al. 2007) and clutch abandonment in reproductive birds (Barron et al. 2010). Long-term effects, often caused by the cumulative impact of a higher wing loading and increased drag leading to reduced flying and feeding efficiencies, can result in decreased body condition (Barron et al. 2010), reduced fecundity (Paton et al. 1991, Demers et al. 2003, Steenhof et al. 2006), or increased mortality (Burger et al. 1991, Paton et al. 1991, Gervais et al. 2006).

Potential adverse effects of transmitters can be minimized by limiting device weight. A transmitter weighing no more than 5% of the body mass is generally assumed to be acceptable, although this has never been experimentally tested in birds (but see Caccamise and Hedin 1985, Aldridge and Brigham 1988, Barron et al. 2010). Several methods have been developed to attach transmitters on birds (e.g., tail mounts, leg mounts, neck collars, and backpacks) but their

suitability varies among species. In large-bodied birds such as raptors, the backpack method generally works well in the field (Snyder et al. 1989, Vekasy and Marzluff 1996, McGrady et al. 2002) including with snowy owls (*Bubo scandiacus*; Fuller et al. 2003), although it has been associated with negative impacts on breeding and/or survival in golden eagles (*Aquila chrysaetos*; Gregory et al. 2003), burrowing owls (*Athene cunicularia*; Gervais et al. 2006), and prairie falcons (*Falco mexicanus*; Steenhof et al. 2006). Researchers should thus be careful when choosing an attachment method and transmitter size and, whenever possible, evaluate any potential negative impacts as these can vary depending of the body mass, habitat, behavior, and life history traits of the studied population.

Snowy owls inhabit the Arctic tundra, one of the most remote and harshest environments on Earth, and are well known for their irruptive movements (Newton 2006). Satellite telemetry is thus an ideal technique to study migration and dispersal in this species (see Fuller et al. 2003 and Therrien et al. 2011 for recent applications). We evaluated annual survival and breeding performance (breeding probability, laying date, clutch size, and nesting success) of adult female snowy owls tracked by satellite for up to 3 years and investigated potential negative effects of transmitters.

Study area

Our study area covered approximately 400 km^2 of Arctic tundra in the southern portion of Bylot Island, Nunavut, Canada (73°N, 80°W). The landscape was constituted of gently rolling hills and river valleys. We searched a 100 km^2 area annually for nesting snowy owls and monitored the fate of all nests found (Gauthier et al. 2004).

Methods

In 2007, we found 17 nests of snowy owls. From 27 June to 11 July, we captured 12 adult female snowy owls on their nest using a bow-net trap. We captured birds during the hatching period (on average, 3.6 young were present at the nest; range: 1 to 7) except for 2 birds where eggs had just started to crack. We weighed all birds to the nearest 10 g using a 3 kg or 5 kg spring scale (Pesola, Kapuskasing, Canada). During handling, we covered birds' heads with a cloth to minimize movements and struggling. We marked females with 30-g satellite transmitters (PTT-100; Microwave Telemetry Inc., Columbia, MD) attached with backpack harnesses made of Teflon ribbon (Bally Ribbons Mills, Bally, PA; Steenhof et al. 2006). The straps of the harness crossed

the breast of the bird and were held in place with a 2-cm^2 leather pad. We knitted together the 2 strap ends of the harness in the back of the transmitters using 9.1-kg fishing line and applied a small amount of 5-minute epoxy glue on the fishing line knots. We fitted harnesses quickly (<10 min) and, after release, we observed the territory and the nest of the marked bird for up to 1 hour from a hidden vantage point to monitor its behavior.

Transmitters, including the harness, fishing line, and glue weighed approximately 39 g and represented 1.8% of the average body mass of the marked females (range: 1.6–2.1%; $n = 12$). Transmitters were programmed to transmit continuously for an average of 5 hours and then turned off for an average of 125 hours from marking through the first winter (up to Feb 2008). During the first spring and summer months (Mar–Jul 2008), the transmitters were programmed to transmit for 5 hours and then turned off for 49 hours. Finally, cycles of 4 hours on and 142 hours off were programmed for the remaining battery life of the transmitters. We received locations of marked owls on a regular basis via the Argos system (Collecte Localisation Satellites 2011). Each location was assigned to a class (0, 1, 2, 3, A, B, or Z) according to its estimated precision. The estimated accuracy of location classes 0, 1, 2, and 3 followed a normal distribution with a standard deviation of >1,000 m, <1,000 m, <350 m, and <150 m, respectively. Location classes A, B, and Z were considered to be of poorer accuracy by the system and we therefore only used locations with an accuracy class ≥1 for all analyses.

No birds returned to the marking site of Bylot Island the summer following manipulations. Nonetheless, between 25 June and 7 July 2008, we were able to visit by helicopter all the sites where satellite-tracked owls had settled with 1 exception, a bird that had settled in the western Canadian Arctic (>1,200 km away from Bylot Island). At each site, the helicopter circled briefly to detect any signs of owl presence before landing. On the ground, 1 to 3 persons searched the area for a few hours and scanned with a spotting scope in order to find the marked bird and determine if it was paired and nesting. When we found a nest (i.e., confirmed breeding), we checked its contents.

We defined clutch size as the maximum number of eggs (or chicks) recorded in a nest. We inferred laying date (defined as the date that the first egg was laid) from the nest contents assuming that 1 egg was laid every other day and that incubation lasts approximately 32 days

(Parmelee 1992). For nests found when all eggs had hatched, we assessed hatching date based on the plumage development and size of young, assuming a normal chick growth curve as reported by Watson (1957). We compared laying dates and clutch sizes of marked birds among years (i.e., before and after marking) using paired t-tests. We also compared laying dates and clutch sizes of marked birds with unmarked birds breeding on Bylot Island in the same years using t-tests. We assessed nesting success (defined as the probability to fledge at least 1 chick) for nests that could be monitored until fledging (defined as when chicks are able to sustain flight). We compared nesting success of marked and unmarked birds on Bylot Island in 2007 using a Fisher's exact test.

We assessed average daily locations of the marked owls using all locations of a given date. We defined settlement on a potential breeding site when movements between 2 successive locations were less than 5 km (settlement date was the midway point between these 2 dates; Ganusevich et al. 2004). Similarly, we inferred departure from the breeding site as the first time that birds were located 5 km away from the nest site (or the center of the cluster of summer locations when the exact position of the nest site was unknown). The departure date was the midway point between this date and the date of the previous location (Ganusevich et al. 2004). We calculated the daily distance moved (as the distance between average daily locations divided by the number of days separating them) and the home range size (100% minimum convex polygon) recorded between the settlement and departure dates. We used this information to infer breeding for birds that could not be visited on the ground during summer 2009 and 2010. We inferred that a bird was breeding if its locations fulfilled 3 criteria. First, the length of time between settlement and departure date had to be at least 46 days, the minimum length of time recorded for a confirmed breeding bird (Table 1). Second, the mean daily movements needed to be within 1 standard deviation of the mean daily movements of confirmed breeders (confirmed breeding birds moved 0.67 ± 0.32 km per day on average, mean $\pm$ SD, $n = 19$). Third, summer home range size needed to be within 1 standard deviation of the mean size observed in confirmed breeding birds (i.e., 18.2 ± 15.2 km^2, $n = 19$). This was a conservative approach to infer reproduction because only 14 of 19 confirmed breeding attempts fulfilled those 3 criteria (Table 1).

During the study period, 4 transmitters stopped moving and generated stationary signals. We were able to visit 2 sites from which stationary signals had been received for >20 weeks. We conducted

a thorough search on the ground for the transmitter and/or for any evidence of an owl carcass around the position provided by the satellite.

We estimated monthly survival rate over a 36-month period using a Kaplan-Meier model for known fate individuals using the program MARK (version 4.3; White and Burnham 1999). One transmitter stopped sending signals while the bird was still moving normally (after 14 months of tracking or 550 hr of transmission time). We assumed that this was because of transmitter failure because the battery had reached 73% of its life expectancy (i.e., 750 hr of total transmission time). Consequently, we assigned an unknown status to this individual after the transmitter failure for the survival analysis. We transformed monthly survival estimates (S_m) into annual survival (S_a) as follows: $S_a = (S_m)^{12}$.

We performed spatial analyses with ArcGIS 9.2 software (ESRI Inc., Redlands, CA) and statistical analyses with SAS 9.1.3 software (SAS Institute, Cary, NC). We captured and handled all birds according to the animal care committee of Université Laval (CPAUL permit #84921). Results are presented as mean ± SE unless otherwise stated.

Results

Short-term effects

No young were hurt and no eggs were broken during capture at the nest. All marked females returned rapidly to their nest after marking (mean = 12 min, range = 3–57 min), and quickly resumed normal activities (i.e., they all incubated the eggs and brooded their chicks).

Average nesting success of snowy owls breeding on Bylot Island was relatively low in 2007 (60%, $n = 15$). However, nesting success did not differ between females that were captured and marked (64%, $n = 11$) and those that were not manipulated (67%, $n = 3$, Fisher's exact test = 0.77, $P = 0.79$); this comparison excludes 1 nest abandoned during laying and for which the female was therefore not available for marking.

Long-term effects

We found an owl carcass at each of the 2 visited locations where transmitters were sending stationary signals. Based on the cessation of movement, those birds died approximately 6 weeks and 17 months after marking. Carcasses did not provide any evidence of entanglement with the

harness and the transmitters were still well positioned on the birds' backs, without any scars on the skin. For the 2 sites with stationary signals that could not be visited, transmitters stopped moving 1.5 months and 5 months after marking. We thus performed the survival analyses with 2 scenarios. We first assumed that all stationary transmitters were associated to dead birds (worst case scenario). We also ran the analyses assuming that the 2 stationary transmitters that we were unable to visit were lost by live birds. Based on the first scenario, monthly survival rate calculated over a 36-month period was 0.987 ± 0.007, or 0.852 ± 0.070 on an annual basis. However, if we consider that only 2 birds died (best scenario based on confirmed mortalities), monthly survival estimates was 0.993 ± 0.005 or 0.923 ± 0.057 on an annual basis.

In 2008, 1 year after marking, all successfully tracked birds settled in confined areas. At all 8 sites where we conducted ground visits, marked birds were resighted and appeared healthy. Transmitters were hidden in the plumage and observations of the antennas sticking out at the back suggested that transmitters were still well positioned on the birds. In all cases, the radio-marked females were paired with a male and no other pair was observed in the vicinity. For 7 of these 8 birds, we found a nest within the cluster of positions provided by the satellites where the bird had settled. Although movement parameters strongly suggest that female F8 was also breeding (see Table 1), we failed to find its nest. This likely resulted from limited searching effort because of logistic and climatic constraints (the only opportunity we had to visit the area was on a foggy and rainy day, which restricted visibility and time spent on the ground) or perhaps a failed nesting attempt. In 2009 and 2010, all successfully tracked birds settled again in confined areas for extended periods of time and, based on the 3 criteria defined from movement patterns of confirmed breeders (see methods), we inferred that all of them initiated a nest, which was confirmed in 1 case in 2010 (Table 1).

Mean clutch size tended to be greater 1 year after the initial capture than before marking (2007: 6.1 ± 0.6; 2008: 7.1 ± 0.8; $t_{1,7} = 1.87$, $P = 0.11$). In 2008, clutch size of marked birds did not differ from unmarked birds breeding on Bylot Island (unmarked birds: 7.0 ± 0.3; $t_{1,24} = 0.19$, $P = 0.85$). Moreover, the only marked breeding bird that was visited in 2010 (the bird returned to our study area 3 years after marking) had a clutch of 7 (compared to 3 in 2007). Mean clutch size of unmarked breeding snowy owls on Bylot Island in 2010 was 6.9 ± 0.3. Finally, females started laying on average 10 days earlier during their first post-marking breeding season (2007: 28 May $\pm$

3 days; 2008: 18 May ± 3 days; $t_{1,7}$ = 2.65, P = 0.04; Table 1). In 2008, laying date of marked birds did not differ from unmarked birds breeding on Bylot Island (unmarked birds: 16 May ± 1 days; $t_{1,23}$ = 1.45, P = 0.19). In 2010, the laying date recorded for the only visited marked female was 30 May (compared to 23 May in 2007). Average laying date of unmarked breeding birds on Bylot Island in 2010 was 23 May ± 2 days.

We recaptured the marked owl that returned to our study area 3 years after the initial capture and removed its transmitter. The transmitter and the harness were both well positioned on the bird and we observed no sign of injury apart a small amount of feather abrasion under the transmitter. The body mass recorded during the early chick rearing period for the recaptured female varied little from 2007 (2.325 kg) to 2010 (2.175 kg; a 6% decline).

Discussion

We did not find any significant negative effect of satellite transmitters on several key life history traits of snowy owls tracked for up to 3 years. We thus conclude that methods used to capture and mark the birds were safe and well adapted to the study species (see also Fuller et al. 2003). However, the limited sample size and the lack of adequate control (unmarked) groups for some comparisons could have reduced our ability to detect subtle effects.

Nesting success of snowy owls breeding on Bylot Island in 2007, the year of initial capture and marking, was relatively low (60%) compared to other years when nesting owls were found (average annual nesting success = 96 ± 3%, range: 85–100%, n = 5 years; J.-F. Therrien, Université Laval, unpublished data). However, nesting success did not differ between marked and unmarked females, indicating that capture and marking was not the cause of the low overall success. The abundance of both collared (*Dicrostonyx groenlandicus*) and brown (*Lemmus trimucronatus*) lemmings, the primary prey of owls, was relatively low on Bylot Island in 2007 compared to other years when owls nested at our study area (0.32 lemmings/ha in 2007 compared to 5.7 ± 2.1 in other years; Chapter 1). Since lemming abundance is a strong determinant of reproductive success of snowy owls (Parmelee 1992, Gauthier et al. 2004), the low nesting success recorded in 2007 was probably a result of low prey abundance.

Although we could not ascertain the reason of death in the 2 retrieved owl carcasses, the transmitter did not appear to be a direct cause as judged by its position on the bird. Also, the

female recaptured in 2010 did not show any sign of injury related to the transmitter or the harness, and was still flying with ease. Based on the 2 confirmed deaths, the maximum estimates of annual survival rate was 92.3% for our 12 owls. Fuller et al. (2003) also reported the death of 1 individual out of 5 radio-marked females tracked for up to 2 years. Although no published survival rates exist for snowy owls in the wild, our estimate is relatively high considering the range of values reported in comparable species. Indeed, annual survival of closely related and similar size species, such as the great horned owl (*Bubo virginianus*), is usually within the range of 80–90% (90.5% for owls with radio-transmitters in Yukon, Rohner 1996; 81–88% for ring recovered owls in Saskatchewan, Houston and Francis 1995). Similar survival estimates have also been reported for smaller owls (e.g., 80–88% in color-banded spotted owls [*Strix occidentalis*]; Foster et al. 1992, Van Deusen et al. 1998, Seamans et al. 2002, Zimmerman et al. 2007). We thus conclude that the tracking of marked snowy owls for up to 3 years does not provide evidence that transmitters impaired their survival.

One of our marked owls died 6 weeks after marking and 2 transmitters became stationary during the first winter for unknown reasons. This could be interpreted as evidence that a few individuals did not adapt well to wearing a transmitter. However, we do not know if the latter 2 transmitters became stationary because the birds died or because they freed themselves of the transmitter. Harnesses used to attach transmitters are made of resistant material but they still need to be smooth and flexible to prevent any harm to the bird. Raptors have previously been observed removing their harness and dropping their transmitter (Buehler et al. 1995, Reynolds et al. 2004, Steenhof et al. 2006). Moreover, these 2 birds had moved over long distances (over 1,000 km each) and for periods of 1.5–5 months before the signals became stationary suggesting that they were able to fly with ease while wearing the transmitter. However, if we assume, under the worst case scenario, that all stationary transmitters were associated to dead birds, this would bring the annual survival of our marked owls to 85.2%, a value that is still within the range of values reported in comparable species (see above).

Even when transmitters do not cause mortality, more subtle effects are still possible. For instance, transmitters may reduce flight performance or feeding efficiency, leading to poor body condition (Barron et al. 2010) or cause pair bond breakage and interfere with pairing (Demers et al. 2003). When animals are disturbed or weakened, one of the first activities that they curtailed is breeding

(Barron et al. 2010). If radio-transmitters have negative effects on owls, we would expect marked individuals to have a reduced clutch size, delay laying, or in the worst case, be unpaired and completely forego breeding. We found that all our successfully tracked birds apparently bred every year during the study period (up to 3 years following marking) and this was confirmed for 8 of the 9 cases where ground checks were possible. Moreover, during the breeding season following the initial capture, all marked birds were paired and bred, laid earlier, and had similar clutches on average to the year before. Their clutch size and laying date did not differ from that of unmarked birds breeding on Bylot Island in the same year although the power of this comparison is weakened by the fact that all marked birds settled >200 km from Bylot Island in 2008. These results therefore strongly suggest that transmitters had no detrimental long-term effects on female snowy owls, as found in several other raptors species (Snyder et al. 1989, Sodhi et al. 1991, Hiraldo et al. 1994, Reynolds et al. 2004).

Management implications

We conclude that harness-mounted satellite transmitters can be safely used on snowy owls in the wild. Their use is likely to provide reliable long-term information on movements, habitat use, reproduction, and survival of this elusive predator that would be otherwise virtually impossible to obtain using conventional techniques. To our knowledge, this study provides the first survival and multi-annual individual reproduction estimates in wild snowy owls. With the anticipated climate changes, especially in Arctic regions, such information on key players of the food webs are of prime importance for management decisions and conservation of the integrity of the tundra ecosystem.

Table 1. Breeding parameters of 12 adult female snowy owls marked with satellite transmitters on Bylot Island, Nunavut, Canada in 2007 and tracked for up to 3 years. Empty cells indicate that information was unknown.

Year	Owl ID	Settlement Date	Laying date	Departure date	Time spent on breeding site (days)	Distance (km) travelled daily X̄	SD	n	Home range (km²)	Breeding attempt Inferred[a]	Confirmed[b]	Nesting success
2007	F1		25 May	6 Sep	104	0.58	0.50	5	11.61	yes	yes	yes
	F2		2 Jun	22 Sep	112	1.25	1.93	8	35.65	no	yes	no
	F3		25 May	15 Sep	113	0.20	0.21	10	2.42	yes	yes	yes
	F4		30 May	10 Aug	72	0.25	0.14	3	0.40	yes	yes	yes
	F5		20 May	5 Jul	46			1			yes	no
	F6		23 May	11 Aug	80	0.48	0.32	6	8.09	yes	yes	yes
	F7		29 May	9 Sep	103	0.45	0.34	7	21.59	yes	yes	no
	F8		4 Jun	26 Jul	52	0.81	0.22	3	3.84	yes	yes	no
	F9		26 May	16 Sep	113	0.94	0.89	13	40.91	no	yes	yes
	F10		24 May	18 Sep	117	1.07	0.72	7	49.43	no	yes	
	F11		12 Jun	7 Sep	87	0.23	0.37	8	1.21	yes	yes	yes
	F12		7 Jun	9 Sep	94	0.36	0.53	8	4.01	yes	yes	yes
2008	F1	23 Apr	08 May	21 Sep	151	0.97	0.91	54	37.79	no	yes	
	F2	23 May	29 May	21 Aug	90	1.08	0.68	20	32.64	no	yes	
	F3	13 May	19 May	18 Jul	66	0.36	0.37	24	3.56	yes	yes	
	F6	2 May	23 May	23 Aug	113	0.93	0.90	36	25.34	yes	yes	
	F8	5 May		10 Aug	97	0.56	0.44	30	18.19	yes	no	
	F9	1 Apr	11 May	08 Aug	129	0.79	0.63	48	23.19	yes	yes	
	F10	9 May	21 May	-[c]	-[c]	0.91	0.91	32	12.78	yes	yes	

	F11	13 May	19 May	24 Aug	103	0.62	0.56	42	12.37	yes	yes
	F12	11 Jun		21 Aug	71	0.81	0.48	30	10.88	yes	
	F1	11 Apr		03 Aug	114	0.47	0.31	15	30.34	yes	
	F3	21 May		04 Sep	106	0.21	0.14	14	10.33	yes	
	F6	14 May		31 Jul	78	0.29	0.18	8	9.23	yes	
2009	F8	25 Jun		27 Aug	63	0.47	0.29	9	11.38	yes	
	F9	9 May		17 Aug	100	0.48	0.25	16	23.19	yes	
	F11	21 Jun		25 Aug	65	0.40	0.38	9	8.31	yes	
	F12	25 Jun		31 Aug	67	0.46	0.29	9	33.09	yes	
	F1	27 Apr		2 Oct	159	0.29	0.14	16	17.82	yes	
	F3	27 Apr		12 Nov	199	0.21	0.26	32	10.71	yes	
	F6	3 May	30 May	-[d]	-[d]	0.53	0.31	9	18.05	yes	yes
2010	F8	23 Apr		-[c]	-[c]	0.25	0.20	7	24.81	yes	
	F9	4 May		-[c]	-[c]	0.29	0.21	14	15.66	yes	
	F11	6 May		11 Sep	128	0.28	0.28	10	15.72	yes	
	F12	19 May		13 Sep	118	0.51	0.68	14	29.54	yes	

[a] Breeding status inferred from movement parameters (see methods)

[b] Breeding status confirmed with ground check

[c] Transmission stopped before the end of the breeding period

[d] Transmitter was removed from the bird when recaptured

Chapitre 5

An avian terrestrial predator of the Arctic relies on the marine ecosystem during winter.

Therrien, J. F., G. Gauthier, and J. Bêty. 2011. An avian terrestrial predator of the Arctic relies on the marine ecosystem during winter. Journal of Avian Biology **42**:363-369.

Résumé

Les prédateurs de l'écosystème terrestre arctique sont confrontés à une longue période de faible disponibilité de proies pendant l'hiver et des subsides provenant d'autres écosystèmes tels que l'environnement marin peuvent contribuer à soutenir leurs populations. Le suivi par satellite de femelles harfangs des neiges adultes a permis de démontrer que la plupart des individus demeuraient à des latitudes élevées dans l'arctique canadien pendant l'hiver et passaient plusieurs semaines (jusqu'à 101 jours) sur la glace de mer entre décembre et avril. L'analyse d'images à haute résolution de la glace de mer prises à l'aide de satellites a démontré que les harfangs ont principalement séjourné à proximité de zones d'eau libres de glace. Ces zones sont fréquemment utilisées pendant l'hiver par plusieurs espèces d'oiseaux marins, des proies potentielles. Une telle utilisation de la glace de mer par un prédateur considéré comme spécialiste de petits mammifères était inattendue. Cela suggère que, pendant l'hiver, les ressources marines permettent de soutenir les populations de harfang des neiges qui est un important prédateur du réseau trophique de la toundra pendant l'été. Comme la dynamique hivernale de la glace de mer est susceptible de changer dans les prochaines décennies en raison du réchauffement climatique, cela pourrait affecter la stratégie d'hivernage de ce prédateur et, ultimement, le fonctionnement de l'écosystème de la toundra.

Abstract

Top predators of the Arctic tundra are facing a long period of very low prey availability during winter and subsidies from other ecosystems such as the marine environment may help to support their populations. Satellite tracking of snowy owls, a top predator of the tundra, revealed that most adult females breeding in the Canadian Arctic overwinter at high latitudes in the Eastern Arctic and spend several weeks (up to 101 days) on the sea-ice between December and April. Analysis of high-resolution satellite images of sea-ice indicated that owls were primarily gathering around open water patches in the ice, which are commonly used by wintering seabirds, a potential prey. Such extensive use of sea-ice by a tundra predator considered a small mammal specialist was unexpected, and suggests that marine resources subsidize snowy owl populations in winter. As sea-ice regimes in winter are expected to change over the next decades due to climate warming, this may affect the wintering strategy of this top predator and ultimately the functioning of the tundra ecosystem.

Introduction

The Arctic tundra is characterized by strong seasonal variations in productivity, which nonetheless remains relatively low throughout the year compared to other ecosystems (Bliss 1986, Gauthier et al. 1996, Krebs et al. 2003). Considering that, the relatively high abundance and diversity of vertebrate predators in the tundra is impressive (Krebs et al. 2003). Terrestrial predators, such as the snowy owl (*Bubo scandiacus*) or the Arctic fox (*Vulpes lagopus*), need to find sufficient prey throughout the year to sustain their basic metabolic needs and withstand the extreme Arctic conditions. This is especially critical during the long Arctic winter because the availability of the primary prey species of the tundra such as small mammals and migratory birds becomes very low due to protection offered by the snow cover or the departure of migratory species.

While wintering at high latitudes can reduce migration costs and allow a quick return to tundra breeding sites in spring, terrestrial predators have to cope with very low prey availability at that time. Even if snowy owls are able to withstand midwinter Arctic conditions out in the open (Gessaman 1972), their regular presence during winter in different regions of southern Canada and northern United States suggests that owls are migrating out of the Arctic when food availability is reduced (Kerlinger et al. 1985, Parmelee 1992). Throughout their breeding range those birds have a narrow, specialised diet almost entirely made of small mammals during summer (Parmelee 1992). For that reason, it has long been thought that snowy owls were moving to southern areas to prey upon similar prey type during the winter (Parmelee 1992). Despite some reports of predation on birds and especially waterfowl (Gross 1944, Campbell and MacColl 1978, Mehlum and Gjertz 1998), several studies analysed snowy owl diet during winter and they all found that small mammals comprised the bulk of the food consumed (reviewed by Detienne et al. 2008).

By tracking several individual owls marked with satellite transmitters over a 2-year period, we have uncovered a hitherto unknown wintering strategy for a typically terrestrial species, the extensive use of Arctic sea-ice. Even if it has been previously reported that snowy owls could feed on seabirds at polynyas and open leads in the ice during the winter in the Arctic (Hudson Bay area of Canada; Gilchrist and Robertson 2000, Robertson and Gilchrist 2003), here we show that this strategy is commonly used among adult female snowy owls breeding in the Eastern Canadian

Arctic. We also discuss the implications of this wintering strategy for the conservation of Arctic predators in the context of global warming and retreating sea-ice.

Methods

In July 2007, we marked 12 breeding female snowy owls on their nest with satellite transmitters over a 115km^2 area on the southern portion of Bylot Island, Nunavut, Canada (73°N, 80°W), using a bow-net trap. We fixed the transmitters (PTT-100, 30g battery-powered; Microwave Telemetry Inc., MD, USA) on the owls using a back-pack harness (Steenhof et al. 2006) made of Teflon ribbon. All animal manipulations were conducted in accordance with the animal care committee of Université Laval (CPAUL permit #84921). We received transmissions at 5-day intervals and retained locations of accuracy ranging from 150 to 1000 m to generate maps of winter movements and to determine the proportion of locations that were over the sea.

We characterized the ice cover around the highest quality owl locations (accuracy of $\leq$ 150m; n = 32) using sea-ice images with a 50-m resolution taken by Radarsat satellites provided by the Canadian Ice Service (Radarsat-1 2007-2008, Radarsat-2 2009). We selected satellite images taken within a 2-days window of each owl location. We associated each location with 10 random points (Fortin et al. 2009) within either a 10 or a 100-km radius (encompassing 80% and 100% of the maximum daily distance traveled by owls during winter, respectively) and we measured distances of all points to the nearest open water patch > 0.2 km^2 (the minimum open water patch size where owls had been observed in winter (Gilchrist and Robertson 2000)). For random points located over open water, we attributed a distance of 0. We confirmed that open water patches could be reliably identified from Radarsat images by comparing pairs of images of the same area taken < 2 days apart under different environmental conditions (because wind, for example, creates ripples on the surface water that change the color on the image). We detected the same open water patches on both images in > 95% of the cases (n = 130). We compared the observed and random distances using conditional logistical regressions with empirical standard errors and individual locations nested within each owl ID to account for repeated measures (Fortin et al. 2009). We performed spatial analyses with ArcGIS 9.2 software (ESRI Inc., Redlands, CA, USA) and statistical analyses with SAS 9.1.3 software (SAS Institute, Cary, NC, USA, 2005).

Results

We successfully tracked 9 owls during the first winter following marking (2007/2008) (Fig. 1), and 8 of them for a second winter (2008/2009) (Fig. 2). All tracked birds wintered at high latitudes (> 55°N) in the eastern Canadian Arctic except for two birds that wintered in temperate areas (one in Newfoundland and one in North Dakota, between 45°N to 51°N). Over the two years, birds that wintered in the Arctic and in temperate areas were located on average 1100 km (n = 13; range: 410 to 1970 km) and 2900 km (n = 4; range: 1715 to 3520 km) from their previous summer nesting site.

All birds but one that overwintered in the Arctic were located over the sea for several weeks during both winters, as well as one of the two birds that wintered in more temperate areas (F8) (median = 41 days, range = 8 to 71 days in winter 2007/2008, and median = 59 days, range = 30 to 101 days, in winter 2008/2009; Table 1). At the time that these locations were recorded (from early December to late April), the area used by owls is almost entirely covered by sea-ice. Owls concentrated their activity in the Hudson and Davis straits and in Hudson Bay at a median distance of 40 km from the coast but sometimes as far as 210 km (Figs. 1 and 2). Individuals that spent the most time on the sea-ice during the first winter adopted the same behavior the following winter (Pearson correlation, r = 0.74, p = 0.04, df = 8). During both winters, owls were significantly closer (average distance ± SEM = 0.48 ± 0.11 km, n = 32) to open water patches identified on the Radarsat images than random points at both spatial scales (1.50 ± 0.09 km, β = -1.49 ± 0.30, χ^2 = 24.3, df = 1, p < 0.001; 4.10 ± 0.39 km, β = -1.40 ± 0.22, χ^2 = 40.7, df = 1, p < 0.001, for the 10 and 100-km scales respectively) (Fig. 3).

Discussion

Our study presents the first quantitative results showing that extensive use of the sea-ice is a common and important wintering strategy for snowy owls in North America, a surprising result for a terrestrial species. Although a previous study revealed that owls could cross between land masses over the sea-ice, the time spent on sea-ice was short and was not indicative of potential

resource use in this habitat (Fuller et al. 2003). Considering the length of time spent on sea-ice by our birds, they must be able to find prey in this environment despite the extremely cold temperatures and winter darkness. Small patches of open water areas at those latitudes are often used by high density of wintering seabirds such as eiders (*Somateria* spp), long-tailed ducks (*Clangula hyemalis*) and black guillemots (*Cepphus grylle*), and snowy owls have been observed attacking seabirds there (Gilchrist and Robertson 2000, Robertson and Gilchrist 2003). Considered a small mammal specialist during the breeding period (Parmelee 1992), this predator thus seems to switch to a more generalist or opportunistic strategy during the winter. Wintering at high latitudes may be advantageous to owls by allowing them to start prospecting very early in spring for areas with high lemming densities, a prerequisite for a breeding attempt (Gilg et al. 2003, Gauthier et al. 2004, Hakala et al. 2006).

Kerlinger and Lein (1986) showed that despite a large overlap, the winter distribution of snowy owls in North America varies according to age and sex, with adult females remaining predominantly in the northernmost part of the wintering range while young, immature birds in the southernmost part. In our study, only adult females that had previously bred were tracked and thus it remains to be seen if the strategy of wintering at high latitude and of using sea-ice is also used by adult males and/or immature birds. Given their larger size than males, females may be more capable or suited to feed on relatively large size prey such as seabirds (see Lind 1993) and may thus be more inclined to winter over sea-ice than males. Similarly, the cost of wintering in the Arctic may be greater in immature birds and especially first-year ones due to their inexperience, which may explain why they tend to winter further south (Kerlinger and Lein 1986). Therefore, further investigations are needed to determine the extent of this wintering strategy in males or immature owls.

Exchanges of energy and nutrients between ecosystems, such as between the marine and terrestrial ecosystems, may be relatively common and may have a strong impact on the functioning of the ecosystems involved (Huxel et al. 2002, Loreau et al. 2003). These exchanges are often asymmetric and may be especially important for the food web of low productivity ecosystems such as isolated oceanic islands or the Arctic tundra (Sanchez-Pinero and Polis 2000, Stapp and Polis 2003). The Arctic fox represents another example of a terrestrial animal that can use the sea-

ice in some regions of the Arctic, preying on seal pups or scavenging polar bear kills, thus living essentially upon marine resources in winter (Roth 2002, Roth 2003, Tarroux et al. 2010). Therefore, our results suggest that energy subsidies from the marine ecosystem may be a general feature of terrestrial Arctic predators and could be essential for the long-term persistence of their populations.

Alterations to the physical environment due to climate change appear less dramatic in the Arctic tundra than in marine ecosystems (ACIA 2005, Solomon et al. 2007). However our novel findings imply that rapid changes occurring in the marine environment may affect terrestrial species as well. With climate warming, the extent of the sea-ice in areas used by wintering owls such as the Hudson and Davis straits has been retreating in recent years and is projected to retreat at an even faster rate in the coming decades (Johannessen et al. 2006). This will likely affect the occurrence of open water patches during winter with cascading effects on the whole associated marine food web, including the number and distribution of seabirds using these environments (Stirling 1997, Mallory et al. 2010). Although retreating sea-ice may lead, in the sort-term, to increased open water areas in winter, it is unclear if this will be associated with an increase in primary productivity and in local seabird abundance or the opposite. For instance, more and larger open water areas could allow seabirds to spread over a wider area, possibly decreasing the local density of prey for owls. Consequently, this could lead to the degradation of an important wintering habitat for them. Alternatively, warmer temperature in the Arctic Ocean may result in an increase in primary productivity and in seabird densities, therefore increasing prey availability for snowy owls during winter. We thus believe that the potential consequences of changes in sea-ice regime on the functioning of the tundra ecosystem have been largely overlooked, and are likely underestimated due to a lack of basic knowledge on several Arctic wildlife species.

Table 1. Movement parameters of 9 adult female snowy owls tracked during the winter period (from 11 December 2007 to 28 April 2008 and from 4 December 2008 to 27 March 2009) in Canada.

Period	ID	Number of locations	Proportion of locations over sea-ice	Time spent over sea-ice (days)
Winter 2007-2008	F1	165	0.33	25
	F2	122	0.26	52
	F3	236	0.34	37
	F4	230	0.05	<1
	F5	194	0.20	41
	F6	261	0.44	71
	F7	182	0.48	88
	F8	133	0.20	8
	F9	94	0.00	0
Winter 2008-2009	F1	86	0.60	73
	F2	17	0.94	30
	F3	72	0.93	86
	F4	116	0.03	<1
	F5	71	0.45	44
	F6	85	0.92	101
	F7	-[a]	-	-
	F8	64	0.25	34
	F9	51	0.00	0

[a]transmitter stopped during summer 2008.

Figure 1. Satellite-tracked movements of 9 adult female snowy owls showing extensive use of sea-ice from 11 December 2007 to 28 April 2008 in the Eastern Canadian Arctic (A). The Hudson and Davis Strait regions where most of the marked owls used the sea-ice during winter are presented in more details (B). All birds were marked on the southern portion of Bylot Island in summer 2007.
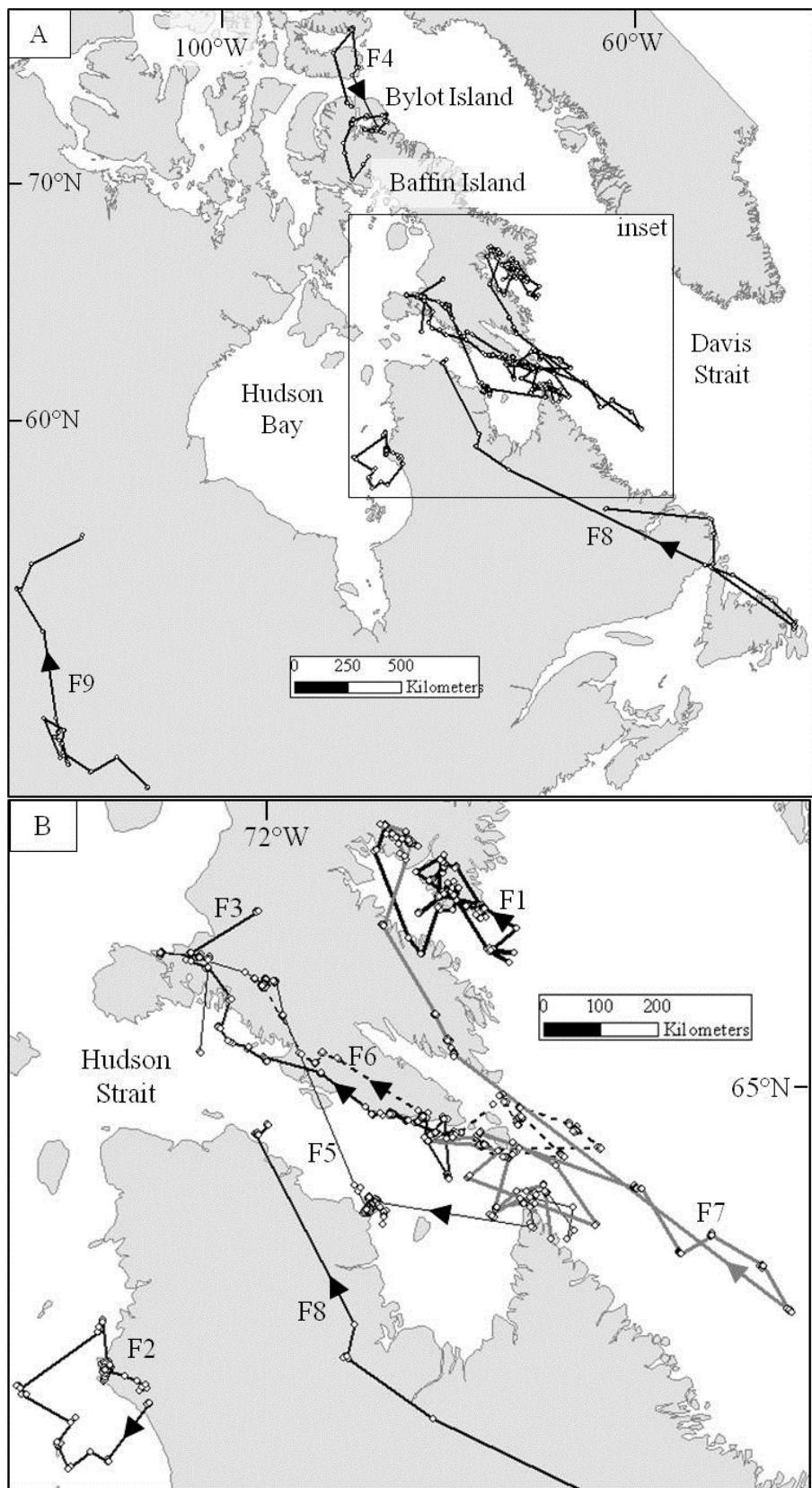
Figure 2. Satellite-tracked movements of 8 adult female snowy owls showing extensive use of sea-ice from 4 December 2008 to 27 March 2009 in the Eastern Canadian Arctic (A). The Hudson and Davis Strait regions where most of the marked owls used the sea-ice during winter are presented in more details (B). All birds were marked on the southern portion of Bylot Island in summer 2007.

Panel A: Map showing F4 near Bylot Island and Baffin Island, an inset region near Davis Strait, Hudson Bay, F2, F8, and F9. Scale bar 0 250 500 Kilometers. Latitude marks 70°N, 60°N; longitude marks 100°W, 60°W.

Panel B: Map showing Hudson Strait, F1, F6, F3, F5, with 72°W and 65°N markers. Scale bar 0 100 200 Kilometers.
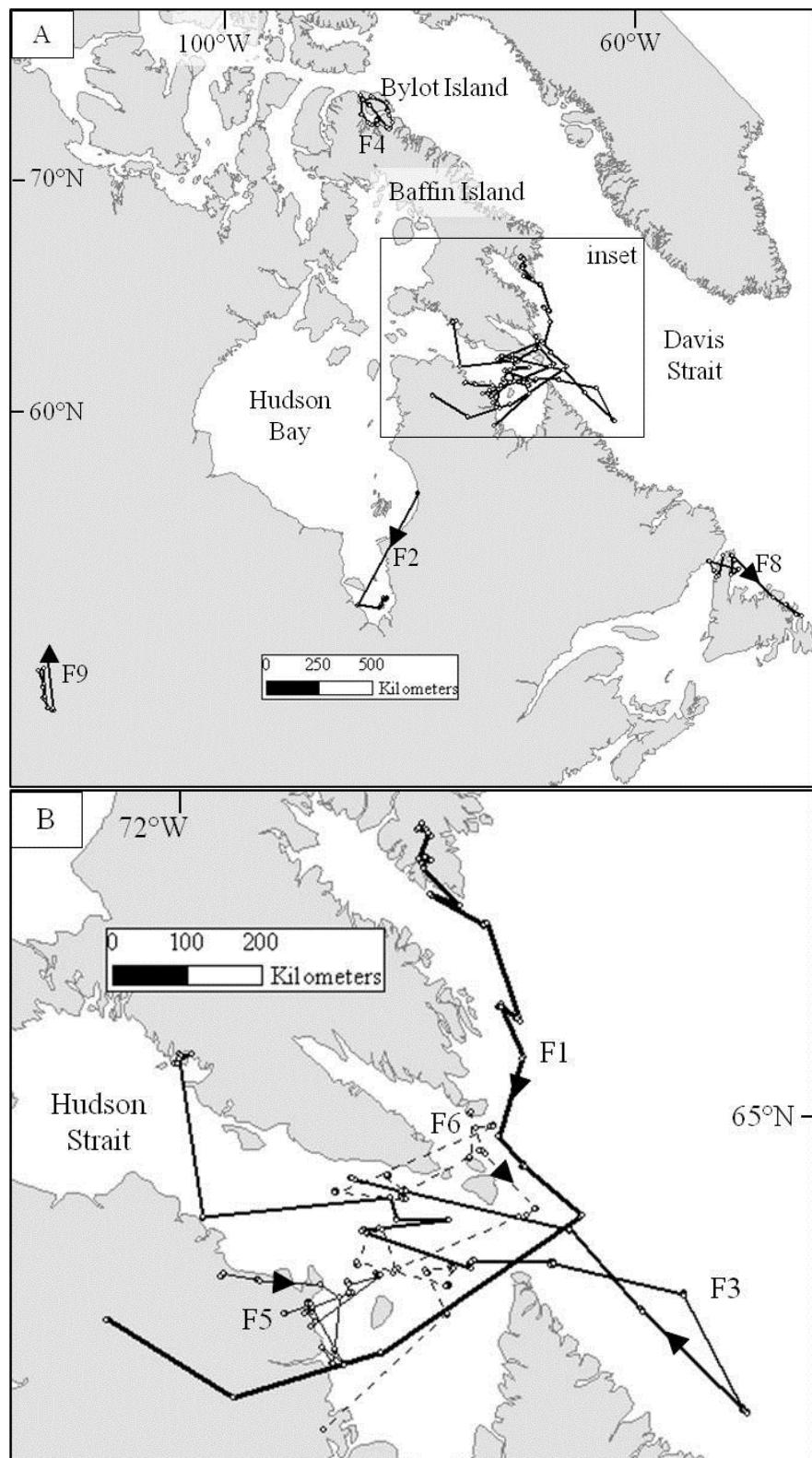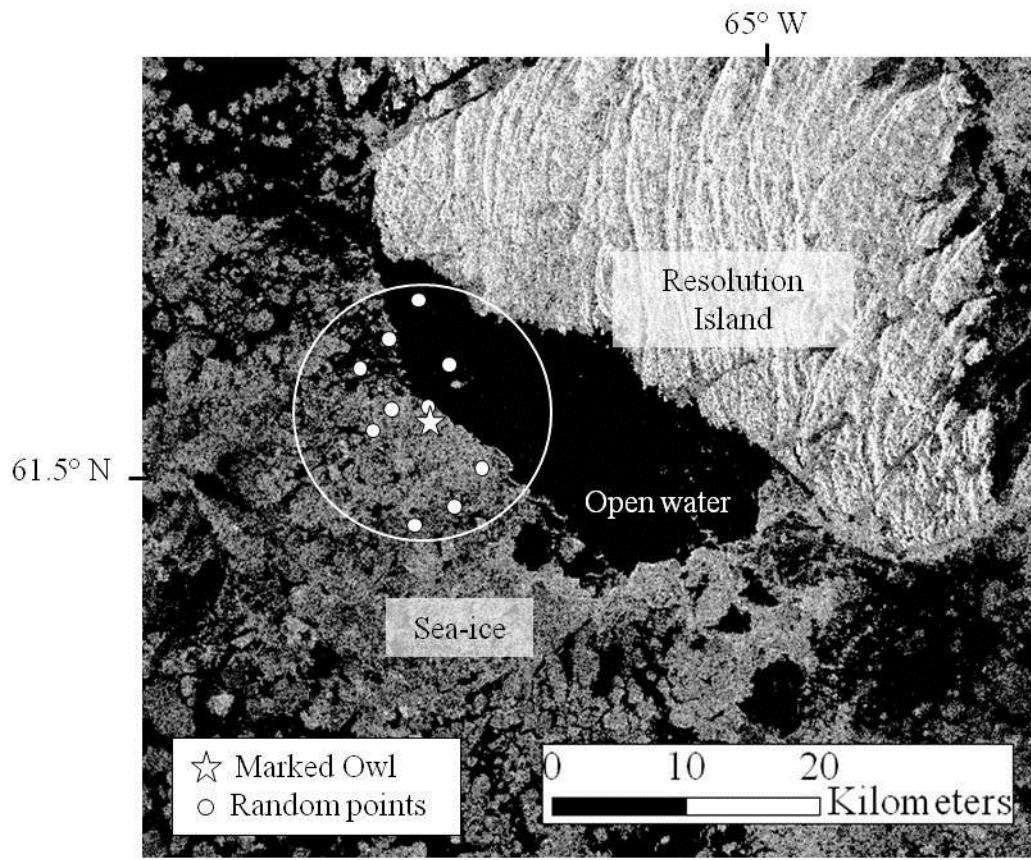
Figure 3. Example of high-resolution sea-ice image taken by Radarsat satellites within 2 days of an actual owl location. Ten random points located within a 10-km radius circle centred on the owl location are displayed.

Conclusion

À travers cette thèse, j'ai intégré plusieurs processus reliés au contrôle des réseaux trophiques comme les relations prédateurs-proies, les mouvements irruptifs, la sélection d'habitat et l'apport de subsides allochtones afin de mieux comprendre le rôle joué par les oiseaux prédateurs dans l'écosystème terrestre arctique. Les défis associés à l'étude de l'écosystème arctique m'ont amené à utiliser différentes techniques (récolte de données empiriques par observation directe, utilisation d'émetteurs satellites, utilisation de caméras à déclenchement automatique, utilisation de photos satellites à haute résolution, etc.) et approches analytiques (temps de premier passage – *first-passage time*, taux de survie d'individus dont le sort est connu – *known-faith survival rate analysis*, fonction de sélection des ressources – *resource selection function*, etc.). La combinaison de ces outils m'a permis d'évaluer plusieurs aspects distincts concernant le rôle des oiseaux prédateurs dans le réseau trophique de la toundra, et plus spécifiquement celui du harfang des neiges, afin d'en extraire des conclusions intégratives. En effet, tous les chapitres présentés sont uniques et indépendants, mais un message global démontrant l'importance des oiseaux prédateurs dans le fonctionnement de l'écosystème de la toundra émerge lorsqu'on unit les composantes.

En plus d'utiliser une panoplie de procédures techniques bien connues et déjà éprouvées, j'ai aussi évalué certaines méthodes afin d'identifier celles procurant les données les plus fiables. En effet, en plus de démontrer que les émetteurs satellites utilisés sur des harfangs des neiges ne semblaient pas affecter les oiseaux marqués (chapitre 4), j'ai évalué différentes méthodes couramment utilisées pour déterminer le régime alimentaire et le taux quotidien de consommation de proies chez les oiseaux (chapitre 2). Cette comparaison de méthodes s'est avérée très pertinente puisqu'elle a permis de démontrer l'importance d'avoir des estimations précises afin d'évaluer la pression de prédation (chapitre 1). Non seulement l'évaluation de l'efficacité des méthodes nous a permis de sélectionner la plus appropriée afin de connaître le régime alimentaire du harfang des neiges avec précision mais elle a aussi permis de démontrer que de faibles variations dans l'estimation provenant d'une méthode peu appropriée pouvaient mener à des conclusions biaisées, surtout dans un écosystème comme la toundra où la biomasse totale est faible. Ainsi, si on avait évalué les taux de consommation de proies quotidien à partir de boulettes de régurgitation, ceux-ci auraient été fortement sous-estimés (chapitre 2), tout comme la pression de prédation imposée par les oiseaux prédateurs (chapitre 1).

Réponse totale des prédateurs aviaires

Mon étude a permis d'appuyer l'hypothèse d'un contrôle par le haut sur l'écosystème terrestre arctique. En effet, les taux de prédation exercés par les oiseaux prédateurs dépassent largement les taux d'accroissement potentiel maximal des populations de lemmings variables à l'Île Bylot et seraient donc suffisants pour réguler cette espèce pendant l'été (chapitre 1). Bien que ceci ne fût pas le cas pour l'autre espèce, le lemming brun, l'impact des prédateurs aviaires était quand même non-négligeable et ceux-ci pourraient avoir un impact significatif sur les populations de cette espèce en combinaison avec les prédateurs mammaliens. Par contre, des résultats équivoques ont été obtenus au site secondaire (Île Herschel) alors que les taux de prédation n'ont pas atteint des niveaux comparables à ceux observés à l'Île Bylot. Plusieurs facteurs ont été évoqués afin d'expliquer ces différences (chapitre 1). Parmi ceux-ci, des différences dans la productivité primaire ou la présence de subsides allochtones (Gauthier et al. 2011, chapitre 5) représentent des avenues de recherche prometteuses. Néanmoins, la valeur de ces résultats n'en demeure pas moins importante, ce type d'étude étant très rare. Ainsi, la simple détermination des taux de prédation à plus d'un site permet non seulement de chiffrer l'impact de la prédation mais aussi de démontrer que l'écosystème de la toundra n'est pas un ensemble uniforme et homogène à l'échelle circumpolaire. Le contrôle du réseau trophique par les prédateurs semble donc agir fortement à certains endroits (Reid *et al.* 1995, Wilson *et al.* 1999, Gilg *et al.* 2006, chapitre 1) mais apparemment beaucoup moins à d'autres (Turchin *et al.* 2000, chapitre 1). Une approche expérimentale, où la pression de prédation, la productivité primaire et/ou les apports allochtones seraient manipulés, permettrait possiblement de déterminer quels facteurs sont les plus importants pour obtenir un type de contrôle donné (par le haut ou par le bas). La pertinence d'une telle démonstration serait considérable, mais l'établissement d'un tel dispositif demanderait un investissement colossal.

Le rôle du harfang des neiges dans le réseau trophique de la toundra est majeur (chapitre 1). Par contre, même si elle est centrale à ma thèse, cette espèce ne constituait pas le prédateur le plus important en termes de pression de prédation sur les lemmings au site d'étude principal (Île Bylot). En effet, de par leurs fortes densités et leurs taux de consommation élevés compte tenu de leur masse corporelle, les labbes à longue queue ont démontré la réponse totale la plus forte.

Plusieurs facteurs, comme par exemple la disponibilité d'habitat de nidification, peuvent influencer cette réponse totale. En effet, à notre site d'étude secondaire (Herschel), la densité de labbes était beaucoup plus faible et l'importance relative des harfangs y était plus grande. Des résultats comparables ont également été obtenus au Groenland où l'espèce imposant la plus forte pression de prédation variait entre le harfang des neiges et le labbe à longue queue entre les années et au cours d'une même année (Gilg *et al.* 2006). Ainsi, dans des sites différents, la pression de prédation imposée par les différentes espèces de prédateurs peut varier et il apparaît important de la mesurer de façon empirique.

Plus spécifiquement, cette étude a permis de démontrer le rôle important joué par les oiseaux prédateurs dans le fonctionnement du réseau trophique de la toundra. En effet, dans plusieurs régions de la toundra, les oiseaux prédateurs démontrent une forte diversité spécifique et une haute densité comparée aux prédateurs mammaliens. On supposait donc qu'ils pouvaient jouer un rôle important, mais relativement peu d'études avaient pu le mesurer (mais voir Pitelka et al. 1955, Gilg *et al.* 2006). Vu leur fort potentiel de mobilité, ces oiseaux démontrent des réponses numériques agrégatives sans délai, contrairement à bien d'autres prédateurs qui réagissent de manière différée à l'augmentation des populations de proies (Andersson & Erlinge 1977, Hanski *et al.* 1991, Hanski *et al.* 1993, Tornberg *et al.* 2005). Cet aspect a été traité au chapitre 3, mais c'est dans le chapitre 1 qu'on voit toute l'importance d'un tel comportement, lorsqu'on combine les réponses numériques aux taux de consommation mesurés.

Mouvements irruptifs, déplacements sur grande distance et dispersion reproductive

L'utilisation d'émetteurs satellites a permis de démontrer la remarquable plasticité comportementale du harfang des neiges (chapitre 3). En lien étroit avec la démonstration que la pression de prédation imposée par les oiseaux prédateurs semble limiter les populations de lemmings variables (chapitre 1), nous avons pu mieux décrire et comprendre la mécanique sous-jacente aux réponses numériques sans délai observées à un site donné. En effet, cet extraordinaire potentiel de mobilité, combiné à une absence de fidélité au site de reproduction (chapitre 3), illustrent comment le harfang des neiges peut envahir un site donné lorsque ses proies préférées

(lemmings) y sont abondantes. Ces comportements caractéristiques du harfang des neiges permettent à ce dernier d'afficher l'exemple ultime du migrateur irruptif décrit par Newton (2006).

Les espèces irruptives ont la particularité d'agir de manière différente de tout ce qui peut sembler bénéfique aux oiseaux et aux mammifères, où la réduction des distances et du temps passé en déplacement et la fidélité au site de reproduction semblent généralement favorisés. La combinaison de plusieurs facteurs tels que la réduction des coûts de déplacements et un fort potentiel reproductif peut probablement expliquer l'évolution de ce type de comportement (chapitre 3). De plus, le harfang des neiges démontre une forte spécialisation alimentaire sur une ressource pulsée, phénomène rare dans le monde animal. Ce type de stratégie alimentaire dans un environnement peu productif comme la toundra n'est apparemment rendu possible qu'en la combinant avec un fort potentiel de mobilité tel qu'observé (chapitre 3).

Dans cette thèse, j'illustre en détails des comportements décrits pour la première fois chez un oiseau, soit la confirmation de reproduction par les mêmes individus durant plusieurs années consécutives dans des sites distincts de plusieurs centaines de kilomètres combinés à des mouvements annuels exploratoires également étendus sur plusieurs centaines de kilomètres (chapitres 3 et 4). Les émetteurs satellites qui ont permis de démontrer ces comportements uniques représentent à ce jour un avancement technologique majeur. Par contre, il ne serait pas surprenant de voir ce type d'émetteurs s'améliorer et ainsi devenir plus petits et légers. Il est donc fort probable que nous pourrons observer ce type de comportement chez d'autres espèces se spécialisant sur des ressources pulsées comme certaines espèces d'oiseaux granivores (Newton 2006). Si on assume que ces oiseaux granivores se comportent également comme des migrateurs irruptifs, la limitation de la ressource par les consommateurs, comme démontré dans le cas du harfang des neiges (chapitre 1), reste par contre à être démontrée chez ces espèces.

Bien que cette thèse procure des résultats inédits et remarquables, certaines limites atteintes en cours d'analyses ouvrent des avenues de recherche intéressantes. En effet, nous n'avons pu, à ce jour, corréler aucun paramètre autre que l'abondance de lemmings aux déplacements observés sur de longues distances. Ainsi, notre compréhension des mécanismes proximaux qui expliquent ces déplacements demeure très limitée. Dans ce contexte, l'acquisition d'informations sur le succès de

nidification passé ou actuel des individus, sur la qualité des sites de nidification choisis et disponibles, la qualité des partenaires rencontrés, l'âge des individus, l'abondance locale des compétiteurs et/ou les conditions climatiques (par exemple la quantité de neige au sol) seraient des avenues de recherches intéressantes.

Notre étude innovatrice s'appuie sur les travaux de Korpimäki (1985) et Korpimäki et Norrdahl (1989, 1991) qui ont déjà démontré des comportements et des effets semblables de la part des oiseaux prédateurs habitant la taïga de Fennoscandie. Par contre, en combinant des résultats détaillés sur la propension aux déplacements (chapitre 3), la pression de prédation effectuée par les espèces au sommet du réseau trophique (chapitre 1) et l'impact d'un apport en ressources allochtones (chapitre 5), on arrive par contre à peu d'études similaires témoignant de résultats comparables. En effet, bien peu d'études ont tenté de mesurer à la fois les mécanismes et leurs impacts sur la dynamique d'un écosystème entier. On peut par contre faire un parallèle avec le loup (*Canis lupus*) qui est connu pour sa capacité à réguler les populations de grands herbivores tels que l'orignal (*Alces alces*) ou le wapiti (*Cervus canadensis*) et dont les mécanismes ont été étudié en détails (McLaren et Peterson 1994, Ripple *et al.* 2001). Par contre, cette régulation semble se faire de façon différente, c'est-à-dire sur une échelle spatiale réduite et avec un délai dans la réponse numérique des prédateurs. On peut donc supposer qu'un contrôle par le haut pourrait s'appliquer aux systèmes où les prédateurs sont mobiles et démontrent de fortes réponses aux variations d'abondance de leurs proies principales. Ainsi, il serait intéressant de voir si différents prédateurs démontrant un fort potentiel de mobilité comme certaines espèces de tortues marines et/ou de requins par exemple, pourraient limiter ou même réguler leurs proies, et évaluer comment elles pourraient le faire.

Apport de subsides allochtones

L'apport de ressources allochtones a été démontré comme étant un élément important dans le fonctionnement de plusieurs écosystèmes (Huxel *et al.* 2002, Loreau *et al.* 2003), quoique ce phénomène demeure encore relativement peu étudié ou pris en compte. Dans la toundra, le renard arctique est un prédateur opportuniste bien connu pour utiliser des ressources provenant de l'écosystème marin (Roth 2002, 2003, Tarroux 2011) ou transporté du sud par les oiseaux migrateurs (Giroux *et al.* 2012). Par contre, jusqu'à tout récemment, le renard semblait être un cas

isolé et l'unique utilisateur de ressources allochtones dans la toundra. En documentant ce comportement chez le harfang des neiges (chapitre 5), nous démontrons ainsi que ce phénomène pourrait être plus répandu qu'on ne le croyait chez les prédateurs arctiques. En effet, suite à la publication de nos résultats (Therrien et al. 2011), des chercheurs travaillant sur la côte ouest du Groenland ont rapporté des comportements similaires chez le faucon gerfaut (*Falco rusticolus*, Burnham et Newton 2011). En ajoutant les labbes au palmarès, eux qui se nourrissent en mer pendant l'hiver (Wiley et Lee 1998, 1999), mais qui consomment d'énormes quantités de proies terrestres pendant la saison estivale, on se rend compte que la plupart des prédateurs du milieu terrestre arctique ont recours à des ressources marines pendant une partie significative de leur cycle vital. Ce phénomène semble donc particulièrement important dans les écosystèmes démontrant une faible productivité primaire comme la toundra et pourrait contribuer à renforcer le pouvoir de régulation de ces prédateurs sur les populations de petits mammifères pendant la saison estivale (chapitre 1). Il n'est pas surprenant, après mûre réflexion, de trouver qu'un apport de ressources externes ait un effet majeur dans un système où l'abondance de ressources autochtones est justement très limitée. Ce type de comportement (utilisation de ressources allochtones) pourrait donc être beaucoup plus répandu qu'on le croit (Gauthier *et al.* 2011), non seulement dans la toundra mais ailleurs également, et avoir des répercussions importantes sur le fonctionnement de plusieurs écosystèmes.

Message final et apport de la thèse

Pour conclure, cette thèse présente des résultats contribuant à une meilleure compréhension des relations prédateurs-proies. Les résultats suggèrent que le potentiel de mobilité et les fortes réponses numériques et fonctionnelles peuvent avoir une importance capitale sur le rôle des oiseaux prédateurs dans l'écosystème terrestre arctique. En intégrant différentes approches issues de l'étude des relations prédateurs-proies, des déplacements irruptifs et des composantes biodémographiques, j'ai apporté différentes perspectives sur les comportements et l'impact des oiseaux prédateurs de la toundra arctique sur les populations de proies. Au-delà de ces résultats, mon travail ouvre des avenues de recherche intéressantes. Parmi celles-ci, une expérience de manipulation de la prédation aviaire et/ou des apports allochtones sur la dynamique des populations de proies, l'étude des déplacements et de l'utilisation de l'espace par des espèces

prédatrices moins connues (la buse pattue par exemple), l'étude des mécanismes proximaux (physiologiques) utilisés par les oiseaux prédateurs pour les guider dans leurs déplacements et la sélection du site de nidification ou la quantification de l'importance des ressources marines dans le régime alimentaire et le bilan énergétique annuel des prédateurs terrestres arctiques en sont quelques-unes qui revêtent un intérêt particulier.

En terminant, mon étude s'est attardée longuement à l'écosystème terrestre arctique. Cet écosystème semble très vulnérable aux altérations d'origine anthropique en général et aux changements climatiques en particulier. Bien que ces perturbations soient susceptibles d'influencer grandement son équilibre (Harrington *et al.* 1999, ACIA 2005, Ims & Fuglei 2005), les prédictions quant à leurs impacts restent très spéculatives (voir par exemple le chapitre 5). Les résultats de la présente thèse permettront ainsi, je l'espère, d'aider à mieux appréhender les risques potentiels encourus et à guider les décisions liées à la gestion des ressources fauniques.

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Annexe 1

# Taux de consommation des prédateurs aviaires en fonction de l'abondance de lemmings (espèces combinées)
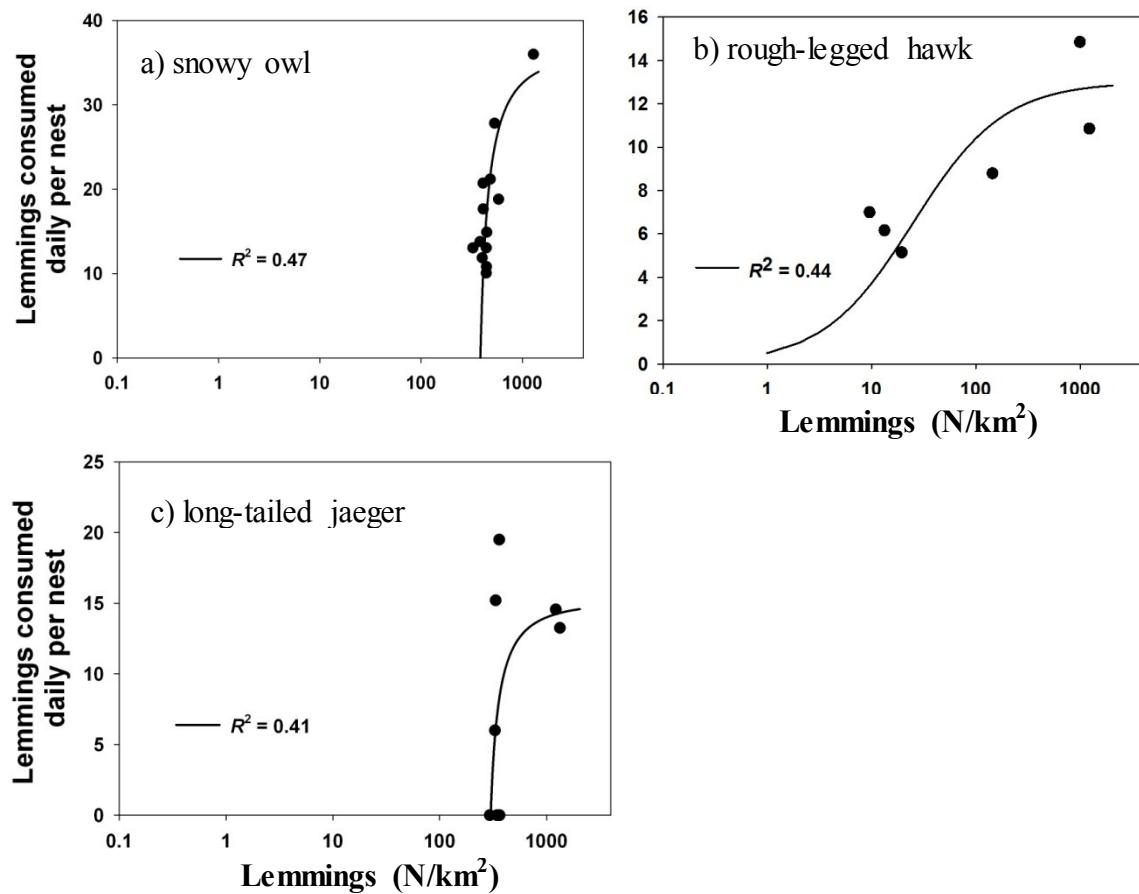
Figure 1. Daily consumption rate by breeding pairs of the main avian predators in relation to daily small mammal density (both species combined) on Bylot Island, Canada, 2007 – 2010.

Annexe 2

Schematic representation of turn angles used to separate between directional and exploratory movements
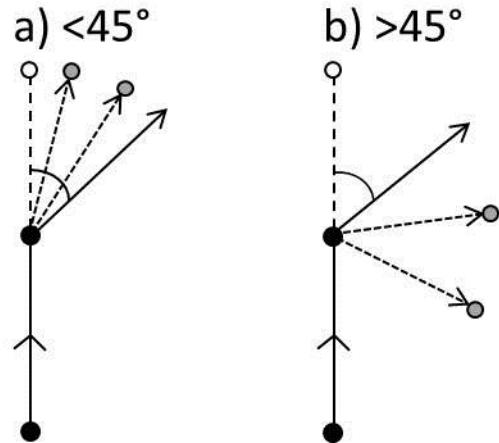
Figure 1. Schematic representation of turn angles used to separate between a) directional and b) exploratory movements of snowy owls marked with satellite transmitters. Black dots represent actual locations of individuals. White dots represent hypothetic locations at exactly 0° (no turn) and gray dots represent hypothetic locations at less (a) or more (b) than 45°.

Annexe 3

Graphiques d'analyses du temps de premier passage (*first-passage time – FPT*) des harfangs des neiges suivis par télémétrie satellite
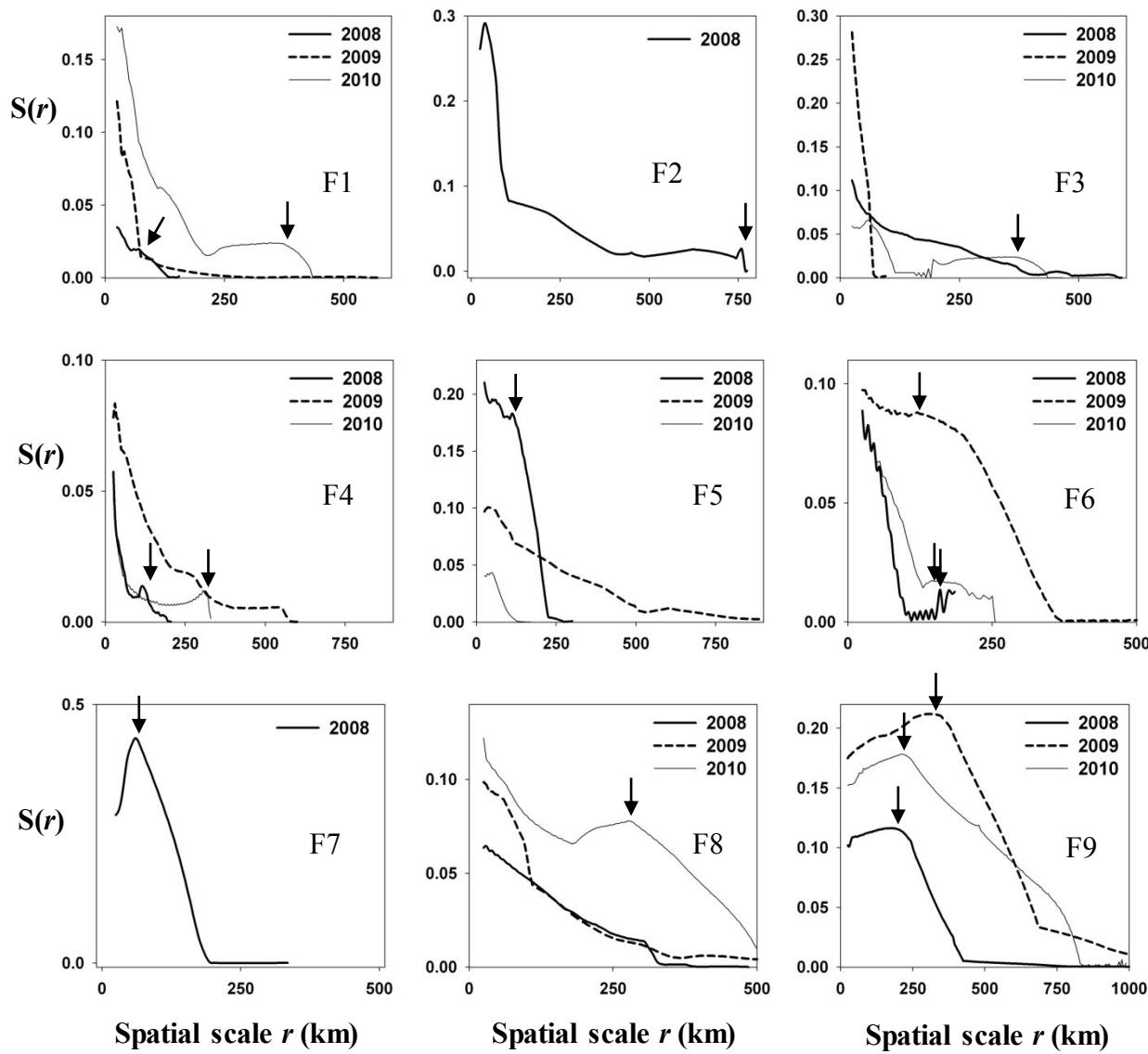
Figure 1. Plots of variance in first-passage time (S(*r*)) in relation to radius *r* during spring exploratory movements of nine adult female snowy owls marked with satellite transmitters on Bylot Island, NU, Canada in 2007 and tracked for up to 3 years. Arrows indicate search area.