

NICOLAS LECOMTE

**RISQUE DE PRÉDATION, HÉTÉROGÉNÉITÉ DE
L'HABITAT ET FIDÉLITÉ AU SITE DE
REPRODUCTION :**
le cas de la Grande Oie des neiges dans le Haut-Arctique

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Résumé succinct

L'objectif de cette thèse est d'examiner les liens entre la dynamique prédateurs-proies, les stratégies de reproduction et la structure spatiale des colonies chez la Grande Oie des neiges (*Chen caerulescens atlantica*). Nous montrons que les habitats humides peuvent fournir des refuges aux oies car leur structure réduit la vitesse d'attaque des nids par les renards arctiques (*Alopex lagopus*). À l'aide d'approches empiriques et expérimentales, nous démontrons que la disponibilité en eau serait un déterminant majeur du succès de nidification via un mécanisme où la distance d'éloignement du nid pour boire module le risque de prédation. Nous avons également trouvé que les oies montrent une fidélité modérée au site spécifique de nidification mais une forte préférence pour nicher dans les milieux humides. Enfin, nous avons détecté une structure génétique à une échelle spatiale fine (quelques kilomètres) entre les sites d'élevage des jeunes mais pas de structure sur la base des sites de nidification à l'intérieur de la colonie. Tout en soulignant l'importance de travailler à différentes échelles spatiales et temporelles, notre travail démontre comment des mécanismes prédateurs-proies subtils peuvent influencer la stratégie de reproduction des oiseaux.

Résumé long

L'objectif de cette thèse est d'examiner les liens entre la dynamique prédateurs-proies, les stratégies de reproduction et la structure spatiale des colonies chez la Grande Oie des neiges (*Chen caerulescens atlantica*) nichant dans le Haut Arctique canadien. Nous avons récolté les données de 2002 à 2005 et exploité certaines bases de données recueillies antérieurement sur l'Île Bylot (Nunavut, Canada). Nous avons identifié des mécanismes pouvant expliquer des différences dans le succès de nidification entre deux types de milieux. Nous avons d'abord montré que les habitats humides peuvent fournir des refuges contre la prédation car leur structure réduirait le succès de chasse de renards arctiques (*Alopex lagopus*; le principal prédateur des oies) en limitant leur vitesse d'attaque des nids. De plus, la qualité de tels refuges varierait en fonction du cycle de lemmings, la principale proie de ce prédateur. La disponibilité en eau serait également un déterminant majeur du succès de nidification. Les femelles augmentent leur risque de prédation lorsqu'elles quittent leur nid pour boire, un élément critique en milieu mésique où l'accès à l'eau est limité. En manipulant expérimentalement la disponibilité en eau, nous avons observé une augmentation du succès de nidification de plus de 20% par rapport à des nids témoins. De plus, nous montrons une relation positive entre l'abondance des pluies et le succès, la présence de mares d'eaux formées par la pluie à proximité des nids réduisant le risque de prédation sur les nids. Nous avons également trouvé que les oies montrent une fidélité modérée au site spécifique de nidification, probablement en réponse aux variations dans les patrons d'enneigement au printemps et le faible coût de changement de site sur le succès de nidification. Par contre, les oies seraient fidèles à l'échelle des habitats, les milieux humides étant favorisés pour leurs avantages en termes de risques de prédation. Enfin, nous avons détecté une structure génétique à une échelle spatiale fine (quelques kilomètres) entre les sites d'élevage des jeunes mais pas de structure sur la base des sites de nidification à l'intérieur de la colonie. Tout en soulignant l'importance de travailler à différentes échelles spatiales et temporelles, notre travail démontre comment des mécanismes prédateurs-proies subtils peuvent influencer la stratégie de reproduction des oiseaux.

Abstract

The main objective of this thesis is to examine factors linking predator-prey relationships, breeding strategies and spatial structure inside colonies of greater snow geese (*Chen caerulescens atlantica*). We collected data from 2002 to 2005 and used some data collected in previous years at Bylot Island (Nunavut, Canada). We first explored how predation, the main determinant of nesting success, was affected by habitat heterogeneity. We showed that wetlands could provide refuges for geese because polygon-patterned grounds decrease travel speed and success of their main predator, the arctic fox (*Alopex lagopus*). The quality of these refuges varied according to the lemming cycle (the main prey of foxes) with foxes feeding on goose eggs during years of low lemming abundance. Our study also demonstrated that water availability is a major determinant of goose nesting success. First, geese nesting in mesic tundra experienced higher predation risks than those nesting in wetlands due to limited availability of water. Second, by experimentally manipulating water availability, we recorded a 20% increase of nesting success relatively to control nests. Third, we showed a positive relationship between rainfall abundance and nesting success. Nests were less exposed to predators because females were able to reach nearby water holes resulting from recent rainfall accumulation. We found a low fidelity to a specific nesting site, which could result from variable patterns of spring snow-melt and the limited consequences of changing sites. Nonetheless, geese showed fidelity towards habitat type yet geese nest preferentially in wetlands where they experienced lower predation risks. Finally, we explored how dispersal strategies could determine patterns of population genetic structure. We detected a fine-scale genetic structure (few km) among rearing sites but not among nesting sites inside the colony. To conclude, this thesis provides a framework to understand population dynamic and distribution by using multiple-scale analyses of mechanisms driving predator-prey relationships.

Avant-propos

Cette thèse commence par une introduction générale suivie par 5 chapitres principaux 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 nouent le fil conducteur liant l'ensemble des chapitres. Bien que je sois l'auteur principal de tous les chapitres, Gilles Gauthier (directeur de thèse) et Jean-François Giroux (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. De la même façon, Louis Bernatchez (membre du comité) a aidé à toutes les étapes des Chapitres 4 et 5. De plus, Vincent Careau a participé au Chapitre 2 par son implication sur le terrain et dans la rédaction. Le Chapitre 1 a été soumis pour publication à la revue *Journal of Animal Ecology* et le Chapitre 3 a été accepté dans *Oecologia*. Quant aux Chapitres 2 et 4, ils seront soumis sous peu aux revues *Ecology Letters* et *Nature*, respectivement. Enfin, le Chapitre 5 a été publié dans la revue *Journal of Field Ornithology*.

En plus des chapitres officiels de la thèse, je voudrais souligner l'existence d'autres articles et manuscrits en lien direct avec ce projet. Notamment, les deux premiers chapitres du mémoire de maîtrise de Vincent Careau pour lesquels j'ai eu un rôle dans l'élaboration, la prise de données, l'analyse et la rédaction. Le premier a été publié dans la revue *Journal of Ethology* et l'autre a été soumis à la revue *Ecoscience*. Également, j'ai eu l'occasion et la chance de superviser Cassandra Cameron pour son initiation à la recherche qui a abouti à la rédaction d'un manuscrit à soumettre à *Wildlife Biology*. Enfin, j'ai pu aussi m'impliquer dans le projet de Marie-Andrée Giroux, en particulier dans les analyses et la rédaction d'un chapitre de sa maîtrise qui devrait être soumis à la revue *Ecology*.

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dont les efforts ont contribué à l'initiation et à l'achèvement de cette étude. En écologie, la recherche est bien loin du modèle avec un chercheur isolé mais tend plutôt à fonctionner selon un modèle s'apparentant à un écosystème où les chercheurs interagissant à de multiples niveaux et augmentant la valeur de leur recherche en favorisant la richesse et la diversité des idées partagées.

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À la rondeur des jours et de la vie

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FIGURE 1. A. Geographical locations of the wintering, staging and breeding areas of greater snow geese (*Chen caerulescens atlantica*) in North America, including the locations of genetic sampling on Bylot Island and on Akimiski Island (1; breeding area of lesser snow geese (*Chen caerulescens caerulescens*)). B. Location of major nesting (dark gray) and brood-rearing (light grey) areas of greater snow geese on Bylot Island (drawn from information in Reed *et al.* (2002) and G. Gauthier, unpubl. data). The main colony is also used as a brood-rearing area by some birds. Geese nesting in the Qarlikturvik valley typically nest in association with snowy owls (*Bubo scandiacus*) only in years of peak lemming abundance. The black arrows show movements of birds between their nesting and brood-rearing areas as inferred by our genetic analyses of birds sampled both on the nesting and brood-rearing sites (see Results). White circles indicated locations of the three sampling nesting sites.97

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FIGURE 3. F_{ST} variation as a function of dispersal rates in both sexes for simulations with $N_e = 1500$. Mean values \pm SE of F_{ST} are obtained after 100 simulations in the software EASYPOP (Balloux, 2001). The dotted line (1) indicates the level of F_{ST} measured for females in our system and (2) the level where F_{ST} is not significantly different from 0 with an alpha threshold of 5%. The shaded square shows the range of dispersal values for males of this species reported in the literature (Rockwell & Cooke, 1977).99

CONCLUSION

FIGURE 1. Schéma conceptuel simplifié représentant l'effet de refuge résultant de la complexité de l'habitat (barrière) sur la prédation du renard arctique ainsi que l'effet limitant de l'eau sur le succès reproducteur des oies, bénéficiant tant au renard qu'aux prédateurs aviaires (e.g. labbe parasite). On suppose ici que l'habitat n'affecte pas la prédation sur le lemming. 120

ANNEXE 2

FIGURE 1. Localisations des sessions de baguages et des sites de nidification où nous avons effectué les prélèvements sanguins respectivement d'adultes et d'embryons. 147

Introduction

L'ensemble des facteurs limitant la répartition et l'abondance des organismes vivants constitue une question centrale de l'écologie depuis les tous débuts de cette science. Appliquée aux populations, cette question intègre une dimension supplémentaire, soit la dynamique démographique et spatiale (Hanski, 1994). Cette dynamique est la résultante de quatre facteurs fondamentaux déterminés par l'ensemble des individus au sein des populations ou entre elles, soient le taux de reproduction, de survie et de dispersion (émigration et immigration). Ainsi, la dispersion est une composante biodémographique centrale en écologie et par extension est largement utilisée dans de nombreuses études de conservation et de gestions de population (e.g. MacDonald & Johnson, 2001), notamment par son effet sur la dynamique des populations (Greenwood & Harvey, 1982; Johnson & Gaines, 1990) mais aussi sur la structure de leur variance génétique (Slatkin, 1985; Ross, 2001).

La dispersion est ici définie comme le processus provoquant le changement de sites entre deux événements de reproduction consécutifs (dispersion de reproduction) ou bien entre le site de naissance et celui où la première tentative de reproduction aura lieu (dispersion natale) (Greenwood, 1980; Greenwood & Harvey, 1982). Le complément de la dispersion est ainsi la fidélité ou philopatrie, i.e. le comportement de retour à un site de naissance ou de reproduction précédente pour se reproduire. Le processus de dispersion peut être décomposé en trois phases : le départ d'un site, le transit et l'arrivée à un site. Nous ne parlerons pas du transit dans cette thèse mais plutôt des effets interagissant avec les décisions d'installation et de départ d'un site de reproduction. Ici, il faut également différencier la dispersion de la migration. En effet, alors que le premier processus lie les événements successifs de reproduction entre les années, le second est en fait un mouvement saisonnier des individus entre des sites de reproduction et de non-reproduction (e.g. site

d'hivernage ou de mue). Il faut aussi souligner que le terme « migration » en écologie moléculaire a un sens tantôt englobant les deux définitions données plus haut, tantôt restrictif en référant uniquement au résultat de la dispersion en termes de brassage génétique. C'est ce dernier sens que j'utiliserai dans le chapitre traitant de génétique (voir plus bas).

Malgré son rôle clé en écologie, l'étude de la dispersion a souffert d'un manque de données empiriques, surtout dû à des difficultés logistiques (Koenig, Van Vuren & Hooge, 1996) et à un manque de méthodologies adéquates tant au niveau démographique (revue dans Nichols, 1996; Blums *et al.*, 2003) que génétique (e.g. Sunnucks, 2000). Les quinze dernières années ont toutefois vu naître plusieurs initiatives d'envergure visant à étudier les déplacements des individus, ainsi que des méthodes d'analyses dérivées des modèles de capture-recapture et de marqueurs génétiques hypervariables. Malgré cela, les mécanismes de dispersion et ses conséquences en termes spatiaux sont encore mal appréhendés (Wiens 2001).

Il existe trois grandes forces guidant l'évolution de la dispersion, soient les interactions d'apparentement (évitement ou interaction préférentielle des apparentés), la compétition pour les ressources (nourriture, territoire, partenaire) ainsi que l'hétérogénéité spatio-temporelle de l'environnement (présence de prédateurs, qualité de la nourriture, type de végétation) (Clobert *et al.*, 2001). Parmi ces forces, l'hétérogénéité semble de plus en plus déterminante pour comprendre les causes proximales de la dispersion dues aux contraintes environnementales (e.g. nourriture, prédation) et propres à l'individu (e.g. condition physique) (Ims & Hjermann, 2001; Ims & Andreassen, 2005). Dans ce contexte, les hypothèses abordant le thème de la dispersion partagent des prédictions avec celles issues des modèles de sélection et d'utilisation d'habitat, en particulier, celles des modèles de distribution idéale (Fretwell & Lucas, 1970; Fretwell, 1972; Rosenzweig, 1991). À l'intérieur de ce cadre théorique, la distribution des individus résulte d'un comportement basé sur une maximisation de la valeur sélective. Bien que les modèles de distribution idéale reposent sur des axiomes peu ou pas observables en nature (e.g. connaissance parfaite des conditions à tout moment, aucun coût de dispersion), l'hypothèse de maximisation de la valeur sélective est abondamment utilisée dans les études de dispersion.

Cette hypothèse de maximisation sous-entend le fait que les individus sont capables d'estimer les variations de valeurs sélective dans l'espace, notamment via des indices directement reliés à la valeur sélective (e.g. Reed *et al.*, 1999). Chez la plupart des espèces animales, le succès reproducteur individuel semble être l'indice le plus utilisé dans les décisions de dispersion (Switzer, 1993, 1997). Par exemple, la prédation des nids semble un facteur majeur de dispersion chez les oiseaux, les reproducteurs quittant les habitats présentant un fort risque de prédation vers les habitats à plus faibles risques (Rosenzweig, 1981; Martin, 1995; Fontaine & Martin, 2006). D'autres indices de la valeur sélective sont également possibles, comme les facteurs propres d'hétérogénéité de l'habitat (présence de prédateurs, qualité de la nourriture, type de végétation) et l'information publique (présence de conspécifiques, succès reproducteurs des voisins) (revue détaillée dans Doligez *et al.*, 2003).

Pour finir, il faut souligner l'importance de l'échelle à laquelle les études examinent la dispersion et l'utilisation de l'habitat (Wiens, 1973, 1989; Kotliar & Wiens, 1990; Orians & Wittenberger, 1991). En effet, que la dispersion soit importante ou non, elle s'exprime toujours relativement à un site donné. Il reste alors à savoir ce que signifie le « site » en question; cette définition est d'ailleurs souvent arbitraire et variable d'une étude à l'autre, limitant les comparaisons inter et intraspécifiques. De plus, il faut être conscient de la limite géographique des études des mouvements des individus. Cette limite va en effet contraindre les distances maximales auxquelles les individus sont susceptibles d'être détectés et la distribution des distances présentera une forme leptokurtique typique résultant, entre autre, d'une décroissance des probabilités de détections des individus avec la distance. Au-delà de ces limitations méthodologiques, il faut d'abord détecter l'échelle à laquelle s'exprimeront les principales contraintes à la dispersion (e.g. la prédation) et ensuite mettre en relation ces contraintes avec les patrons de dispersion observés à l'échelle appropriée, dans les limites physiques de l'aire d'étude. C'est dans ce cadre que je place ma thèse, en abordant d'abord la dispersion à fine échelle dans le contexte des interactions prédateurs-proies en lien avec l'hétérogénéité spatiale et temporelle de l'environnement à différentes échelles, puis en examinant les conséquences de la dispersion sur la structure génétique des populations pendant la période de reproduction.

Interaction prédateurs-proies et habitat

Les interactions prédateurs-proies peuvent être déterminantes dans la compréhension des patrons de dispersion et de distribution des populations. Les proies tendent en effet à disperser en fonction des risques de prédation et les prédateurs se déplacent à leur tour en fonction de leurs proies (revue par Weisser, 2001). Dans cette thèse, je ne traite pas directement des effets du mouvement des proies sur leurs prédateurs mais je me concentre plutôt sur la compréhension des patrons de dispersion des proies dans un paysage où le risque de prédation est variable.

La notion d'hétérogénéité de l'habitat prend toute son importance dans les modèles de stabilité des relations prédateurs-proies (e.g. Murdoch & Oaten, 1975; Caswell, 1978; Holt, 1984; McNair, 1986). Au sein d'un paysage hétérogène, certains types d'habitat peuvent ainsi présenter des refuges contre les prédateurs pour la proie, par exemple à cause de la structure physique intrinsèque du milieu qui limite le succès de chasse des prédateurs (e.g. Dickman, 1992; Beukers & Jones, 1997) ou encore par la présence d'espèces agressives qui protègent un territoire où les prédateurs sont exclus (revue par Haeming, 2001). De plus, des différences de valeur sélective entre les refuges (e.g. limitation partielle ou exclusion totale des prédateurs) peuvent aussi avoir une grande influence sur le sens de la dispersion des proies. Dans cette thèse, l'emphase sera placée surtout sur les refuges qui ont seulement un effet de limitation partielle de la prédation afin de comprendre les mécanismes qui peuvent faire varier la valeur des refuges. De plus, la valeur d'un refuge peut varier grandement selon la communauté de prédateurs en cause (Hogstad, 1995; Schmidt & Whelan, 1998). Par exemple, ceci peut se produire si la structure du milieu joue un rôle de filtre variable en fonction du type de moyen de locomotion utilisé par les prédateurs (Schmidt, 1999). Ces approches à prédateurs multiples se retrouvent majoritairement dans les études utilisant les systèmes aquatiques (e.g. Huang & Sih, 1991; Warfe & Barmuta, 2004) et sont encore peu nombreuses en écologie terrestre (Schmidt, 1999).

Même si les refuges sont la plupart du temps appréhendés pour leur qualité intrinsèque dans le cadre théorique des interactions trophiques directes, celle-ci peut également varier en fonction de l'abondance des autres proies utilisées par les prédateurs via un mécanisme de

changement de proie consommée. Ainsi, lorsqu'une proie A diminue en abondance, une augmentation de la prédation sur une proie B est possible, et inversement lorsque la proie A devient plus disponible (Hogstad, 1995; Abrams & Matsuda, 1996; Schmidt, 1999). Dans les systèmes terrestres, de telles interactions trophiques indirectes ont été peu étudiées (Abrams & Matsuda, 1996; Bêty *et al.*, 2001) et encore moins dans un contexte de complexité de l'habitat.

Dispersion et structure des populations

En milieu naturel, l'organisation spatiale des populations a un impact important sur la dynamique démographique mais aussi sur les changements évolutifs. La dispersion joue un rôle clé dans cette organisation car son intensité détermine en grande partie le lien entre les populations (Hanski, 2001; Hanski & Gaggiotti, 2004). Ce mécanisme est central aux approches méta-populationnelles et de biologie de la conservation, notamment en ce qui a trait à la fragmentation (Schitckzelle, Mennechez & Baguette, 2005). D'un point de vue évolutif, le flux de gènes résultant de la dispersion peut déterminer en grande partie l'homogénéisation ou bien l'isolation génétique des populations entre elles (e.g. Slatkin, 1985; Bohonak, 1999; Ross, 2001). Ainsi, la dispersion est surtout vue comme une force qui peut contrer les effets de dérive génétique et de la consanguinité, en particulier en jouant sur la taille effective des populations, et par la même occasion limiter la différenciation génétique (Slatkin, 1985; Lenormand, 2002). C'est pourquoi les animaux avec de grandes capacités de dispersion (e.g. les grands mammifères carnivores, les oiseaux migrateurs) sont souvent considérés comme ayant un faible potentiel de structuration génétique (voir revue dans Bohonak, 1999; Pilot *et al.*, 2006). Ces idées ont toutefois été remises en question car des études récentes ont démontré que la différenciation génétique des populations peut être rapide et forte à fine échelle spatiale même en présence de taux de dispersion non-négligeable si la dispersion est directionnelle (Garant *et al.*, 2005; Postma & vanNoordwijk, 2005). C'est dans ce contexte de nouvelles explorations du lien entre structures génétiques et spatiales que je situe mon travail de doctorat.

En milieu naturel, une fidélité à un site de reproduction qui diffère entre les sexes peut créer un patron de structuration génétique des populations à fine-échelle spatiale (Sugg *et al.*,

1996; Coltman, Pilkington & Pemberton, 2003). Plusieurs hypothèses sont avancées pour expliquer un tel phénomène. La compétition pour les ressources et les partenaires ainsi que les effets de la consanguinité peuvent varier de façon importante entre les sexes (Greenwood, 1980; Chesser, 1991; Queller, 1994). Malgré les divergences entre ces hypothèses, les mécanismes d'appariement (e.g. période d'appariement et choix du partenaire) semblent être étroitement liés aux biais de dispersion entre les sexes (Greenwood, 1980), notamment afin d'éviter les coûts potentiels de consanguinité que pourrait entraîner une philopatrie similaire pour les deux sexes (Chesser, 1991). Chez les mammifères, les mâles dispersent plus que les femelles qui ont tendance à former des regroupements matrimoniaux dont les liens sociaux sont durables. Par contre, chez les oiseaux, les femelles sont généralement beaucoup moins philopatriques que les mâles, avec comme résultat que ceux qui occupent des territoires voisins sont souvent étroitement apparentés (Greenwood, 1980; Greenwood & Harvey, 1982). Le nombre d'études de structure génétique liant les mécanismes d'appariement et les biais de dispersion est grandissant mais il existe encore peu de données portant sur des espèces aux systèmes sociaux peu développés (e.g. Coltman, Pilkington & Pemberton, 2003) et présentant des patrons de dispersion différents de la norme (e.g. forte dispersion des mâles chez les Anserinae).

Objectifs de la thèse

Dans cette thèse, mes objectifs sont d'examiner l'effet des relations prédateurs-proies ainsi que l'hétérogénéité spatio-temporelle de l'habitat sur la dispersion d'un oiseau herbivore nichant dans le Haut-Arctique. Mon plan d'attaque de cette problématique vise d'abord à comprendre les variations du risque de prédation au nid, tant du point de vue des prédateurs que des proies, à plusieurs échelles spatiales et temporelles. Dans ce contexte de risque de prédation, j'examine ensuite le déterminisme des patrons de dispersion de reproduction. Afin d'élargir davantage la portée de ces résultats, j'explore les conséquences des processus de dispersion, en terme de structure spatiale et génétique, sur la distribution des individus à de multiples échelles spatiales. Ainsi, ma thèse intègre différents niveaux d'analyses des

relations trophiques et des stratégies individuelles, éléments déterminants de la dynamique des populations et des écosystèmes.

Modèle d'étude

La Grande Oie des neiges (*Chen caerulescens atlantica*) est l'espèce centrale de cette thèse. Plusieurs facteurs font de cette espèce un modèle intéressant afin de mesurer les patrons de dispersion d'un oiseau et leurs mécanismes sous-jacents.

C'est d'abord une espèce longévive et itéropare, ce qui permet de suivre les événements de reproduction consécutifs d'un même individu sur plusieurs années. Cette espèce effectue également un seul événement de reproduction par année, i.e aucune seconde couvée au cours de la période de reproduction. Cette caractéristique permet ainsi l'étude de la dispersion sur une base annuelle uniquement, qui ne confond donc pas dispersion saisonnière et annuelle. Comme chez l'ensemble des Anserinae (oies-bernaches-cygnes), cette espèce est dite monogame avec des liens intra-couple durables (Mowbray, Cooke & Ganter, 2000; Demers *et al.*, 2003), ce qui fait que les stratégies d'utilisation d'habitat de reproduction ne seront que très peu biaisées par la relocalisation des individus divorcés. Un autre biais possible pourrait être la relocalisation d'individus dont le partenaire est mort mais la survie annuelle des adultes est relativement élevée (env. 83%, Gauthier *et al.*, 2001), ce qui limite encore l'effet de ce paramètre sur l'évaluation des patrons de dispersion. Enfin, comme beaucoup d'autres espèces d'oiseaux (Lima & Dill, 1990; Fontaine & Martin, 2006), la prédation aux nids cause en grande partie les échecs de nidification de la Grande Oie des neiges (Bêty *et al.*, 2001), ce qui limite les autres effets potentiels (e.g. condition des individus, parasitisme) et facilite la compréhension des patrons de succès de nidification et de dispersion.

La Grande Oie des neiges est aussi une espèce nidifuge (i.e. les jeunes quittent le nid peu de temps après l'éclosion); il existe donc un découplage spatial et temporel entre le site de nidification et le site d'élevage (e.g. Mainguy *et al.*, 2006), et une dynamique fort différente au niveau de l'utilisation de l'habitat durant ces deux phases de la reproduction. Cette caractéristique segmente également la détermination du succès reproducteur en succès de

nidification et succès à l'envol. Étant donné la forte influence du succès de nidification sur le succès reproducteur (Lepage, Gauthier & Menu, 2000), je peux utiliser avec confiance le succès de nidification (départ d'au moins un jeune du nid) comme base aux idées de modèles optimaux d'utilisation d'habitat.

La simplicité du réseau trophique de la toundra arctique, dans lequel l'oie joue un rôle d'herbivore important (Gauthier *et al.*, 2004), offre l'avantage d'un nombre limité d'acteurs, facilitant la mesure des mécanismes impliqués, notamment des relations prédateurs-proies. Ainsi, par ordre décroissant d'importance, les principaux prédateurs d'œufs des oies sont le Renard arctique (*Alopex lagopus*) et les prédateurs aviaires tels le Labbe parasite (*Stercorarius parasiticus*), le Goéland bourgmestre (*Larus hyperboreus*) et le Grand corbeau (*Corvus corax*) (Bêty *et al.*, 2002). À cet assemblage, il faut ajouter la présence d'une autre proie herbivore essentielle aux prédateurs de cet écosystème, les lemmings. J'utiliserai leurs fluctuations d'abondance comme principale source de variation temporelle du risque de prédation des oies pour comprendre la réponse des prédateurs dans le temps et dans l'espace.

À cause d'une forte croissance démographique de la population de la Grande Oie des neiges depuis 30 ans (Gauthier *et al.*, 2005), les sites de reproduction subissent une pression de broutement accrue. À de nombreux endroits dans l'Arctique, les oies sont les herbivores les plus abondants et ceux ayant le plus d'impact sur la végétation de ces habitats fragiles (Gauthier, Rochefort & Reed, 1996). Dans le Haut-Arctique, l'habitat utilisé principalement par les oies durant la reproduction présente une dichotomie intéressante, prémisse d'une expérience dans un contexte naturel: d'une part, on retrouve les milieux humides, à la structure topographique complexe, tourmentée par les coins de glace, riches en source d'eau potable comme des étangs et en nourriture préférée par les oies (Gauthier, Rochefort & Reed, 1996; Lepage, Gauthier & Reed, 1996; Fortier & Allard, 2005). D'autre part, on a les milieux dits mésiques (i.e. relativement bien drainés) où les accidents topographiques sont limités, les sources d'eau restreintes à quelques lacs et étangs et la végétation relativement pauvre en espèces préférées par les oies.

Enfin, la concentration de la Grande Oie des neiges sur l'Île Bylot (Reed, Hughes & Boyd, 2002) en fait un terrain de choix pour tester des hypothèses nécessitant un fort taux de recapture visuelle et une taille d'échantillon importante. Le paysage de toundra arctique de ce lieu facilite également cette approche, notamment pour l'ouverture du milieu qui facilite l'observation à grande distance et une visibilité continue sur 24 h du au soleil de minuit permettant des observations du comportement des prédateurs même la nuit.

Organisation de la thèse

Les deux premiers chapitres sont intimement reliés car ils permettent de comprendre les principaux facteurs responsables des variations spatiales et temporelles du risque de prédation présent au sein des colonies de la Grande Oie des neiges. Le premier chapitre traite cet aspect du point de vue des prédateurs en testant l'hypothèse que la complexité de l'habitat diminue l'efficacité de certains prédateurs et par là-même crée un refuge pour la proie. En incorporant des approches dérivées de la théorie de l'approvisionnement avec une approche centrée sur la structure de l'habitat, j'évalue les variations temporelles et spatiales du risque de prédation. En particulier, je contraste le rôle des deux types de prédateurs (renards vs oiseaux) à l'échelle des habitats, une comparaison encore peu abordée dans les études de relations prédateurs-proies (Schmidt, 1999).

Dans le deuxième chapitre, j'aborde le risque de prédation cette fois-ci du côté de la proie (oeufs d'oies au nid). L'élément-clé est le comportement de la proie par l'entremise de la distance d'éloignement des oies de leurs nids lors des pauses d'incubation, moment où la majorité de la prédation se produit (Cooke, Rockwell & Lank, 1995; Bêty *et al.*, 2001). Bien que de nombreuses études sur les oies aient montré l'importance de l'alimentation durant ces pauses (e.g. Thompson & Raveling, 1987; Afton & Paulus, 1992; Reed, Hughes & Gauthier, 1995), je présente ici des évidences inédites du rôle-clé de la disponibilité de l'eau pour le succès de nidification. Pour ce faire, j'utilise des contrastes naturels en termes d'abondance d'eau durant l'incubation (milieux de nidification humides vs mésique, années plus ou moins pluvieuses) mais aussi je manipule la disponibilité de l'eau à proximité des nids. Ce chapitre me permet de développer un aspect très peu connu de l'effet de l'eau dans ces écosystèmes.

Le troisième chapitre me permet de placer les résultats des chapitres précédents dans le contexte de la dispersion de reproduction des femelles de la Grande Oie des neiges. J'examine ainsi comment l'hétérogénéité de l'habitat et le succès reproducteur influencent les patrons de dispersion d'individus marqués. L'échelle d'analyse est cruciale lorsque l'on travaille sur l'utilisation de l'habitat et la fidélité au site (Greenwood & Harvey, 1982; Wiens, 1989). J'aborde la dispersion à l'échelle du site précis de nidification (distance euclidiennes entre nids d'une année sur l'autre) ainsi qu'à l'échelle des habitats, notamment via l'utilisation de modèles multi-états de capture-recapture. Plusieurs études soulignent le manque de données empiriques pour comprendre des effets combinés sur le comportement de dispersion (e.g. Clobert *et al.*, 2001; Cam *et al.*, 2004), et ce chapitre vise justement à explorer ces nouvelles avenues.

Le quatrième chapitre vise à comprendre l'impact de la dispersion dans la structure génétique et spatiale des colonies d'oies à Bylot. Mon objectif est de montrer à quel point les structures observées peuvent être dynamiques selon le moment de la reproduction et d'explorer des modèles pouvant expliquer les patrons observés. De la même façon qu'au chapitre précédent, je tiens à souligner l'importance de l'échelle à laquelle l'étude est effectuée afin de comprendre les patrons observés. En particulier ici, j'explore les structures génétiques à une échelle spatiale fine, une échelle encore peu explorée, en particulier chez les espèces aux groupements sociaux peu complexes. Placé dans un contexte de dispersion biaisée par le sexe, ce chapitre remet en question l'idée d'une faible structure génétique chez des espèces comme la Grande Oie des neiges en analysant les patrons de variabilité génétiques durant les deux étapes de la reproduction des oiseaux nidifuges, la nidification et l'élevage des jeunes.

Finalement, le cinquième et dernier chapitre présente un aspect éthique et méthodologique du prélèvement sanguin chez les oiseaux. Ce chapitre vise à mesurer l'impact d'une nouvelle technique de récolte de sang utilisé précisément dans le chapitre 4. Afin de valider cette technique, je compare les avantages et inconvénients qu'elle encoure avec ceux d'autres techniques existantes et j'évalue les conséquences possibles sur la survie des oiseaux prélevés.

Chapitre 1

HABITAT LABYRINTHS AS REFUGES FROM TERRESTRIAL PREDATORS: TEMPORAL AND SPATIAL VARIATION OF PREDATION RISK IN ARCTIC-NESTING GEESE

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Résumé

Nous avons examiné comment la complexité de l'habitat peut fournir des refuges contre la prédation pour des oiseaux nichant à même le sol, modulant par la même occasion les interactions prédateurs-proies. Dans l'Arctique, les Grandes Oies des neiges (*Anser caerulescens atlanticus* L.) nichent souvent dans les milieux humides, milieux où la structure est perturbée par de multiples réseaux entremêlés de canaux d'eaux. Nous avons testé l'hypothèse selon laquelle le renard arctique (*Alopex lagopus* L.), le prédateur principal des œufs d'oies, était défavorisé dans cette structure hétérogène d'habitat, notamment lors de son activité de chasse. Nous avons également examiné comment les cycles d'abondance de lemmings, la proie principale des renards, pourraient également influencer le lien entre la structure de l'habitat et la prédation des renards sur les œufs d'oies. Les résultats d'une expérience avec des nids artificiels a d'abord indiqué que les renards sont plus rapides à détecter des nids non défendus que les prédateurs aviaires en milieu mésique alors que la relation inverse était observée en milieux humides. De plus, les renards ont passé en moyenne 3.5 fois plus de temps entre deux attaques consécutives sur de vrais nids d'oies dans les milieux humides que dans les milieux mésiques. Par contre, aucune différence n'a été détectée pour les oiseaux prédateurs. Sur une période de 11 ans, le succès de nidification en milieux humides (65%) a toujours été supérieur à celui des milieux mésiques (56%) mais l'ampleur de cet écart a été supérieure durant les creux de populations de lemmings (15%) que durant toutes les autres phases du cycle de lemming (5%). Le succès des nids situés à la limite des parcelles de milieux humides a également été inférieur au succès des nids centraux, suggérant un gradient d'accessibilité des nids au sein des milieux humides pour les renards. Notre étude supporte donc l'hypothèse selon laquelle l'hétérogénéité spatiale des milieux humides fournit des refuges partiels aux oiseaux nichant dans l'Arctique quant à la prédation par les renards mais pas pour les prédateurs aviaires. Nos résultats démontrent également que les cycles de lemmings affectent indirectement les interactions complexes entre la structure de l'habitat, le changement de proie par les prédateurs et le succès de chasse des renards.

Abstract

We investigated how habitat complexity could provide predator refuges for ground-nesting birds and affect predator-prey interactions. In the Arctic, greater snow geese (*Anser caerulescens atlanticus* L.) often nest in wetlands that form intricate networks of water channels. We tested the hypothesis that the ability of the arctic fox (*Alopex lagopus* L.), the main predator of goose eggs, was impaired by this structurally heterogeneous habitat. Lemmings, the main prey of foxes, show strong population cycles. We also examined how their fluctuations influenced the interaction between habitat structure and fox predation on goose eggs. An experimental approach with artificial nests suggested that foxes were faster in finding unattended goose nests than avian predators in mesic tundra whereas the reverse was true in wetlands. Foxes spent 3.5 times more time between consecutive attacks on real goose nests in wetlands than in mesic tundra. Their attacks on goose nests were also half as less successful in wetlands than in mesic tundra whereas no difference was found for avian predators. Nesting success in wetlands (65 %) was always higher than in mesic tundra (56 %) but the difference between habitats was higher during lemming crashes (15 %) than during other phases of the lemming cycle (5 %). Nests located at the edge of wetland patches were also less successful than central ones, suggesting a gradient in accessibility of goose nests in wetlands for foxes. Our study supports the hypothesis that the structural heterogeneity of wetlands provides a partial refuge from predation by foxes (but not avian predators) for arctic-nesting birds. Our results also demonstrate that cyclic lemming populations indirectly alter the spatial distribution of productive nests due to a complex interaction between habitat structure, prey-switching and foraging success of foxes.

Introduction

Spatial heterogeneity is widely recognized as an ecological process affecting predator-prey interactions (e.g. Murdoch & Oaten, 1975; Caswell, 1978; Holt, 1984; McNair, 1986). Heterogeneity can either positively or negatively affect predator foraging by altering their behaviour and physical abilities (Briand & Cohen, 1987; Holt, 1987; Hixon & Menge, 1991; Whitehead & Walde, 1992) or by regulating encounters between predators and prey (Murdoch & Oaten, 1975). For instance, heterogeneity can improve foraging success of predators with ambush tactics by providing plenty of sites with visual obstructions from which they can attack (Janes, 1985) and by decreasing their visibility to prey (Coen, Heck & Abele, 1981; Metcalfe, 1984; Schooley, Sharpe & Van Horne, 1996). In contrast, predators that actively search for and pursue prey are often less efficient in heterogeneous landscapes because it interferes with their ability to manoeuvre and/or visually detect prey (e.g. Warfe & Barmuta, 2004).

By reducing predator efficiency, heterogeneous habitats thus provide prey with partial refuges from predators (Dickman, 1992; Beukers & Jones, 1997; Eklöv, 1997; Babbitt & Tanner, 1998), although refuge value for prey may differ between avian and mammalian predators (Nour, Matthysen & Dhondt, 1993; Schmidt, 1999). In addition, benefits of living in a refuge may also vary temporally, depending on the functional response of predators to different prey (Hogstad, 1995; Schmidt & Whelan, 1998; Schmidt, 1999). According to foraging theory, a decrease in availability of the main prey should increase predation rate on alternative ones, even if they use refuges (Hogstad, 1995; Abrams & Matsuda, 1996; Schmidt, 1999). Despite numerous studies on the ecological consequences of refuges, the extent to which habitat heterogeneity regulates predator-prey interactions remain uncertain (McCoy & Bell, 1991; Grabowski, 2004). Incorporating habitat structure within foraging theory is a promising but neglected framework (Schmidt, 1999) that requires fine-scale empirical investigations of predator-prey interactions.

The Arctic tundra is a good model to study predator-prey dynamic due to the simplicity of species assemblages and its habitat heterogeneity (e.g. Angerbjorn, Tannerfeldt & Erlinge, 1999; Bêty *et al.*, 2002). One of the main terrestrial predators, the arctic fox (*Alopex*

lagopus L.; hereafter fox), often acts as a lemming specialist (Angerbjorn, Tannerfeldt & Erlinge, 1999). However, goose eggs, especially snow geese (*Anser caerulescens* L.), are important alternative prey for foxes in many areas (Bantle & Alisauskas, 1998; Anthony, Barten & Seiser, 2000; Bêty *et al.*, 2001). In addition, several avian predators such as gulls, jaegers and ravens also prey on both goose eggs and lemmings in this system, and predation is usually the most important cause of nest failure in geese (e.g. Bêty *et al.*, 2001). Snow geese nesting in the Arctic often use two major habitat types, wetlands and mesic tundra (Lepage, Gauthier & Reed, 1996). Wetlands generally consist of a network of polygon-patterned grounds with water channels (e.g. Ellis & Rochefort, 2004) that can impede foraging behaviour of foxes but not birds (Hughes, Reed & Gauthier, 1994), and thus represent a more structurally heterogeneous habitat than mesic tundra. This habitat dichotomy provided a natural experiment to study the process of egg predation as the outcome of an interaction between multiple predators and two prey, geese and lemmings.

We investigated the role of wetlands as refuges for nesting snow geese by testing the hypothesis that the main predator of goose eggs, foxes, was hampered in more structurally heterogeneous habitats. Based on foraging theory, we predicted that (1) foxes would be more efficient than avian predators in acquiring goose eggs in mesic tundra than in wetlands; (2) goose nests in mesic tundra would experience higher predation by foxes, leading to a lower nesting success than in wetlands; (3) this nest success differential would be highest during years of lemming crashes because foxes then switch to geese; and (4) nests located in the centre of wetland patches would be less vulnerable to foxes than those on the edge due to their reduced accessibility. To test these predictions, we first measured nest detection rate by predators in the two nesting habitats using artificial nest experiments during contrasting years of lemming abundance. Second, we looked at temporal and spatial changes in foraging success of foxes and avian predators on real goose nests during one complete lemming cycle. Finally, we compared the success of snow goose nests between habitats at two spatial scales over 3 lemming cycles.

Material and methods

Study area

Data were collected between 1995 and 2005 at the Bylot Island goose colony, Nunavut, Canada (72°53'N, 79°54'W). This island is the most important breeding site for greater snow geese (*A. c. atlanticus* L., snow geese hereafter), with more than 20,000 breeding pairs (Reed, Hughes & Boyd, 2002). Wetlands and mesic tundra are the two dominant habitat types although the latter is 10 times more abundant than the former (Masse, Rochefort & Gauthier, 2001). Wetlands are mostly found in polygon-patterned ground created by frost action in the ground of lowland tundra (Gauthier, Rochefort & Reed, 1996; Fortier & Allard, 2005). Low-centre and high-centre polygons often form heterogeneous, intricate labyrinths of lakes, ponds, and narrow water channels that can considerably hamper the movement of walking predators (Fig. 1). Wet meadows have a rich cover of graminoids (*Dupontia fischeri* R. Br., *Eriophorum scheuchzeri* R. Br., and *Carex aquatilis* R. Br.), which are the preferred food-plants of snow geese (Gauthier, Rochefort & Reed, 1996). Mesic tundra is found in drier lowlands, gentle slopes of small hills and low altitude plateaus. This habitat is dominated by shrubs with a sparse cover of forbs and graminoids (Gauthier, Rochefort & Reed, 1996).

Two species of small mammals occur on Bylot Island, brown lemmings (*Lemmus sibiricus* Kerr) and collared lemmings (*Dicrostonyx groenlandicus* Traill). The most important avian predators are parasitic jaegers (*Stercorarius parasiticus* L.), glaucous gulls (*Larus hyperboreus* Gunnerus) and common raven (*Corvus corax* L.). All methods described below were approved by the Animal Care Committee of Université Laval following guidelines of the Canadian Animal Care Council.

Lemming monitoring

We estimated lemming abundance annually from 1995 to 2005 with snap-trap surveys. Traps were deployed at the end of July along two pairs of transects (250-m long, 100-m apart within each pair), one pair in wetlands and one in mesic tundra. Following the

protocol of Shank (1993), we baited 25 Museum Special traps per transect with a mix of peanut butter and rolled oats. We set traps 10-m apart on each transect for 10-11 days, and we checked them daily. A lemming abundance index was calculated as the number of lemmings caught per 100 trap-nights over the whole trapping period. To improve estimates of sampling effort, we corrected this index by subtracting 0.5 night for each sprung trap (with lemming or not) (Beauvais & Buskirk, 1999).

Artificial nest experiments

We assessed differences in goose nest detection rate between avian predators and foxes in the two nesting habitats using artificial nests. We conducted 6 experiments in each habitat type in 2003 and 5 in 2004, using different locations each time. Goose eggs were simulated with domestic chicken eggs, which are smaller but similar in shape and colour than goose eggs. In each experiment, we randomly placed 10 nests in a 1-ha plot (100 X 100 m). Nests contained two eggs placed in artificial bowls made with goose down collected in real nests in previous years. We covered the eggs with down as females do before departing their nest (Bêty & Gauthier, 2001) to prevent biases in predation pattern, especially for avian predators (Opermanis, 2004). Thus, artificial nests mimic real nests during incubation recesses when they are left unattended by females (Reed, Hughes & Gauthier, 1995). Nest locations were marked with short bamboo canes (15-cm high) placed 10 m away. We wore rubber gloves during nest deployments and visits to avoid human odour on down and eggs. Nests were checked after 4, 8, 12 h and 1, 2, 3, 6 and 8 days of exposure to predation. A nest was considered depredated when at least one egg had been destroyed or removed. We used nest remains to identify predators (birds or fox) following Bêty *et al.* (2002).

Behavioural observations

From 2002 to 2005, we monitored the behaviour of predators in the main goose colony to determine habitat constraints on their foraging behaviour. We observed predators throughout the 24-h daylight period of the Arctic during the goose incubation period (9 June - 6 July). From three blinds, we used binoculars (10 X) and spotting scopes (20-60 X)

to cover the same area (2.8 km²) each year of the study; nest densities and habitat in this area were representative of those encountered in the whole goose colony.

Every time a predator (fox or bird) entered the observation area, we continuously recorded its activity and habitat use (focal animal sampling) with a digital recorder. When 2 predators were present, we sampled the closest one, except if it was not actively foraging. Foxes were identified by the distinctive patterns of their fur as calibrated by (Bêty *et al.*, 2001) (shedding from winter to summer fur). We defined a nest attack as any attempt by a predator to take goose eggs and attacks were considered successful when at least one egg was taken. We recorded the time between two nest attacks by actively foraging predators as an index of habitat constraints on movements. We controlled for the confounding effect of nest density on this index by counting the number of nests within each patch of habitat where the predators were observed foraging.

Goose nest monitoring

We systematically searched for nests in different areas of the goose colony during egg laying and early incubation from 1995 to 2005. We placed a marker 10 m from each nest and recorded its position using a Global Positioning System receiver (± 5 m after 2000 and ± 20 m before). We classified nesting habitats as wetland or mesic tundra (for nests found before 2003, habitat was assigned a posteriori by reporting the nest position on a detailed habitat map; Chapter 3). We estimated an annual index of nest density as the maximum number of nests found within the same fixed area (9.64 ha) each year, both including wetlands and mesic tundra. This provided an index of temporal variation in nest aggregation at the colony scale.

We revisited nests once during incubation and at hatching to monitor their fate, without inducing biases in nesting parameters (Schubert & Cooke, 1993; Bêty & Gauthier, 2001). We determined laying date of the first egg (nest initiation) and the number of hatched goslings per nest following Bêty *et al.* (2001). A nest was considered successful if at least one egg hatched. Finally, we also defined total clutch size as the maximum number of eggs found in a nest, after the start of incubation.

Data analysis

We examined differences in detection rates of artificial nests between avian predators and foxes using two approaches. We first compared the proportion of nests predated by foxes at the end of each experiment between the two habitats with a two-way ANOVA (factors were habitat and year), using the SAS software version 9 (SAS, 2002). We considered each plot with artificial nests as the experimental unit. We ranked transformed data since the dependent variable was not normally distributed. Because ANOVA on ranks has low power for testing interactions (Seaman, Walls & Wise, 1994), we tested interactions using the aligned rank test procedure (Salter & Fawcett (1993). Second, we tested for differences in predation rate between the two types of predators in each habitat using a log-rank survivorship test with the JMP-IN 4.0 software (SAS, 1989-2001), considering the number of visits as the sampling unit and the predation rate as the total number of nests preyed upon between two visits.

We also used two approaches to test for habitat constraints on predator foraging behaviour. We first analyzed the travel time between consecutive nest attacks by foxes according to year, lemming cycle phase, habitat and nest density where travelling occurred with a generalized linear mixed-effects model (lmer command in the Matrix library of the R 2.2.1 statistical program. Ihaka & Gentleman, 1996; Bates & Maechler, 2006). Mixed-effect models included predator identity as a random effect to avoid pseudo-replication (Machlis, Dodd & Fentress, 1985). For this analysis and the following ones, we coded the lemming phase as a categorical variable (crash years vs. other years), because Bêty *et al.* (2001) showed that predator foraging behaviour was mostly driven by the dichotomy of lemmings absence vs. presence. Second, we examined the effect of habitat, nest density where travelling occurred and lemming phase on foraging success (i.e. proportion of successful attacks) by predators. For foxes, we used generalized estimating equations (GEE) with a logit link function (SAS, 2002), which takes into account that multiple attacks by the same individual are not independent (See Bêty *et al.*, 2002 for details on the procedure). For avian predators (unknown identity), we used a multiple logistic regression model (SAS, 2002). The significance of independent variables was assessed with a Wald statistic, which is distributed as a χ^2 (Trexler & Travis, 1993). All independent variables were standardized

and multi-collinearity among them was not significant. Because the distance of attending parents from the nest is critical in determining the success of predator attacks (Bêty *et al.*, 2002. N. Lecomte, unpubl. data), we restricted analyses to cases where goose pairs were at the nest or very close to it (<10 m), thus avoiding confounding interactions between habitat and presence/absence of parents near the nest.

We examined the effect of habitat on goose nesting parameters at two scales. First, at the whole-colony scale, we compared success between nests located in different wetland patches and the mesic habitat surrounding them throughout the colony. Second, we examined wetland edge effects on nesting parameters in a restricted area near the centre of the colony where both habitats occurred and sample size was sufficient. We subdivided this area into three sections of similar surface area (9.4 ha): centre and edge of the wetland patch and the immediate surrounding mesic habitat (Fig. 2A).

We compared annual nest density, total clutch size, number of hatched goslings per nest and laying date among habitats and years with a two-way ANOVA for unbalanced design (SAS, 2002). Nests with clutch sizes of one were rare (2 %) and were removed from the analysis as suggested by Lepage, Gauthier & Menu (2000). Because laying date was not normally distributed, we ranked transformed data and used the same approach than for artificial nest plots. We computed pair-wise comparisons among nest types using a Tukey-Kramer adjustment for multiple comparisons of Least Square Means. We considered each goose nest as independent because individual snow geese can defend their nests against predators and the fate of a nest is independent of the fate of its nearest neighbours (Bêty *et al.*, 2001).

We estimated nesting success with the daily nest survival (S) procedure of program MARK v4.2 (Dinsmore, White & Knopf, 2002). We included the age of the nest at the time of discovery (date found minus estimated laying date) as an individual covariate in the model because predation rate can vary during the nesting period (Bêty *et al.*, 2002). We considered the model with full time (t ; i.e. years), habitat (h), incubation day (linear effect; d), and *age* effects with relevant interactions as the most general model. To select the most parsimonious model, we used the Akaike's Information Criterion modified for small

sample size (lowest AICc value) and the relative weight of evidence in favour of a particular model (ω AICc) (Burnham and Anderson 1998). In presence of uncertainty in model selection (Δ AICc < 4), we estimated model-weighted average parameter values and their unconditional standard errors (Burnham & Anderson, 1998). We estimated nesting success as the product of daily nest survival for the mean duration of laying and incubation (27 days). We formally tested the effect of specific time-dependent covariates (lemming phase and annual nest density) on nest survival using the analysis of deviance (ANODEV; Annexe 1) (Agresti, 2002). Finally, we estimated the proportion of variation in nest survival explained by those variables with the ratio of differences in deviance of various models (analogous to a r^2 ; Annexe 1) (Skalski, Hoffmann & Smith, 1993; Agresti, 2002).

For all data, normality was checked with the Kolmogorov-Smirnov test (Lilliefors option). All probabilities are two-tailed and the alpha level was set to 0.05. Unless mentioned otherwise, values are reported as means \pm 1 SE.

Results

Annual variation in lemming abundance

Trapping data showed strong cyclic variation in the lemming population (Figure 2). Peak abundance occurred in 1996, 2000 and 2004 as indicated and crashes in 1995, 1999 and 2002-2003. Overall, snowy owls nested only in lemming peak year. Typically, the lemming cycle on Bylot Island shows crash years just before peaks (Gauthier *et al.*, 2004), not the reverse as found for rodent cycles in Northern-Europe (e.g. Angerbjörn, Tannerfeldt & Lundberg, 2001). Thus, our study spanned 3 complete lemming cycles.

Nest detection and foraging success of predators

The mean proportion of predation on artificial nests due to foxes was much higher in mesic tundra (63 %) than in wetlands (23 %; $F_{1, 21} = 18.9$, $P < 0.001$). This suggests that habitat type affected probability of predation of unattended nests by foxes. However, the difference

between the two habitats was lower in 2004 (32 %), the lemming peak year, than in 2003 (43 %), the lemming crash year (interaction habitat*year, $F_{1,21} = 8.71$, $P = 0.007$).

Overall, predation rate of artificial nests did not differ between habitats ($\chi^2_1 = 0.17$; $P = 0.68$) or between predator types ($\chi^2_1 = 1.63$; $P = 0.2$). However, predation rates differed between foxes and avian predators within habitats (mesic tundra: $\chi^2_1 = 13.56$, $P < 0.001$; wetlands: $\chi^2_1 = 5.29$, $P = 0.02$). In mesic tundra, 50% of all nests preyed upon after 8 h vs. 1 day for those preyed upon by birds. On the other hand, 50% of nests preyed upon by foxes in wetlands were preyed upon after 1 d vs. 12 h for those preyed upon by birds.

We conducted 764 h of observation over 103 days during which we recorded 110 h and 27 h of foraging behaviour by foxes and avian predators, respectively. Overall, we observed 1105 attacks by foxes on nests defended by snow geese (range: 7-8 foxes per year) and 580 attacks by avian predators. Time spent travelling by foxes between two nest attacks was 2.3-fold higher in wetlands (103 ± 11 s) than in mesic tundra (44 ± 4 s; $F_{1,203} = 49.5$, $P < 0.001$). Nest density where travelling occurred ($F_{1,203} = 0.76$, $P = 0.38$) and the lemming phase ($F_{1,203} = 2.21$, $P = 0.14$) had no effect on travelling time between nests. In all years, fox attacks on nests were more successful in mesic tundra (16 %, annual range 15-22) than in wetlands (7%, range 2-10; $\chi^2_1 = 16.13$; $P < 0.001$), with no effect of nest density ($\chi^2_1 = 0.34$; $P = 0.55$) and lemming phase ($\chi^2_1 = 0.87$; $P = 0.35$). In contrast, habitat did not affect avian predator success in attacking nests (2% for both habitats; annual range 1-3; $\chi^2_1 = 0.01$; $P = 0.93$), nor did nest density ($\chi^2_1 = 0.80$; $P = 0.37$), nor the lemming phase ($\chi^2_1 = 0.49$; $P = 0.48$).

Habitat effects on nesting parameters

Overall, laying dates did not differ between habitats across the goose colony (Table 1). However, there were large annual variations ($F_{9,2795} = 674.4$, $P < 0.001$), ranging from 9 June in 2003 to 17 June in 1999, and a significant interaction between year and habitat ($F_{10,2090} = 4.09$, $P < 0.001$). Pair-wise comparisons indicated that laying date was 1 day earlier

in wetlands than in mesic tundra in 2003 ($P = 0.005$). We found no difference in clutch size between habitats but the number of hatched goslings per successful nest was 13 % higher in wetlands than in mesic tundra (Table 1).

The top four models in our analysis were supported by the data and suggested that daily nest survival differed among habitats and years, increased with the day of incubation, and possibly with the age that a nest was found (Table 2). Overall, even though nesting success varied considerably among years, it was always higher in wetlands (64.7 %) than in mesic tundra (56.4 %; Fig. 3). The phase of the lemming cycle in interaction with the habitat type explained 42 % (r_{DEV}^2) of the annual variation in nest survival (model (6) vs. models (1) and (10), Table 2). On average, nesting success in wetland was 15% higher than in mesic tundra in years of lemming crashes compared to 5% during other phases of the lemming cycle (ANODEV of model (6) vs. models (1) and (10), $F_{2,18} = 6.57$, $P < 0.01$; Table 2). Finally, despite a 13-fold variation in annual nest density (median = 563 nest/km², range 83 to 1104), we found little evidence for an effect of an annual nest density in interaction with habitat on nesting success (ANODEV of model (8) vs. models (1) and (10), $F_{2,18} = 0.43$, $P = 0.65$; $r_{DEV}^2 = 0.04$; Table 2).

Edge effects on nesting parameters

We found no difference in annual nest density, egg laying date, clutch size and number of hatched goslings among nests located in the centre or the edge of the same wetland patch or in the surrounding mesic habitat ($P > 0.07$ for all tests). Nonetheless, nesting success differed among years and nest location, increased with the day of incubation, and possibly with the age that a nest was found (Table 3). Nesting success was always higher in the centre of the wetland patch (77.8 %; annual range: 46.5 – 96.0 %) than at the edge (73.2 %; range: 35.0 – 95.3 %), or in the surrounding mesic habitat (63.8 %; range: 18.9 – 91.9 %; Fig. 2B).

Discussion

Our study demonstrates how habitat heterogeneity and the temporal variation in prey availability can act together to influence predator-prey interactions in an Arctic landscape. Habitat heterogeneity attenuated the risk of predation by foxes (main predator) in wetland patches, which provided a suitable refuge for snow goose nests (alternative prey). Despite the importance of predation in community dynamics, causal links between habitat and predator-prey interactions are rarely understood (Schmidt, 1999). Here, we propose a mechanism to explain about how habitat heterogeneity can affect predator efficiency and ultimately the prey reproductive output.

Habitat and predator efficiency

Few studies have explored the differential effects of habitat on multiple predators and their prey (Nour, Matthysen & Dhondt, 1993; Hogstad, 1995; Swisher, Soluk & Wahl, 1998; Warfe & Barmuta, 2004). Our study illustrates how habitat structure differentially influenced both nest detection probability and foraging success of avian and mammalian predators.

Experiments with artificial nests (which mimic nests with no parental defence) suggest that foxes were faster in finding unattended goose nests than avian predators in mesic tundra whereas the reverse was found in wetlands. Behavioural observations further showed that travel time by foxes between nests increased in wetlands compared to mesic tundra. The labyrinth of ponds and water channels represents obstacles that hamper fox movements while searching for prey in wetlands. In contrast, predatory birds can search for prey with equal ease while flying over mesic and wetland habitats. These results could imply an habitat-mediated exploitative competition between the two groups of predators where constraints on movements modulate prey detection rate (Holt, Grover & Tilman, 1994).

The success of attacks by avian predators on real nests (i.e. with parental defence) was much lower than foxes, indicating that parental nest defence is more efficient in deterring avian predators than mammalian ones (Schmidt, 1999; Bêty *et al.*, 2001). In addition, foraging success of avian predators on real nests was not affected by habitat type, contrary

to foxes. Consequently, goose nests in mesic tundra should suffer additive predation from both avian predators and foxes whereas nests in wetlands, though equally affected by avian predators, should suffer a reduced predation pressure by foxes. The lower success observed for nests at the edge of wetlands compared to those in the centre provides further evidence that habitat structure imposes constraints on prey accessibility and/or foraging success of foxes.

Despite an abundant literature on interactions between space use and habitat structure, few studies have addressed the direct effect of habitat structure on foraging speed under natural conditions (e.g. Vasquez, Ebensperger & Bozinovic, 2002). Our study shows how habitat heterogeneity can affect the velocity of a foraging terrestrial predator. When attacking goose nests, foxes are mostly successful when they rush toward the nests (Samelius & Alisauskas, 2001). Thus, any habitat constraint on running speed is likely to decrease foraging success of foxes by giving more time to snow geese to fly back to their nest when they are away (e.g. during incubation recesses) and to defend it before foxes are able to rob eggs. Even if other factors may contribute to high nesting success of snow geese in wetlands (e.g. better feeding opportunities), we suggest that the topographic heterogeneity of wetlands and its consequence on foraging success of foxes is a key factor enhancing goose nesting success in this habitat.

Refuge value of habitats

No refuge is perfectly safe, and the degree of protection that they offer may change according to temporal variations in habitat characteristics (e. g. presence or absence of leaves in trees, Santos & Telleria, 1991) or alternative prey abundance (Hogstad, 1995; Schmidt & Whelan, 1998). Polygon-pattern ground in wetlands show a low rate of transformation (Ellis & Rochefort, 2004), so we expect little temporal variation in habitat structure at the time-scale of our study (11 years). In contrast, cyclic variation in lemming abundance influenced the difference in nesting success between habitats, presumably because variations in the abundance of the main prey changed the value of alternative prey for predators. During lemming crashes, foxes are known to switch to goose eggs (Bêty et al. 2001, Gauthier et al. 2004) and the increase in predation rate fell disproportionately upon

nests in mesic tundra due to their accessibility, thereby enhancing the role of wetlands as refuges for snow geese. On the other hand, when lemmings are moderately to very abundant, foxes feed primarily on lemmings and much less on goose eggs, and this mostly benefits nests in mesic tundra, thereby reducing the relative value of wetlands as a predator refuge. This evidence strengthens the link between rodent dynamic and nesting success of arctic birds (e. g. Bêty *et al.*, 2001) but also highlights that spatial variation in nest predation risk can modify this link. Predator-prey studies should thus be conducted at an appropriate spatio-temporal scale to account for variable habitat structure effects on different predators and variation in refuge value driven by prey-switching behaviour.

Predation pressure is a major selective force that shapes the evolution of anti-predator strategies in prey, which often use refuges to increase their fitness (Lima & Dill, 1990; Martin, 1995). Other types of predator refuges have already been described in arctic nesting waterfowl, such as islands, cliffs, steep slopes or even association with aggressive nesting raptors that provide an active protection (e.g. Tremblay *et al.*, 1997; Bêty *et al.*, 2001; Ebbinge & Spaans, 2002; Prop & Quinn, 2003). The use of wetlands by nesting snow geese (Chapters 2 & 3; this Chapter) could be viewed as another anti-predator strategy because of the foraging constraints imposed by this habitat on the main terrestrial predator. Bêty *et al.* (2001) reported positive density-dependant nesting success through predator swamping (dilution effect. Ims, 1990). However, we found that annual nest density had less effect on success than nesting habitat or the abundance of the main prey.

Based on previous studies conducted at our study site (Tremblay *et al.*, 1997; Bêty *et al.*, 2001), nesting in association with aggressive raptors like snowy owls (*Bubo scandiacus* L.) seems to provide a better predator refuge than nesting in wetlands, probably because raptors exclude both avian and mammalian predators, even when snow geese are absent from their nest. However, snowy owls breed only in lemming peak years (i.e. every 3 or 4 years; Gauthier *et al.* 2004) and defend only a small territory around their nest. Conversely, wetlands are available for nesting every year and cover a greater proportion of the landscape than raptor territories, hence allowing many snow geese to nest in this refuge. The effect of spatio-temporal variations in the availability and value of predator refuges on

habitat selection processes and colony settlement patterns deserve further investigations in arctic-nesting geese.

Conclusion

Most environments represent a mosaic of different habitats that could provide a variety of refuge for prey. In tundra ecosystems, wetland patches offer high quality nesting habitat for snow geese by acting as a partial predator refuge against their main terrestrial predator. Cyclic lemming populations regularly and indirectly alter the spatial distribution of productive nests due to a complex interaction among habitat structure, prey-switching and foraging success of foxes. Our results also suggest a link between environmental heterogeneity and community dynamics. Further studies are needed to measure how refuges stabilize bird populations in the arctic by providing islands of protection within the tundra. Understanding interactions between habitat and behaviour that underlie trophic dynamics may therefore improve our ability to predict the consequences of habitat change at the population and community levels.

TABLE 1. Effect of habitat on nesting parameters of snow geese at the whole colony scale (data from 1995 to 2005) on Bylot Island. Mean \pm 1 SE except for dates (median). Sample sizes are shown in parentheses.

Nesting parameter	Habitat		<i>F</i>	<i>P</i>
	Wetlands	Mesic tundra		
Laying date	12 June (1206)	12 June (1865)	3.33	0.068
Clutch size	3.4 \pm 0.04 (911)	3.3 \pm 0.03 (1297)	0.17	0.678
Hatched goslings	1.94 \pm 0.03 (1042)	1.68 \pm 0.02 (1711)	9.16	0.002

TABLE 2. Model selection for the effect of habitat type on daily nest survival (S) of snow geese on Bylot Island, 1995-2005 (n = 3024 nests). The most relevant models are ranked by their AICc value. For each model, the difference in AICc values is given in relation to the most parsimonious model (ΔAICc), the model's AICc weight (ωAICc), the number of estimable parameters (np) and the deviance.

Type of Model	Model	ΔAICc	ωAICc	np	Deviance
With time variation	(1) $S_{(h*t)+d}$	0.00	0.54	23	5133.87
	(2) $S_{(h*t)+d+age}$	1.84	0.21	24	5133.72
	(3) S_{h+t+d}	2.49	0.15	13	5156.38
	(4) $S_{h+t+d+age}$	3.65	0.08	14	5155.54
	(5) $S_{t+d+age}$	22.42	0.00	13	5176.31
With time- dependent covariates	(6) $S_{(h*PHASE)+d}$	233.23	0.00	5	5403.13
	(7) $S_{h+PHASE+d}$	259.29	0.00	4	5431.19
	(8) $S_{(h*DENS)+d}$	408.48	0.00	5	5578.37
	(9) $S_{h+DENS+d}$	425.20	0.00	4	5597.09
Without time variation	(10) S_{h+d}	425.87	0.00	3	5599.77

Subscripts: *age* = age of the nest when found (date found minus the nest initiation date), *d* = linear effect of incubation day, *DENS* = annual nest density, *PHASE* = lemming cycle phase (crash years vs. other years), *h* = habitat effect (wetlands vs. mesic tundra), *t* = year, + = additive effect, * = interactive effect.

TABLE 3. Model selection of the effect of nest location (wetland centre vs. wetland edge vs. surrounding mesic) on daily nest survival (S) of snow geese on Bylot Island, 2000-2003 and 2005 ($n = 745$ nests). The most relevant models are ranked by their AICc value. For each model, we give the difference in AICc values relative to the most parsimonious model (ΔAICc), the model's AICc weight (ωAICc), the number of estimable parameters (np) and the deviance.

Model	ΔAICc	ωAICc	np	Deviance
(1) $S_{(LOC^*t)+d}$	0.00	0.66	16	1033.91
(2) $S_{(LOC^*t)+d+age}$	1.39	0.33	17	1033.29
(3) $S_{(LOC^*t)}$	16.34	0.00	15	1052.25
(4) $S_{(L^*t)+d}$	28.48	0.00	11	1062.39
(5) $S_{LOC+t+d}$	30.67	0.00	8	1080.61
(6) $S_{LOC+t+d+age}$	32.39	0.00	9	1080.33

Subscripts: age = age of the nest when found (date found minus the nest initiation date), d = linear effect of incubation day, LOC = nest location without constraint, L = nest location where S is constrained to be equal between wetland edge and centre, t = year, $+$ = additive model, $*$ = model with interaction.

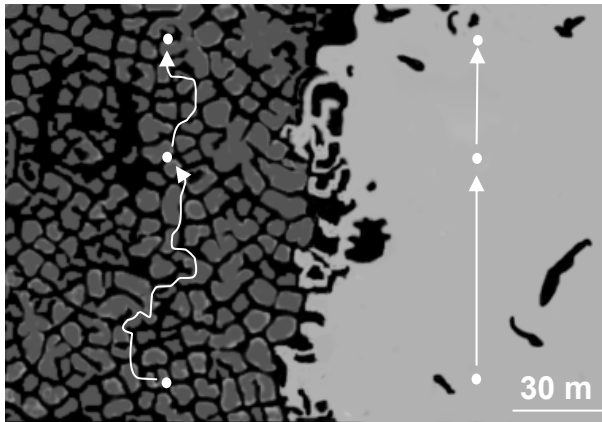


FIGURE 1. Constraints imposed by habitat structure on arctic foxes foraging in a snow goose colony. Figure based on an aerial photograph of a portion of the colony showing two hypothetical paths of a fox (white arrows) travelling between goose nests (white circles) while avoiding water, one in mesic habitat and one in wetlands; wetlands are in grey, ponds and water channels in black, and mesic tundra in light grey.

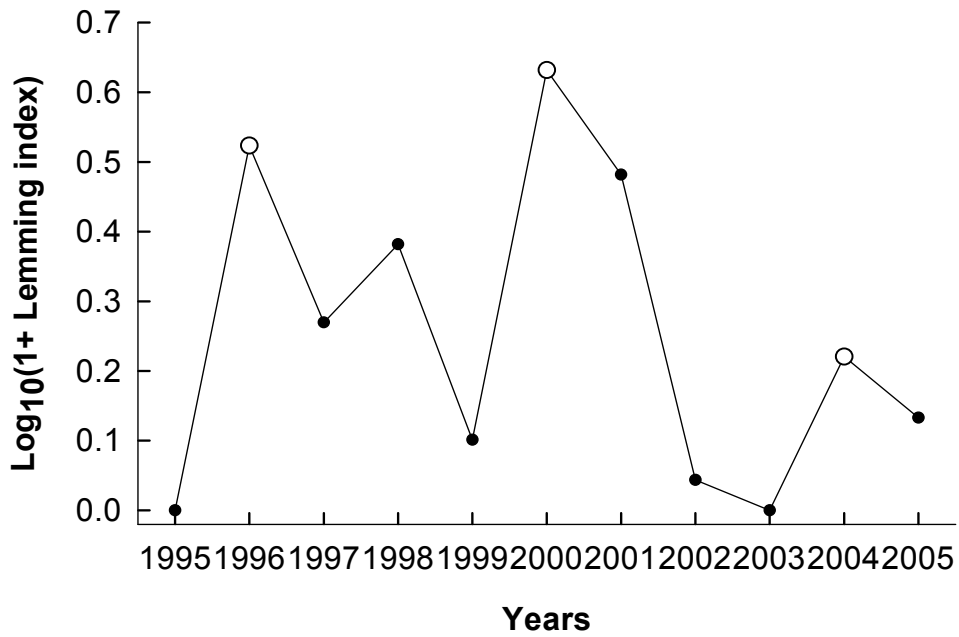


FIGURE 2. Index of lemming abundance (\log_{10} [1 + pooled number of *Lemmus sibiricus* and *Dicrostonyx groenlandicus* caught per 100 trap-nights]) on Bylot Island, Nunavut. Open circles indicate years with snowy owls nesting on Bylot Island.

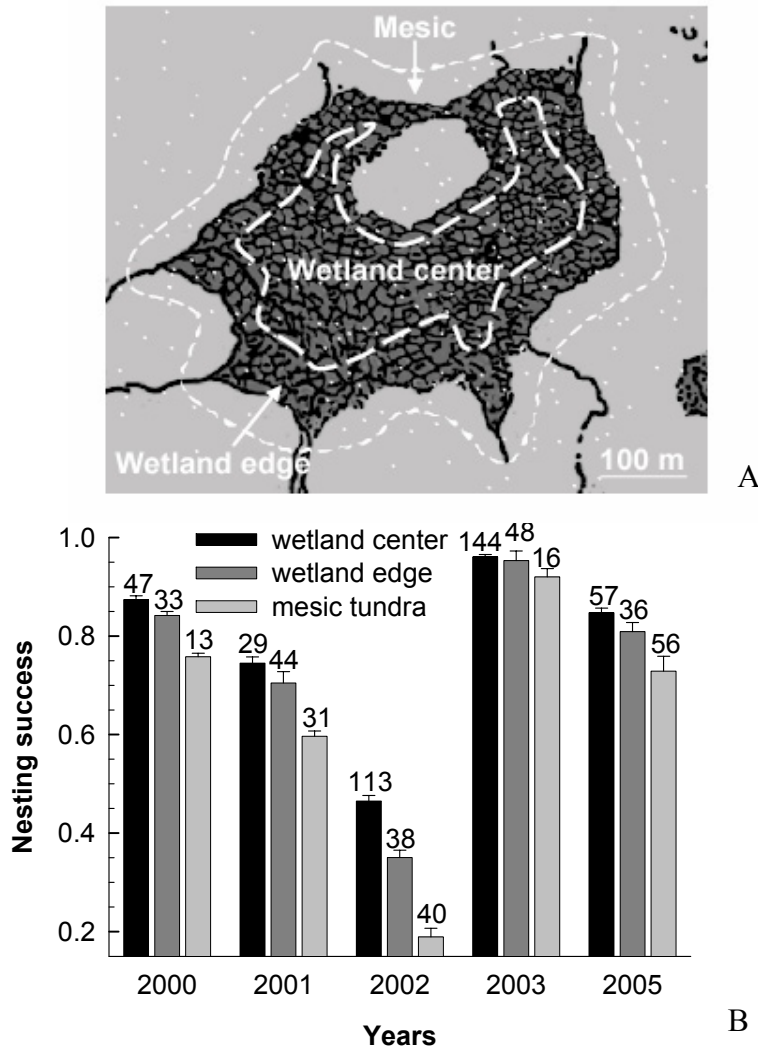


FIGURE 3 A. Representation of a subset of the colony based on an aerial photograph showing the distinction between wetland centre, wetland edge and the surrounding mesic habitat. Wetlands are in grey, ponds and water channels in black and mesic tundra in light grey. White dots show the distribution of goose nests in 2003 for illustration purposes. B. Mean (+ 1 SE) annual success of snow geese nests located either in the wetland centre, at the edge, or in mesic tundra on Bylot Island, 2000-2003 and 2005 (parameter values averaged over 2 top models in Table 3; see methods). Numbers over bars represent sample size.

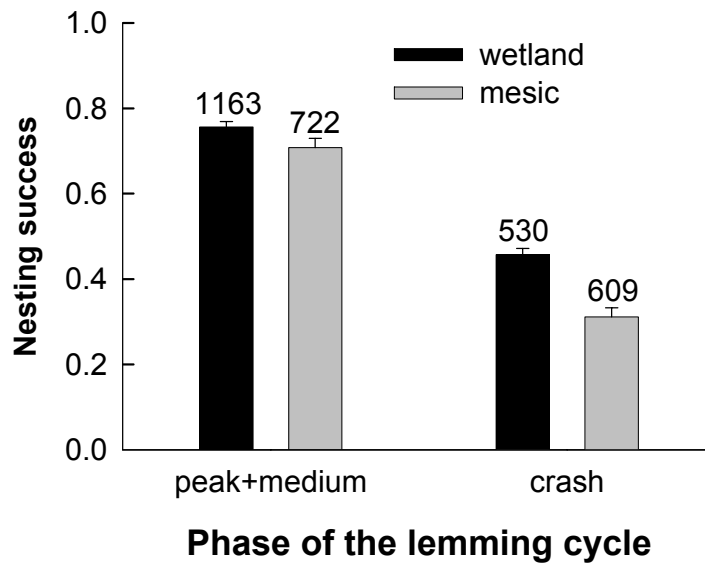


FIGURE 4. Mean (+ 1 SE) annual success of snow goose nests in two habitats on Bylot Island, 1995-2005 (parameter values averaged over 4 top models in Table 2; see methods). Numbers over bars represent sample size. The number of years following the lemming peak is also shown for each calendar year.

Chapitre 2

A LINK BETWEEN WATER AVAILABILITY AND NESTING SUCCESS MEDIATED BY PREDATOR-PREY INTERACTIONS IN THE ARCTIC

Lecomte, N., Gauthier, G. & Giroux, J.-F. 2006. Manuscrit soumis à *Ecology Letters*.

Résumé

Bien que l'eau soit un facteur limitant très important dans les processus éco-physiologiques, les réponses écologiques des organismes aux disponibilités en eau restent encore mal comprises. Dans cette étude, nous démontrons un lien entre cette disponibilité et la reproduction de la Grande Oie des neiges (*Anser caerulescens atlanticus*). Cette espèce niche dans un environnement arctique où normalement l'eau n'est pas considérée comme une ressource limitante. Dans les milieux où l'eau est peu disponible (milieux mésiques), les oies sont plus susceptibles de s'éloigner de leur nid afin d'atteindre une source d'eau que les oies nichant en milieux humides, et par la même occasion, dépasser une distance limite (10 m) où la défense du nid devient inefficace contre les prédateurs. Après une pluie, les oies ont réduit de moitié leur distance d'éloignement en utilisant les dépressions dans le sol remplies par l'eau de pluie. Le succès de nidification a toujours été supérieur en milieux humides relativement aux milieux mésiques mais cette différence était plus forte durant les années de faible abondance de pluie (11%) que durant les années pluvieuses (3%). Lorsque nous avons manipulé la disponibilité de l'eau à proximité des nids en ajoutant des bacs d'eau, nous avons mesuré une baisse de la distance d'éloignement du nid par les oiseaux et une augmentation du succès de nidification relativement à des nids témoins. Ces résultats suggèrent que les variations dans les régimes de précipitations dus aux changements climatiques peuvent avoir un impact sur les espèces arctiques, en modifiant notamment les interactions prédateurs-proies.

Abstract

Although water is an important limiting factor of physiological processes, ecological responses to water availability remain poorly understood. Here, we document a link between water availability and reproduction of greater snow geese (*Chen caerulescens atlantica*), inhabiting an Arctic environment where water is not usually considered a limited commodity. To reach water sources during incubation recesses, geese nesting in mesic tundra (low water availability) were more likely to travel beyond a distance threshold where nest defence becomes inefficient against predators compared to wetlands (high water availability). After a rainfall, geese half reduced their distances because they used temporary water holes. Nesting success was always higher in wetlands than in mesic tundra but this difference was higher in years of low rainfall than in those of high rainfall (11 and 3%, respectively). Water-supplemented nests showed lower predation risks and a higher success than control nests. This suggests that variations in precipitations brought by climate changes could have a large impact on some arctic species by influencing top-down interactions between predators and prey.

Introduction

Water can be a strong limiting factor for several physiological processes (e.g. Bartholomew & Cade, 1963; Klaassen, 2004). However, water availability can also affect demographic processes such as survival and reproduction, as shown for species living in arid environments (Newton, 1998). In the context of global warming, major changes in precipitation patterns and water availability are expected in most biomes (IPCC, 2001). Although future variations of hydrologic cycles could be as great as changes in air temperature, their potential impacts on ecosystems and organisms have received far less attention than the latter (Hodkinson *et al.*, 1999; Allen & Ingram, 2002). Yet, understanding how animals respond to hydrologic variability is fundamental for any projection of the impacts of future climate change (Bolger, Patten & Bostock, 2005).

There is growing evidence that rainfall can affect animal productivity either positively or negatively. For example, increased water levels and flooding can lead to egg loss and reduced survival in ground-nesting birds (e.g. Thompson & Furness, 1991; Ratcliffe, Schmitt & Whiffin, 2005). In arid environments, the amount of precipitation is positively linked with clutch size and reproductive success because it increases water availability at the onset of egg-laying (Coe & Rotenberry, 2003). This link is usually assumed to be mediated through an increase in food availability rather than water per se (bottom-up control) (Blancher & Robertson, 1987; Gibbs & Grant, 1987). In contrast, the effect of rainfall on predation has been neglected (Morrison & Bolger, 2002), despite its importance in ecological systems (top-down control) (Ostfeld & Keesing, 2000). Although there are some examples of how weather can affect predator efficiency (e.g. Post *et al.*, 1999), we know very little about how climatic conditions may affect prey behaviour and hence predation risk (Morrison & Bolger, 2002).

In birds, nest predation can have a considerable impact on reproductive success (Martin, 1995). Incubating birds must balance the conflicting needs of foraging and protecting their nest because, when they leave to feed, predation risk of unattended eggs often increases (Thompson & Raveling, 1987). Change in resource availability during incubation could then affect egg predation rate if this influences the time spent off the nest by incubating

parents (thereafter called recess). Much emphasis has been placed on food availability or feeding behaviour during recesses (Martin & Ghalambor, 1999) but constraints imposed by water requirements have been largely ignored, even though they can be significant in species that fast during incubation (Le Maho *et al.*, 1981).

We investigated how water availability affected nesting success in an arctic-nesting species, the snow goose (*Chen caerulescens*). In this species, predation is the primary cause of nest failure and occurs mostly when females leave their nest to drink or feed during incubation (Cooke, Rockwell & Lank, 1995; Bêty *et al.*, 2001. this study). Although males can limit egg losses by attacking and chasing off predators (Samelius & Alisauskas, 2005), they often follow their mate during recesses, leaving the nest unprotected. We tested the hypothesis of a link between water availability and nesting success mediated through predation. We first predicted that geese nesting in mesic tundra where water is scarce should be more vulnerable to predation than those in wetlands because they had to travel a greater distance to drink during recesses (Fig. 1). Therefore, predators should find more unattended nests in mesic tundra than in wetlands. We tested these predictions by monitoring the behaviour of incubating females during recesses and the foraging behaviour of predators in the two habitats during four breeding seasons. We also hypothesized that rainfall should increase water availability and thus decrease predation risk as distance to drinking sources is reduced, especially in mesic tundra. We therefore predicted that difference in nesting success between wetland and mesic tundra should vary with rainfall, increasing in drier years and decreasing in wetter years. We tested this prediction by comparing the nesting success of geese in the two habitats in relation to rainfall over an 11-year period. Finally, to eliminate the confounding factor of differences in food quality between wetlands and mesic tundra (i.e. wetlands have more food plants preferred by geese) (Gauthier, Rochefort & Reed, 1996), we experimentally manipulated water availability by supplementing nesting pairs with water. We predicted that pairs that were provided with water should stay closer to their nest during recesses and achieve higher nesting success than controls.

Materials and Methods

Study site

Data were collected between 1995 and 2005 on Bylot Island, Nunavut, Canada (72°53'N, 79°54'W). This island is the most important breeding site for greater snow geese (*Chen caerulescens atlantica*), with more than 20,000 breeding pairs, the majority of which are nesting in the same colony (Reed, Hughes & Boyd, 2002).

Wetlands and mesic tundra are the dominant habitats with mesic tundra covering 10 times more area than wetlands (Masse, Rochefort & Gauthier, 2001). Wetlands are mostly found in polygon-patterned ground created by frost action in the lowland tundra (Gauthier, Rochefort & Reed, 1996). Low-centre and high-centre polygons often form a heterogeneous, intricate network of lakes, ponds, and narrow water channels that hamper the movement of walking predators (Fig. 1; Chapter 1). Wetlands have a rich cover of graminoids (*Dupontia fischeri* R. Br., *Eriophorum scheuchzeri* R. Br., and *Carex aquatilis* R. Br.), which are the preferred food-plants of geese (Gauthier, Rochefort & Reed, 1996). Mesic tundra is found in drier lowlands, gentle slopes of small hills and low altitude plateaus. Standing water is scarce in mesic tundra and is only found in isolated small ponds or streams (Fig. 1) and between hummocks (low mounds of earth formed by winter freezing) following a rainfall. This habitat is dominated by scattered shrubs and a sparse cover of forbs and graminoids (Gauthier, Rochefort & Reed, 1996).

The predator community of Bylot Island is relatively simple with only one major terrestrial predator, the arctic fox (*Alopex lagopus* L.; hereafter fox), and a few avian predators, parasitic jaegers (*Stercorarius parasiticus* L.), glaucous gulls (*Larus hyperboreus* Gunnerus) and common ravens (*Corvus corax* L.) (e.g. Bêty *et al.*, 2002).

Mean daily temperature during the study was 3.7°C (annual range: 1.0 to 7.7°C). Each year, we recorded daily rainfall (mm) manually from 1 June to 15 August with a rain gauge.

Behavioural observations

From 2002 to 2005, we carried out behavioural observations of foraging predators and incubating geese. We observed predators and geese throughout the 24-h daylight period of the Arctic during the incubation period (9 June-6 July). From three blinds, we used binoculars (10 X) and spotting scopes (20-60 X) to cover an area of 2.8 km² where both nesting habitats (wetlands and mesic tundra) were present and where nest densities were representative of those encountered in the whole colony. The number of goose nests under observations ranged annually from 100 to 500. We continuously scanned incubating females and, every time a female was seen departing from a nest, we started a stopwatch and observed it continuously until she resumed incubation. Upon departure, we measured the distance travelled to the nearest water source to drink. Distance was either estimated visually using 250 geo-referenced sticks located in the colony, or a posteriori with a measuring tape (median precision of 1.5 m). For each drinking event, we recorded whether the water source was permanent (ponds, rivers) or temporary (small depression at the surface of the tundra). We recorded all nest attacks by predators during the absence of the female, noted the predator involved, and whether it was successful (i.e. at least one egg taken) or not. We defined an attack as any attempt by a predator to take goose eggs. Foxes were identified individually by the distinctive patterns of their fur (shedding from winter to summer fur).

Goose nest monitoring

We systematically searched for goose nests in different areas of the colony during egg laying and early incubation. For each nest, we determined the habitat (wetland or mesic tundra) and revisited them once during incubation and again at hatching to monitor their fate. We estimated nest density as the maximum number of nests found within the same fixed area (9.64 ha) each year. We determined laying date of the first egg (nest initiation) following Bêty et al. (2001). A nest was considered successful if at least one egg hatched. We defined total clutch size as the maximum number of eggs found in a nest, after the start of incubation. At hatch, we counted the total number of goslings in the nest.

Water supplementation experiment

During the entire incubation period in 2005, we supplemented 40 randomly chosen nests in the colony with water, split equally between wetlands and mesic tundra. For each nest, we used two dark brown plastic containers with a volume of ca. 8-L (width×depth×length = 11.7×20.8×34.1 cm). We buried them in the ground in opposing directions, at distances from the nest ranging from 3 to 6 m. This distance was smaller than the 10-m threshold distance beyond which geese are much less effective in protecting their nest against predators during recesses (Bêty *et al.*, 2001). This distance also ensured that water supplementation was restricted to the parents of focus nests as geese are territorial in the vicinity of their nest (Cooke, Rockwell & Lank, 1995). We filled containers with water from neighbouring ponds for the first time one or two days after the onset of the incubation period and refilled them as needed during incubation to ensure that water was present until hatch. A sample of non-manipulated nests observed and monitored in the same year (see above) was used as control.

We conducted behavioural observations at the 40 experimental nests using the same methods previously described, and we monitored their fate until hatch. We also recorded nest attendance by males at the experimental nests and at 49 control nests randomly chosen in the colony. Nest attendance was defined as the percentage of total time spent close to the nest (≤ 10 m) during periods of observations (see also Samelius & Alisauskas, 2001). We detected no widowed females as attending males were seen at least once at all nests under observation.

Data analysis

We first explored the effect of water on predation risk by comparing the distance traveled by females from their nest to a drinking site between years and habitats with two-way ANOVAs. Second, we compared this distance between days following significant rainfall (i.e. presence of > 20 mm of rainfall in the preceding 3 days) and those that did not. We also used a χ^2 statistic to compare the success of predators' attacks in the two nesting habitats during recesses.

We examined the combined effects of habitat and rainfall on goose nesting success with the daily nest survival (S) procedure of program MARK v4.2 (Dinsmore, White & Knopf, 2002). We included the age of the nest at the time of discovery (date found minus estimated laying date) as an individual covariate in the model because predation rate can vary during the nesting period (Bêty *et al.*, 2002). We considered the model with full time (t ; i.e. years), habitat (h), incubation day (linear effect; d), and age effects with relevant interactions as the most general model. To select the most parsimonious model, we used the Akaike's Information Criterion modified for small sample size (AICc) and the relative weight of evidence in favour of a particular model (ω AICc) (Burnham and Anderson 1998). In presence of uncertainty in model selection (Δ AICc $<$ 4), we estimated model-weighted average parameter values and their unconditional standard errors (Burnham & Anderson, 1998). We estimated nesting success as the product of daily nest survival for the mean duration of laying and incubation (27 days). We determined the proportion of variation in nest survival explained by the presence of rainfall (time-dependent covariate), based on the ratio of differences in deviance of various models (analogous to a r^2 ; Annexe 1) (Skalski, Hoffmann & Smith, 1993; Agresti, 2002). We parameterized rainfall as a binary variable to contrast years with higher (wet years) and lower (dry years) rainfall than average. Finally, we formally tested the effect of rainfall on nest survival using the analysis of deviance (ANODEV; Annexe 1) (Agresti, 2002).

For the water supplementation experiment, we determined the effect of habitat on the use of water containers vs. natural sources of water with a Generalized Estimating Equations model (GEE) and a logit link function. This procedure accounts for the non-independence of multiple observations on the same individuals (see Bêty *et al.*, 2002 for details on the procedure). We used a generalized linear mixed regression model to examine the effects of habitat and experimental treatment (fixed effects) on distance travelled to drink by females during recesses, adding female identity as a random effect. We determined the effects of habitat and experiment on male nest attendance with a GEE. We compared the mean number of hatchlings per successful nests between the two habitats and between experimental vs. control nests with a two-way ANOVA. Because the dependant variable was not normally distributed, we ranked transformed data and we tested interactions using the aligned rank test procedure as recommended by Salter & Fawcett (1993). We compared

nesting success between experimental and control nests following the same procedure presented earlier (Dinsmore, White & Knopf, 2002). Finally, to test for possible confounding factors affecting nesting success, we compared laying date and clutch size between habitats and experimental and control nests with two-way ANOVAs using rank transformed variables as described earlier.

Statistical analyses other than nest survival were performed using SAS software (Institute, 2002). We considered each goose nest as independent because individual geese can defend their nests against predators and the fate of a nest is independent of the fate of its nearest neighbours (Bêty *et al.*, 2001). For all data, normality was checked with the Kolmogorov-Smirnov test (Lilliefors option). All probabilities are two-tailed and the alpha level was set to 0.05. Unless mentioned otherwise, values are reported as mean \pm 1 SE.

Results

Rainfall and water availability

Between 1995 and 2005, the mean total precipitation during the incubation period was 51.6 mm, with an almost four-fold inter-annual variation (range: 27 to 123 mm; Fig. 2). During incubation, most precipitation falls as rain, although snow occasionally occurs. After significant precipitation events, rainwater persisted in small pools and/or in shallow depressions between hummocks for 1–3 d (N. Lecomte, pers. obs.), thereby increasing the availability of drinking water for geese in the landscape.

Goose use of water and predator attacks

We observed 102 incubation recesses in 96 nests. After departure from the nest, drinking was the first activity performed by females in 89.3 % of the case ($n = 91$) whereas feeding behaviour was the first activity in 8.8 % of recesses ($n = 9$) and preening in 1.9 % ($n = 2$). Only 10.8 % ($n = 11$) of all recesses involved no drinking by females and occurred when the birds had to precipitately return to their nest due to presence of a predator.

During recesses, females nesting in mesic tundra traveled 3.8 times farther from their nest to drink compared to those nesting in wetlands (mesic: 37 ± 3 m; wetland: 9 ± 3 m; $F_{1,98} = 57.7$, $P < 0.001$), with no difference between years ($F_{1,98} = 0.001$, $P = 0.97$). During the 3 d following a significant rainfall, distance travelled to drink decreased in both habitats (mesic tundra - before rain: 39 ± 3 m, after: 19 ± 5 m; wetlands - before rain: 13 ± 3 m, after: 6 ± 1 m; $F_{1,74} = 13.5$, $P < 0.001$). This occurred because females drank in temporary water depressions rather than in permanent water sources (ponds, rivers).

During recesses, females nesting in mesic tundra were 13.9 times more likely to exceed the 10-m threshold distance from the nest where predation risk increases (Bêty et al. 2002) than females nesting in wetlands. As a result, both avian and terrestrial predators were more successful in robbing eggs in mesic tundra (89 % of success, $n = 200$) than in wetlands (79 %, $n = 77$; $\chi^2_1 = 4.3$; $P = 0.038$) during incubation recesses.

Water availability and nesting success

Between 1995 and 2005, we monitored the fate of 1331 and 1693 nests in wetlands and mesic tundra, respectively. During these years, daily nest survival differed among habitats and years, increased with the day of incubation, and possibly with the age that a nest was found, as suggested by the four top models in Table 1. Contrasting precipitations between dry and wet years in interaction with habitat types (model (6); Table 1) explained 34% (r^2_{DEV}) of the variation in nest survival (this model vs. models (1) and (8), Table 1). Overall, nesting success of geese was always higher in wet than in dry years, and the difference in success between habitats was higher during dry years (11 % on average) than during wet ones (3 %; ANODEV of model (6) vs. models (1) and (8), $F_{2,18} = 4.54$, $P = 0.025$; Table 1, Fig. 3). This suggests that rainwater was more beneficial for pairs nesting in mesic tundra than for those nesting in wetlands.

Water supplementation and goose behaviour

In 2005, we observed 44 incubation recesses for the 40 nests equipped with water containers, and 30 recesses for 30 control nests. Both females and males used water

containers, either for drinking or bathing. Females in wetlands used nearly 4 times more natural sources of water to drink ($n = 15$) than the water containers ($n = 4$), whereas geese in mesic tundra used containers more often (11 times in natural sources vs. 14 in containers; GEE $\chi_1^2 = 5.1$, $P = 0.02$).

When we considered only the use of natural sources of water, distances travelled from the nest to these sources still differed between habitats in experimental nests (mesic: 38 ± 7 m, wetlands: 9 ± 7 m; $F_{1, 26} = 18.7$, $P < 0.001$). However, distances travelled to natural sources did not differ between experimental (31 ± 6 m) and control nests (23 ± 6 m; $F_{1, 54} = 0.93$; $P = 0.33$), with no interaction between habitats and the experimental treatment ($F_{1, 54} = 0.94$; $P = 0.34$). When considering the use of all water sources (containers and natural), females with water containers in mesic tundra were 2.2 times less likely to exceed the 10-m threshold distance when they left the nest to drink (38 % of cases; $n = 21$) than females without water containers (84 % of cases; $n = 13$). In comparison, females with water containers in wetlands were only 1.2 times less likely to exceed the 10-m threshold than those without containers (26 % vs. 35 %; $n = 15$ and 17, respectively). Overall, nest attendance by males was higher for experimental nests (93 %) than for control ones (70 %, $n = 89$; GEE $\chi_1^2 = 4.73$; $P = 0.03$), with no effect of habitat ($\chi_1^2 = 0.01$; $P = 0.90$).

We did not find difference in the mean number of hatched goslings per successful nests between the four groups of nests (3.18 ± 0.09 ; mesic vs. wetlands nests and experimental vs. control nests: $F_{1, 117} = 0.10$, $P = 0.92$). Yet, the daily nest survival analysis provided strong support for a treatment effect (Table 2). Overall, success increased by almost 20% in nests with water containers (89 %) compared to control ones (68 %) in both habitats (Fig. 4). Finally, there was no difference in laying date and clutch size between experimental and control nests or between habitats ($P > 0.05$ for all tests).

Discussion

Our study demonstrates that water availability had a positive effect on the nesting productivity of geese, and that this effect was due to a change in nest predation risk through the behaviour of geese during incubation recesses. The presence of abundant and

permanent water source close to nests enhanced the quality of wetland habitat for geese, especially in dry summers with limited rainfall. Most studies showing ecological effects of water availability in birds have dealt with species inhabiting arid environments (Tieleman, Williams & Visser, 2004; Williams & Tieleman, 2005). Here, we show that water availability can also have demographic consequences in a species inhabiting the Arctic environment where water is not usually considered a limited commodity.

Predation-mediated water effect

Predation has a large influence on breeding tactics and success of birds (Lima & Dill, 1990; Fontaine & Martin, 2006). Any abiotic factors imposing constraints on prey behaviour has the potential to indirectly affect their susceptibility to predation, although empirical evidence is lacking (Schmidt, 1999). Our study provides such evidence as both environmental conditions and life-history of the prey interacted to influence “top down” (i.e. predation) processes.

Reproductive output of many species is often limited by food resources, a “bottom-up” control (e.g. Martin, 1987; Nagy & Holmes, 2005). This is supported by many food supplementation experiments that showed an increase in breeding success (Boutin, 1990). However, to our knowledge, the 20% increase in nesting success found in our study is among the strongest ever reported. Moreover, even though we manipulated a resource (i.e. water), this increase resulted from a top-down effect. Several studies showing a strong effect of food supplementation on reproductive success were conducted during years of low natural food availability (e.g. Siikamäki, 1998). Our experiment, however, was conducted in 2005, the year with the highest recorded amount of rainfall since the beginning of our monitoring. This suggests that drinking water is a strong limiting resource and that incubating females benefit from any sources of water close to their nest, such as those appearing after a rainfall.

It is somewhat surprising that the treatment also increased nesting success in wetlands where water is abundant relatively close to the nest. It is highly unlikely that the presence of water containers deterred predators like foxes from experimental nests as those were

small and inconspicuous (buried in the ground and same colour than the tundra soil). A possible explanation is that females using water containers in both habitats had an unobstructed view of the surrounding while drinking. In contrast, small ponds or water channels in wetlands are often located in depressions surrounded by polygon rims, which would hinder the vision of drinking females, thereby limiting their detection of predators (e.g. Kahlert, 2003). Increasing water availability near the nest not only reduced the distance travelled by females during incubation recessed but also increased overall nest attendance of males. Since nest protection is more efficient by both pair members than by a single mate (Samelius & Alisauskas, 2001), increased attendance by males may have contributed to the higher success of manipulated nests.

Given the benefits accrued to birds having access to drinking water close to their nest, we would expect that proximity to predictable water resources should be an abiotic factor influencing nest site selection. Not only drinking water is more available in wetlands than in mesic tundra, but the intricate network of water channels in wetlands also impede movements of terrestrial predators like foxes (Chapter 1). In accordance with these observations, we have found that female snow geese prefer to nest in wetlands (Chapter 3).

Water economy in the Arctic

Comparative studies showed a link between incubation constancy and body mass in waterfowl (Thompson & Raveling, 1987). For example, large goose species generally take fewer recesses less frequently than smaller ones due to their relatively lower mass-specific metabolic rate and greater amount of nutrient reserves (Afton & Paulus, 1992). Although these authors have typically emphasized energetic constraints to explain interspecific variations in incubation patterns, we argue that water requirement may be an additional constraint on recess frequency. Indeed, geese are likely to face high water needs during reproduction. First, animals suffer an increased tendency to dehydrate under cold and windy conditions such as those typically encountered during the Arctic summer (Willmer, Stone & Johnston, 2000). Second, birds face major physiological challenges to regulate their water balance while fasting during incubation (Le Maho *et al.*, 1981). In eider ducks (*Somateria molissima*), Criscuolo *et al.* (2000) suggested that birds adjusted their drinking

behaviour during incubation recesses to regulate their body water while fasting. Anecdotal evidence also suggests that snow geese have high evaporative water loss, and hence requirements. J. Larochelle, (pers. com.) and Ratté (1998) reported high water loss by goslings during experiments in metabolic chambers, and geese feeding in farmlands typically return to roosting ponds in mid-day to drink under sunny conditions, though not under overcast skies or rain (Béchet *et al.*, 2003). We therefore contend that the water economy of birds, which has received little attention in comparison to food habits even after the seminal paper of Bartholomew & Cade (1963), has been hitherto underrated in reproductive studies of birds.

Change in rainfall abundance resulting from climate warming could be at least as great as change in air temperature but future trends in precipitations are especially difficult to predict (Allen & Ingram, 2002). Although mapping spatial variation in precipitation levels in coming years is a challenge, simulations nonetheless predict a mean increase of 10 % in the next 20 years (6 mm/ month) around the Canadian Arctic, a larger increase than for the world as a whole (IPCC, 2001; ACIA, 2005). Given that goose nesting success is positively linked to rainfall, we could expect some changes in goose productivity in the future under such a scenario. However, the net change in reproductive success to changing precipitation regimes will be difficult to predict because, with the concomitant expected temperature warming, the relative availability of wetland and drier mesic tundra habitats and the proportion of geese nesting in these two habitats may also change, in addition to their nesting success in each habitat. Our results nonetheless suggest that the latter variable will be strongly influenced by an interaction between physiological water requirements and nest predation.

Conclusion

In this study, we showed a critical interaction between abiotic and biotic factors, which provided a link between climate and goose nesting success via a top-down effect. The role of water in the functioning of tundra ecosystems is only beginning to emerge in the literature (Hodkinson *et al.*, 1999) and our study provides an illustration of it. How much birds like geese will balance their water requirements with nest predation risk in face of

both rising temperature and precipitation remains an open question for the moment. Further studies are needed to quantify the projected effects of rainfall and temperature changes on the dynamic of arctic-bird populations.

TABLE 1. Model selection for the effect of habitat type (wetland vs. mesic tundra) and annual rainfall on daily nest survival (S) of greater snow geese on Bylot Island, 1995-2005 ($n = 3024$). The most relevant models are ranked by their AICc value. For each model, the difference in AICc values is given in relation to the most parsimonious model (ΔAICc), the model's AICc weight (ωAICc), the number of estimable parameters (np) and the deviance.

Type of Model	Model	ΔAICc	ωAICc	np	Deviance
	(1) $S_{(h*t) + d}$	0.00	0.54	23	5133.87
	(2) $S_{(h*t) + d + age}$	1.84	0.21	24	5133.72
With time variation	(3) $S_{h + t + d}$	2.49	0.15	13	5156.38
	(4) $S_{h + t + d + age}$	3.65	0.08	14	5155.54
	(5) $S_{t + d + age}$	22.42	0.00	13	5176.31
With time-dependent	(6) $S_{(h*P) + d}$	273.71	0.00	5	5443.58
covariates	(7) $S_{h + P + d}$	308.36	0.00	4	5480.23
Without time variation	(8) $S_{h + d}$	425.87	0.00	3	5599.77

Subscripts: age = age of the nest when found (date found minus the nest initiation date), d = linear effect of incubation day, h = habitat (wetlands vs. mesic), P = precipitations (dry vs. wet years), t = year, + = additive effect, * = interactive effect.

TABLE 2. Model selection for the effect of experimental increase in water availability on daily nest survival (S) of greater snow geese nesting in two habitats (wetlands vs. mesic tundra) on Bylot Island, 2005 ($n = 300$). The most relevant models are ranked by their AICc value. For each model, the difference in AICc values is given in relation to the most parsimonious model (ΔAICc), the model's AICc weight (ωAICc), the number of estimable parameters (np) and the deviance.

Model	ΔAICc	ωAICc	Np	Deviance
(1) S_{c+age}	0.00	0.37	3	402.69
(2) S_c	1.33	0.19	2	406.03
(3) $S_{c+h+age}$	1.93	0.14	4	402.63
(4) S_{c+d}	3.02	0.08	3	405.71
(5) S_{c+h}	3.30	0.07	3	406.00
(6) $S_{c+h+d+age}$	3.92	0.05	5	402.61
(7) S_{h+age}	9.92	0.00	3	411.96

Subscripts: age = age of the nest when found (date found minus the nest initiation date), c = experimental treatment (i.e. presence of water container), d = linear effect of incubation day, h = habitat (wetlands vs. mesic), + = additive effect.

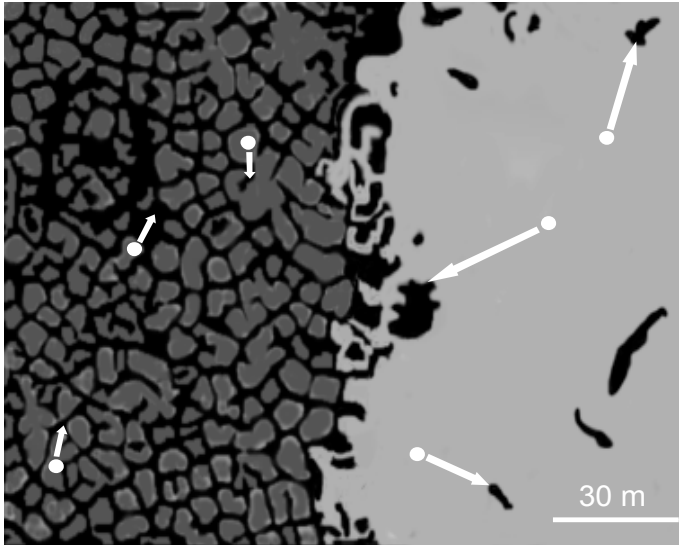


FIGURE 1. Constraints imposed by habitat on water supply in a snow goose colony. Figure based on an aerial photograph of a portion of the colony showing hypothetical goose nests (white circles) and movements during incubation recesses (white arrows) towards permanent water sources (black) either in wetlands (dark grey) or in mesic tundra (light grey).

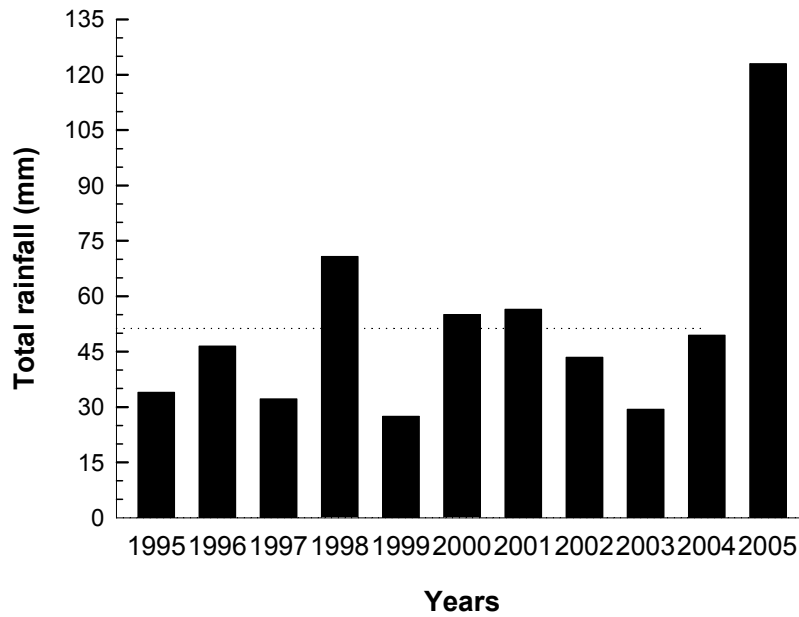


FIGURE 2. Annual rainfall abundance on Bylot Island during the snow goose nesting season (12 June to 25 July), 1995 to 2005. The dotted line shows the long-term average.

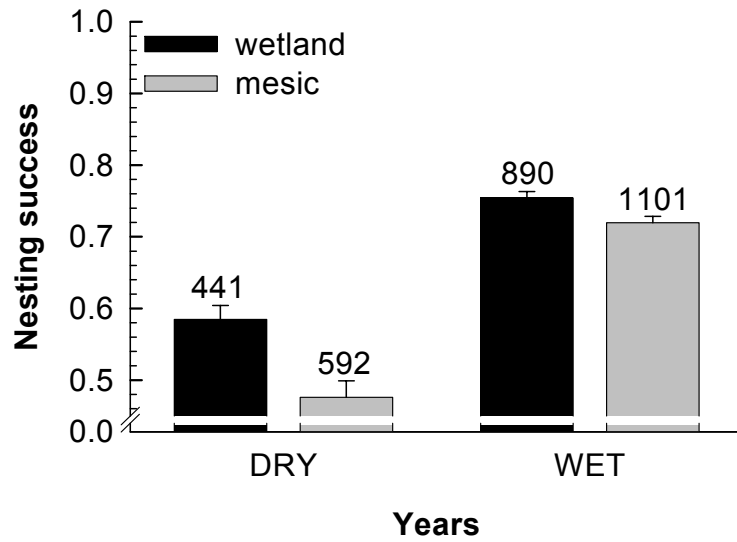


FIGURE 3. Mean (+ 1 SE) annual nesting success of snow geese on Bylot Island as a function of the habitat and annual precipitations. Wet and dry years correspond to years with rainfall abundance higher and below the 1995-2005 average, respectively.

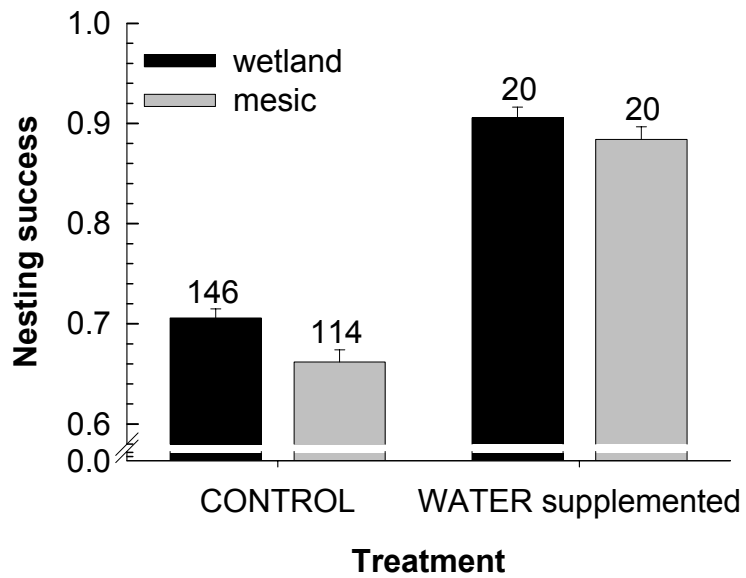


FIGURE 4. Mean nesting success (+ 1 SE) of experimental (i.e. with water containers) and control snow goose nests in two habitats on Bylot Island, 2005. Numbers over bars indicate sample size.

Chapitre 3

BREEDING DISPERSAL IN A HETEROGENEOUS LANDSCAPE: THE INFLUENCE OF HABITAT AND NESTING SUCCESS IN GREATER SNOW GEESE

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Résumé

Malgré de nombreuses études portant sur la dispersion de reproduction, il reste beaucoup d'incertitudes quant à l'effet combiné de l'hétérogénéité de l'habitat et du succès reproducteur précédent sur la fidélité à un site de nidification, et ce, à diverses échelles spatiales. Dans ce contexte, nous avons exploré les facteurs affectant la dispersion de reproduction chez la Grande Oie des neiges (*Anser caerulescens atlanticus*). Cette espèce arctique est caractérisée entre autre par l'utilisation lors de la nidification de deux habitats contrastés (humides et mésiques). De plus, la disponibilité de l'habitat au moment de la ponte variable d'une année sur l'autre est fonction du patron de fonte de neige. De 1994 à 2005, nous avons suivi individuellement le succès de nidification et la dispersion de reproduction de femelles marquées. Nous avons trouvé que ces femelles présentaient une fidélité modérée à l'échelle d'un site précis de nidification, avec notamment une variabilité individuelle considérable dans les distances de dispersion entre deux tentatives de nidification. Cette variabilité peut être partiellement due à la variabilité interannuelle dans les patrons de fonte de neige. Malgré cette contrainte environnementale, les différences d'habitat à l'échelle de la colonie de nidification ont par contre eu un effet sur le succès de nidification et sur les patrons d'établissement des nids. Les femelles nichant dans les milieux humides ont eu un meilleur succès de nidification que celles nichant en milieu mésique. De plus, les oies semblent répondre de manière adaptative à cette hétérogénéité spatiale en présentant une fidélité à leur habitat de nidification, indépendamment des patrons de fonte des neiges. D'une année sur l'autre, les oies étaient plus susceptibles de disperser des milieux mésiques vers les milieux humides, quelque soit leur succès reproducteur l'année précédente et sans coûts apparents en terme de performance reproductrice immédiate. Le caractère imprévisible des patrons de fonte de neige et le faible coût d'un changement de site pourraient favoriser la dispersion des sites de reproduction, la qualité de l'habitat pourrait maintenir la fidélité à l'échelle des habitats.

Abstract

Despite numerous studies on breeding dispersal, it is still unclear how habitat heterogeneity and previous nesting success interact to determine nest site fidelity at various spatial scales. In that context, we investigated factors affecting breeding dispersal in greater snow geese (*Anser caerulescens atlanticus*), an Arctic breeding species nesting in two contrasting habitats (wetlands and mesic tundra) with variable pattern of snow-melt at the time of settlement in spring. From 1994 to 2005, we monitored the nesting success and breeding dispersal of individually marked females. We found that snow geese showed a moderate amount of nest site fidelity and considerable individual variability in dispersal distance over consecutive nesting attempts. This variability could be partly accounted for by the annual timing of snow-melt. Despite this environmental constraint, habitat differences at the colony level consistently affected nesting success and settlement patterns. Females nesting in wetlands had higher nesting success than those nesting in mesic tundra. Moreover, geese responded adaptively to spatial heterogeneity by showing fidelity to their nesting habitat, independently of snow-melt pattern. From year to year, geese were more likely to move from mesic to high quality wetland habitat, regardless of previous nesting success and without cost on their subsequent nesting performance. The unpredictability of snow-melt and the low cost of changing site apparently favour breeding site dispersal although habitat quality promotes fidelity at the scale of habitat patches.

Introduction

Dispersal and its complement, fidelity, are key biological processes of population dynamic, linking patterns of animal movement, habitat use and reproductive strategies at different spatio-temporal scales (review in Clobert *et al.*, 2001). Dispersal is traditionally divided between natal dispersal (the movement of juveniles from the natal site to the site of first breeding or potential breeding) and breeding dispersal (the movement between breeding sites of individuals that have previously reproduced) (Greenwood, 1980; Greenwood & Harvey, 1982).

Even though breeding site fidelity is often high, especially in long-lived species, many ecological factors may affect its intensity, both inter- and intra-specifically (MacDonald & Johnson, 2001). Under the assumption that settlement pattern should maximize fitness (Holt & Barfield, 2001), breeding site fidelity is predicted to be inversely related with habitat heterogeneity in space and time but positively related to the cost of dispersal (Switzer, 1993 and references therein). When habitat quality is predictable from year to year, dispersal of an individual may be favoured, for instance after a reproductive failure (e.g. Wiklund, 1996). According to the public information hypothesis, individuals may also use information provided by conspecifics for habitat choice (Boulinier *et al.*, 1996; Danchin, Boulinier & Massot, 1998; Valone & Templeton, 2002; Doligez *et al.*, 2003). In contrast, unpredictable habitats should promote fidelity independently of previous reproductive outcome. In that case, previous knowledge on the distribution of local resources and predation risks are additional factors that should promote a high fidelity (Greenwood, 1980). Despite numerous efforts to study the proximate conditions leading to high or low rates of breeding dispersal, it is still unclear how habitat heterogeneity and previous nesting success interact to determine nest site fidelity at various spatial scales (Greenwood & Harvey, 1982; Clobert *et al.*, 2001).

Until recently, understanding the causes and consequences of dispersal have been limited both by practical difficulties in the field and the lack of statistical tools to adequately model the spatial movements of marked animals (review in Bennetts *et al.*, 2001). When used in combination with information on habitat use, the recently-developed multi-state capture-

recapture models by Brownie *et al.* (1993) now offer a powerful framework to examine these questions (e.g. Blums *et al.*, 2003; Cam *et al.*, 2004). We used this approach to study individual movement patterns across habitats of nesting greater snow geese (*Anser caerulescens atlanticus*). We monitored marked individuals of this colonial, long-lived species in the High Arctic over an 11-year period.

Lepage *et al.* (1996) inferred a low breeding site fidelity in this species based on the use of different nesting areas in consecutive years on Bylot Island (Nunavut, Canada). However, Lepage *et al.* (1996) did not use marked individuals and failed to consider habitat use at the individual level. Greater snow geese nest either in wetlands or mesic tundra. Wetlands offer the best feeding opportunities (Gauthier, 1993; Hughes, Reed & Gauthier, 1994; Gauthier, Rochefort & Reed, 1996; Massé, Rochefort & Gauthier, 2001) and a lower predation risk on eggs than mesic tundra due to the presence of water that can impede movements of terrestrial predators (Reed, Hughes & Gauthier, 1995, Chapter 1). Wetlands may thus offer a higher fitness payoff than mesic tundra. This dichotomy in habitat quality provided an opportunity to investigate how habitat heterogeneity within a colony affected breeding site fidelity and the probability of moving across habitats among dispersers. Our main objective was thus to explore the links between habitat heterogeneity, nesting success and breeding dispersal of greater snow geese. We first measured habitat availability and annual snow-melt pattern, which may affect availability in arctic-nesting species. During the breeding period, we measured how choice of nesting habitat affected nesting success. To investigate adaptive responses in breeding dispersal and habitat use, we tested whether settling decisions were influenced by the fate of previous nesting events. We predicted that the distance between nesting sites in year i to year $i+1$ would be lower after a success than after a failure. We also predicted that the habitat with greater nesting success would attract more settlers, thereby increasing nest density. Finally, we predicted that, if dispersal was costly, nesting parameters (nest initiation date, clutch size, nest success) in year $i+1$ would be affected by dispersal distance between years i and $i+1$.

Material and methods

Study area and species

Data were collected on Bylot Island, Sirmilik National Park, Nunavut Territory, Canada, between 1990 and 2005. This island is the primary breeding site for greater snow geese, with more than 20,000 breeding pairs, the majority of which are nesting in the same colony (Reed, Hughes & Boyd, 2002). Wetlands and mesic tundra are the two dominant habitat types although the latter is 10 times more abundant than the former (Massé, Rochefort & Gauthier, 2001). Wetlands are typically found in small patches scattered through a mesic landscape and most wetlands occur in polygon-patterned ground created by frost action in the ground of lowland tundra (Gauthier, Rochefort & Reed, 1996; Fortier & Allard, 2005). Low-centre polygons form lakes and ponds whereas high-centre ones are surrounded by water channels. Both types have a rich cover of graminoids, the preferred food-plants of greater snow geese (Gauthier, Rochefort & Reed, 1996; Massé, Rochefort & Gauthier, 2001). Mesic tundra is found in drier lowlands, gentle slopes of small hills and low altitude plateaus. Standing water is scarce there and is found only in isolated small ponds or streams. This habitat is dominated by prostrated shrubs with a sparse cover of forbs and graminoids (Gauthier, Rochefort & Reed, 1996).

The greater snow goose is a precocial species that form permanent, monogamous pair bonds (Mowbray, Cooke & Ganter, 2000). Like all waterfowl, greater snow geese show a female-biased philopatry and nest site selection is primarily driven by females (thus, breeding dispersal should not be influenced by rearing). Nest site use ends at hatch because soon after hatching (<1 d), goslings leave the nest with their parents to distant brood-rearing areas (Mainguy et al. 2006).

Field methods

We caught greater snow geese over a 7-day period in early August every year from 1990 to 2005. With the help of a helicopter, groups of moulting geese and their young were herded into corral traps by people on foot (see Menu, Gauthier & Reed, 2001 for details). Most of

the captured birds were successful nesters with their young of the year, as most non-breeders and failed-nesters had left the island to moult elsewhere or had regained flight capacity at the time of banding (Reed *et al.*, 2003a). All birds captured for the first time were fitted with a metal U.S. Fish and Wildlife Service leg band. A sample of adult females was chosen randomly and fitted with individually coded plastic neck bands. The banding protocol was approved by the Animal Care Committee of Université Laval in accordance with the guidelines of the Canadian Animal Care Council.

During laying and incubation (June-July), we systematically searched the main nesting colony for neck-banded females with a spotting-scope (20-60 X). Searches for marked females were also conducted at secondary nesting areas where geese occasionally nest, mostly in association with snowy owls (*Buteo scandiaca*) (Bêty *et al.*, 2001). We placed markers 10 m from the nests and recorded the position using a Global Positioning System receiver (GPS; ± 20 m before 2000 and ± 5 m thereafter). We classified nesting habitats as wetland or mesic tundra (for nests found before 2003, habitat was assigned a posteriori by reporting the nest position on a detailed habitat map; see below). We revisited nests once during incubation and again at hatching. Following Bêty *et al.* (2001), we determined laying date of the first egg and considered nests as successful if at least one egg hatched.

We mapped habitat types of the main breeding colony using digitized vertical aerial photographs (approx. scale 1:13,000). Wetlands, mesic tundra, rivers, lakes, ponds and xeric habitats were classified into different layers in an ArcGIS database (ESRI, 2004). We ground-truthed the accuracy of this database in the field with 1000 points located randomly in the landscape and found that 98.7 % of the locations were correctly assigned to a given habitat (± 5 m). We assessed the proportion of land within each habitat that was suitable for nesting. The criteria used were: 1) mesic sites with no standing water and/or no rocks; 2) dry polygon rim of low-centre wet polygons; and 3) the dry central portion of high-centre polygons. During snow-melt, percentage of snow-cover in the colony was estimated visually every 2-day annually. Each year, we used the value recorded at the median date of nest initiation to evaluate snow-cover constraints on settling pattern.

Data analysis

Nesting success

We estimated nesting success of marked females with the daily nest survival (S) procedure of program MARK v4.2 (Dinsmore, White & Knopf, 2002). This is an improvement over previous methods (e.g. Mayfield method, Johnson, 1979) because it does not assume constant daily nest survival probabilities and allows the use of individual covariates. We included the age of the nest at the time of discovery (date found minus estimated laying date) as an individual covariate in the model because predation rate varies during the incubation period (V. Careau & N. Lecomte, unpubl. data). There was no reason to believe that this effect varied among habitats so we only modelled year specific relationships between ‘age’ and nest survival. We considered the model with full time (t ; i.e. years), habitat (h), incubation day (linear effect; d), and age effects with relevant interactions as the most general model. We used the Akaike’s Information Criterion modified for small sample size (AICc) to select the most parsimonious model (lowest AICc value, Burnham & Anderson, 1998). We estimated nesting success as the product of daily nest survival for the mean duration of laying and incubation (27 days).

Movements between habitats

We used multi-state models to estimate survival, re-encounter, and transition probabilities of marked nesting females with maximum likelihood methods (Lebreton & Pradel, 2002). States were the two nesting habitats, wetland and mesic tundra. We modelled habitat (h) and time (t) effects on apparent survival probability (denoted S), re-encounter probability (p), and transition probability (Ψ). The first encounter of a female at a nest was considered as the initial marking. We started by fitting a general model with full habitat and time effects and their interactions (denoted by asterisks) (S_{h*t} , p_{h*t} , Ψ_{h*t}). We ran goodness-of-fit (GOF) tests for multi-state models (Pradel, Wintrebert & Gimenez, 2003) using program U-Care 2.2.1 (Choquet *et al.*, 2001).

We used the AICc for model selection and report the relative weight of evidence in favour of a particular model (ω AICc) (Burnham & Anderson, 1998). We analyzed our data with

the program MARK v4.2 (White & Burnham, 1999). In presence of uncertainty in model selection, we used the model averaging procedures implemented in MARK to estimate model-weighted average parameter values and their unconditional standard errors.

Other statistics

We used the average nearest neighbour module in ArcGIS (ESRI, 2004) to detect possible clustering in the distribution of wetland patches (z test) because a heterogeneous distribution might bias our ability to detect marked females and to measure breeding dispersal in both habitats equally. We used the median rather than the mean to describe dispersal distance because the distribution was highly skewed. We compared inter-annual distance in nest sites between successful and failed breeders and between individuals nesting in different habitats with the Mann-Whitney U -test. We compared inter-annual distances between nest sites and the average radii of habitat patches to look for evidence of patch change by nesting females (U -tests), as suggested by Clark and Shutler (1999). The use of Euclidian distances did not bias dispersal measure because the distribution of wetland patches was homogenous across the study area (see results).

We used a χ^2 statistic to compare the distribution of nests across habitats with habitat availability. We compared nest densities of marked females between habitats with a t -test. We used correlation analyses to measure the association between breeding dispersal and snow-cover. Finally, we used a logistic regression model (Trexler & Travis, 1993) to test the null hypothesis that nesting success was not affected by breeding dispersal distance.

These statistical analyses were performed using the SAS software (SAS, 1989-2001). For all data, normality was checked with the Kolgomorov-Smirnov test (Lilliefors option). All probabilities are two-tailed and significance level was set at 0.05. All means are reported with SE, unless mentioned otherwise.

Results

Habitat availability

Within the snow goose breeding colony, 147 wetland patches covered a total area of 4.9 km² distributed over 94.9 km² of mesic tundra. The mean area of wetland patches was 0.034 km² (range: 0.001-0.250) with a mean perimeter of 1.10 km (range: 0.01-10.00). Because wetlands consisted in a mixture of ponds, wet areas and dry sites, only 51% of the habitat in wetland patches (2.5 km²) was suitable for nest establishment compared with 99% in mesic tundra (94.0 km²). The spatial distribution of wetland patches in the colony did not differ from a random distribution pattern ($z = -0.70$, $P = 0.48$). The timing of snow-melt varied annually and the snow-cover at the peak of egg-laying ranged from 40 to 85% (average: 63%).

Nesting success and habitats

From 1990 to 2005, we found the nests of 565 marked females. Top models indicated that daily nest survival differed among habitats and years, increased with the day of incubation, and possibly with the age that a nest was found (Table 1). Because of uncertainty introduced by the latter effect, we averaged daily nest survival across the two top models before transforming it into nesting success. Nesting success was always higher in wetland (73.0 % \pm 0.1; range: 54 – 85 %) than in mesic tundra (47.9 % \pm 0.4; range: 3-84 %) but varied considerably among years, with success being lowest in 1999 and highest in 2000 (Figure 1).

Breeding dispersal

Among the 565 marked females found nesting, 2, 8, and 59 females were seen nesting four, three, and two years in a row, respectively. The median inter-annual distance between two consecutive nests was 215 m ($n = 59$) with considerable variation among individuals (range 1 to 28,936 m; Figure 2) although 67 % of geese moved < 500 m (females used only once to avoid pseudo-replication). Even when the two females that had moved outside the main colony were excluded from the analysis, the median inter-annual distance between nests

was 210 m (range: 1 to 4,378 m). Only two females nested in the same nest bowl or very close (inter-annual distance < 5 m, below the GPS accuracy). When examining individuals for which we had more than two successive dispersal movements in a row, we found variation in breeding dispersal for the same female, with maximum distances between nests ranging from 69 to 4,322 m (median = 374 m, $n = 10$).

We found no effect of nesting success in year i on the distance between nest sites in years i and $i+1$ ($U = 131$, $P = 0.22$, $n = 54$). Similarly, habitat used in year i had no effect on the distance between years i and $i+1$ ($U = 338$; $P = 0.785$, $n = 54$).

Inter-annual distances between nest sites of females that initially nested in wetlands (median = 172 m; range 3 to 28,936, $n = 17$) exceeded the median radius of wetland patches (115 m, $n = 58$; $U = 564.50$, $P = 0.03$). Among females that nested during two successive years in wetlands, 9 out of 11 changed wetland patch.

Probability of movements between habitats

The GOF test of the general multi-state model indicated no lack of fit ($\chi^2_{33} = 24.4$, $P = 0.86$). We detected no habitat effect on re-encounter and survival probabilities (models 3 and 8, respectively in Table 2). This further suggests that habitat heterogeneity had no effect on our ability to detect individuals.

The best model in Table 2 retained equal transition probabilities between the two habitats and time effect on capture probabilities ($S p_t \Psi$) although the second model, which assumed a habitat effect on transition probabilities ($S p_t \Psi_h$), was also realistic ($\Delta AICc < 2$). Because of this uncertainty, we used parameter values averaged between these two models. Although the probability that females would move from wetlands to mesic tundra (0.173 ± 0.049) was slightly higher than the converse (0.160 ± 0.039), the fidelity of females to their nesting habitat was high in both habitats (wetlands: 0.827 ± 0.049 , mesic tundra: 0.840 ± 0.039). However, since the availability of mesic tundra for nesting is 37.6 times higher than wetlands (94.0 vs. 2.5 km²) in the breeding colony but the ratio in transition probabilities between the two habitats was nearly equal (1.1), then the observed probability of moving

from wetlands to mesic tundra was 34.7 times lower ($37.6/1.1$) than expected by chance alone.

Use vs. availability of nesting habitat

Overall, we found the nests of 124 marked females in wetlands and 441 in mesic tundra. When taking into account the availability of these two habitats, marked females showed a strong preference for nesting in wetlands ($\chi^2_1 = 233$; $P < 0.001$; females seen in two or more years were used only once). Similarly, average nest density of marked females was higher in wetlands than in mesic tundra ($5.34 \text{ nests/km}^2 \pm 1.48$ vs. 1.78 ± 0.50 ; $t_{16} = 2.32$, $P = 0.033$). Distances between nest sites in years i and $i+1$ increased with snow-cover in year $i+1$ ($r = 0.91$; $P = 0.03$; $n = 7$ years), yet the proportion of females nesting in wetlands did not change with snow-cover ($r = -0.41$, $P = 0.27$, $n = 9$ years).

The relative timing of nesting and clutch size in year $i+1$ did not vary with dispersal distance between year i and $i+1$ (initiation: $r = -0.07$, $P = 0.76$, $n = 25$; clutch size: $r = 0.37$, $P = 0.08$, $n = 22$). Similarly, breeding dispersal distance had no effect on nesting success in year $i+1$ ($\chi^2_1 = 0.17$; $P = 0.68$; $n = 37$).

Discussion

Herein, we show that habitat differences at the colony scale affect settlement patterns and nesting success in greater snow geese. Even though wetlands were a relatively scarce habitat, geese preferentially settled in wetlands and benefited from a greater nesting success than in mesic tundra. Although geese showed fidelity to their previous year's nesting site, they were more likely to move from low-quality mesic tundra habitat to high-quality wetland habitat when accounting for the relative area covered by the two habitats.

Nest site vs habitat fidelity

Lepage et al. (1996) previously suggested low site fidelity in greater snow geese on Bylot Island based on the distribution of nests of unmarked birds. This apparent low fidelity was surprising considering the disadvantages often associated with breeding dispersal; e. g.

losing familiarity with a site (Smith, 1978; Shutler & Weatherhead, 1994; Badyaev & Faust, 1996), the costs of acquiring knowledge in unfamiliar areas (Greenwood, 1980; Rohwer & Anderson, 1988; Gauthier, 1990; Anderson, Rhymer & Rohwer, 1992) and the risk of possibly nesting in sub-optimal habitats. In this study, we used marked individuals and showed that, even though very few females re-used the same exact nest sites, about two thirds dispersed relatively short distances (<500 m) between consecutive years. Although our results show that greater snow geese exhibit levels of breeding dispersal comparable to other goose species (Table 3), they nonetheless indicate one of the lowest level of site fidelity. However, care should be taken when comparing different studies of dispersal because of variations in detection probability and the scale of covered area, with long-distance movements being more likely to be missed than shorter ones (Van Noordwijk, 1995).

There was considerable intra- and inter-individual variation in breeding dispersal, ranging from specific site fidelity (nest almost in the same bowl) to dispersal far away from the studied colony. Breeding dispersal is sensitive to the scale of observation (Wiens, 1989), and thus, we cannot rule out the possibility that the magnitude of dispersal in our study is biased towards short distances. Nonetheless, our results suggest that some individuals may be using different breeding dispersal tactics depending on environmental conditions in specific years. The two longest movements we documented were individuals that moved away from the main colony to nest in association with snowy owls (*Bubo scandiacus*). By nesting in the vicinity of owl nests, females gained protection from predators such as arctic foxes (*Alopex lagopus*), which are excluded from raptor territories (Haeming, 2001). Such symbiotic nesting, however, is infrequent and limited because snowy owls nest only during peak lemming years (once every 3 to 4 years) and at low density (Bêty *et al.*, 2001).

The increased level of breeding dispersal in years of late snow-melt indicates that the snow-melt pattern interfered with fidelity to a specific site (Lepage, Gauthier & Reed, 1996). Because nesting early is important to increase reproductive success (Lepage, Gauthier & Menu, 2000; Bêty, Giroux & Gauthier, 2004), females may select a new nest site when the one used the previous year is covered by snow. Hence, greater snow geese may trade-off between the benefits of nesting at their previous nest site and the laying at an optimum date.

Conversely, we found evidence of fidelity at another spatial scale, the one of the habitat type (mesic tundra or wetlands). Moreover, fidelity to a specific habitat was not affected by snow-cover. By remaining faithful to one habitat, females may minimize the costs of dispersal to a new nesting site by using the same habitat year after year. As we measured no effects of dispersal distance on nesting parameters, costs of dispersal should be low, thereby allowing inter-annual movements of individuals in case of reduced habitat availability due to snow-cover.

Nesting habitat use

From an individual perspective, dispersal can be closely linked to habitat selection theory (Ronce *et al.*, 2001), where fitness maximization is a central tenet (Holt & Barfield, 2001). Our study reveals asymmetric movements between habitats, with greater snow geese preferring to settle in wetlands where both nesting success and food quality are higher than in mesic tundra. Predation is the principal determinant of nesting success in this species but is also inversely density-dependent at the colony scale (e.g. Bêty *et al.*, 2001). Therefore, high nesting density in wetlands could not only be an adaptive response to this high quality habitat, but may also enhance habitat quality through a positive feedback loop, thus affecting the nest habitat selection process.

To make adaptive choice, individuals usually have to rely on proximate cues of quality when choosing habitats that are heterogeneous in time and space (Doligez, Danchin & Clobert, 2002 and references therein; Doligez *et al.*, 2003). Some researchers have suggested that individuals rely on past breeding experience to assess the quality of a site (Switzer, 1993, 1997), which may explain why birds are often more likely to move following a breeding failure than a success (e.g. Cooke & Abraham, 1980; Gauthier, 1990). However, our results show that previous nesting success has little impact on settlement in the following year.

Two other strategies of breeding habitat selection are possible. First, birds may use environmental cues correlated to nesting success, such as vegetation types or topographic features (Clark & Shutler, 1999). The two main nesting habitats recognized in this study

differ in many ways (e.g. vegetation, abundance of water, presence/absence of polygon tundra; (Gauthier, Rochefort & Reed, 1996), and birds could use such cues at this scale. However, Tremblay et al. (1997) showed that vegetation and topographic features in the immediate nest vicinity (i.e. at a small scale) had no effect on nesting success of greater snow geese. Alternatively, there is growing evidence that public information provided by conspecifics (presence of neighbours or their local breeding success) may be an important cue used by individuals in their breeding settlement decision (Boulinier *et al.*, 1996; Valone & Templeton, 2002; Danchin *et al.*, 2004). Since movements are biased towards wetlands where both average nesting success and density is consistently higher than in mesic tundra, fidelity to habitat type could be explained by the public information hypothesis. According to this hypothesis, we would also expect little heterogeneity in nesting success within individual habitat patches or among similar habitat patches across the colony, two predictions for which we have some evidence (Reed, Gauthier & Pradel, 2005). However, in order to conclusively discriminate between the environmental cues and the public information hypotheses, experimental manipulation of nesting success would be required.

Conclusion

We conclude that nesting greater snow geese showed adaptive responses in their use of habitat. Direct benefits of fidelity to specific nest sites but not to a particular habitat are reduced due to (1) the unpredictable snow conditions in the Arctic at the critical time of nest establishment and (2) the occasional symbiotic association with aggressive raptors. Future work should aim at determining precisely the benefits associated with nesting in wetlands and to what extent predation may influence the distribution of geese at the landscape level.

TABLE 1. Model selection for the effect of habitat type on daily nest survival (S) of greater snow geese on Bylot Island, from 1998 to 2005 ($n = 666$ nests). The most relevant models are ranked by their AICc value. For each model, we give the difference in AICc values relative to the most parsimonious model (ΔAICc), the model's AICc weight (ωAICc), the number of estimable parameters (np) and the deviance.

Model	ΔAICc	ωAICc	np	Deviance
(1) S_{h+t+d}	0	0.671	10	2695.67
(2) $S_{h+t+d+age}$	1.72	0.284	11	2695.38
(3) $S_{(h*t)+d+age}$	6.18	0.030	17	2687.82
(4) $S_{(h*t)+d}$	7.79	0.013	18	2687.42
(5) S_{t+d}	23.34	<0.001	8	2721.01
(6) $S_{h+d+age}$	33.02	<0.001	9	2730.69

Subscripts: age = age of the nest when found (date found minus the nest initiation date), h = habitat effect (wetlands vs. mesic), d = linear effect of incubation day, t = year, + = additive effect, * = interactive effect.

TABLE 2. Model selection of movements between habitats of 155 nesting female greater snow geese on Bylot Island, from 1996 to 2005. Parameters include survival (S), re-encounter (p), and transition (Ψ) probabilities and the 8 most relevant models are ranked by their corrected AICc value. For each model, we give the difference in AICc values relative to the most parsimonious model (ΔAICc), the model's AICc weight (ωAICc), the number of estimable parameters (np) and the deviance.

Model	ΔAICc	ωAICc	np	Deviance
(1) $S p \Psi_h$	0	0.497	5	190.46
(2) $S p \Psi$	1.39	0.248	4	194.18
(3) $S p_h \Psi$	6.54	0.021	5	195.07
(4) $S p \Psi_t$	12.04	0.001	13	180.73
(5) $S p_t \Psi_h$	12.24	0.001	14	177.74
(6) $S p_t \Psi$	12.61	0.001	13	181.29
(7) $S_t p \Psi_h$	15.23	<0.001	13	183.92
(8) $S_h p \Psi_h$	16.63	<0.001	16	175.39

Subscripts: h = habitat (wetlands or mesic tundra), t = year.

TABLE 3. Comparison of inter-annual median distances (m) between nest site locations of individual females in three goose species.

Species	Median	Range	<i>n</i>	Area (km ²) and period of study	References
Canada goose	5	0-50	100	West Midlands, UK, (~100)	(Lessells, 1985)
<i>Branta Canadensis</i>				1977-1979	
	50			Varenes, CA	Giroux, JF, unpublished data
Cackling Canada goose	150	0-2,280	140	Kuskokwim Delta, Alaska, USA (3.6)	(Fowler, 2005)
<i>Branta canadensis minima</i>				1994-1997	
Lesser snow goose	155	3-6,000	467	La Pérouse Bay, MB, CA, (~36)	(Cooke & Abraham, 1980)
<i>Anser caerulescens caerulescens</i>				1974-1978	
Black brant	200	0-4,600	371	Tutakoke River, Alaska, USA, (~12)	(Lindberg, Sedinger & Rexstad, 1995)
<i>Branta bernicla nigricans</i>				1987-1993	
Greater snow goose	215	1-28,936	54	Bylot Island, Nunavut, CA (600)	This study
<i>Anser caerulescens atlanticus</i>				1998-2005	

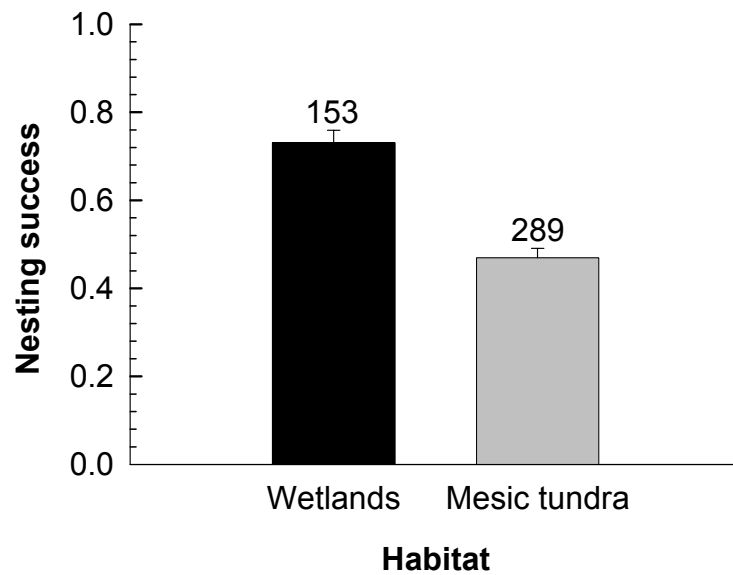


FIGURE 1. Annual nesting success of marked greater snow geese in high-(wetland) and low-(mesic tundra) quality habitat on Bylot Island from 1998 to 2005. Means + 1 SE with sample size over bars are presented.

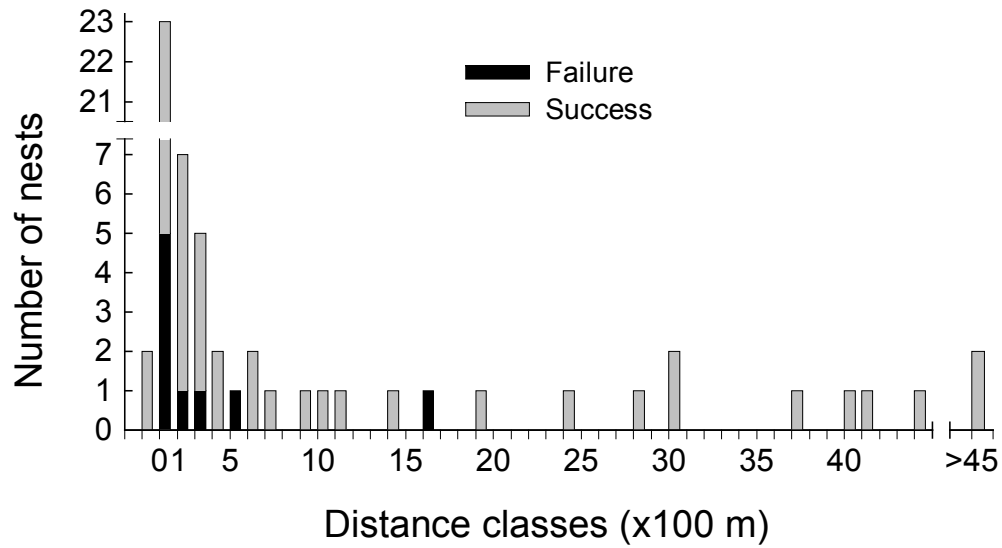


FIGURE 2. Frequency distribution of inter-annual distances between two consecutive nest sites of female greater snow geese according to the reproductive outcome (failure or success) in the first year of nesting, Bylot Island, 1998 to 2005. Nests are grouped by 100-m intervals. The <0 interval include nests at ≤ 5 m (the accuracy of our measuring instruments) and the interval >4,500 m includes two distances, 25,116 m and 28,936 m.

Chapitre 4

FINE-SCALE GENETIC STRUCTURE IN A COLONIAL BIRD: BALANCING SEX-BIASED DISPERSAL AND REARING SITE FIDELITY

Lecomte, N., Gauthier, G., Bernatchez, L., Giroux, J.-F. & Milot, E. 2006. Manuscrit à soumettre à *Nature*.

Résumé

Nos a priori sur les composantes biodémographiques d'une espèce guident souvent notre compréhension de sa structure spatiale et génétique. Selon la théorie, l'observation de forts flux géniques associés à la dispersion entraînent une homogénéisation génétique des populations. Toutefois, il a été proposé que des mécanismes de dispersion non-aléatoire pourraient permettre une différenciation génétique entre population naturelles, à fine échelle spatiale. Par contre, il n'est pas encore certain qu'une telle divergence génétique puisse s'établir sous un fort régime de dispersion de naissance et de reproduction. En utilisant des marqueurs de polymorphismes de longueurs de fragments amplifiés (AFLP - Amplified Fragment Length Polymorphism) chez la Grande Oie des neiges (*Anser caerulescens atlanticus*), nous présentons des évidences de regroupements génétiques à fine échelle spatiale correspondant à des sites d'élevages distincts et séparés de 5 à 30 Km. Une telle structure est surprenante étant donné que l'appariement se fait à 3,000 Km des quartiers de reproduction et l'existence d'un fort taux de dispersion chez les mâles. De plus, nous montrons que les individus répartis dans les différents sites d'élevage sont en fait mélangé durant la nidification et ce, sans regroupement préférentiels entre individus de sites d'élevage identiques. Lorsque les conditions favorables permettent la nidification d'individus en dehors de la colonie, ceux qui le font se répartissent en fonction de leur appartenance à un site d'élevage précis. Chez les oiseaux nidifuges, les approches génétiques basées sur les sites de nidification plutôt que sur les sites d'élevage peuvent donc apporter des patrons très différents de structuration génétique à fine échelle spatiale. Cette divergence pourrait être due à une fidélité aux sites de nidification beaucoup plus flexible qu'aux sites d'élevage.

Abstract

Our understanding of the spatial and genetic structure of populations is commonly driven by our a priori knowledge of life-history traits of the target species. When high rates of gene flow through dispersal are observed, models predict genetic homogenization of populations. Recently, non-random dispersal has been advanced as a mechanism promoting genetic differentiation at fine-spatial scales in natural populations. However, it remains unclear whether such genetic divergence could arise when both natal and breeding dispersal are thought to be high. Using AFLP (Amplified Fragment Length Polymorphism) markers in greater snow geese (*Anser caerulescens atlanticus*), a species where male-biased dispersal is thought to be high, we document a fine-scale genetic clustering between spatially distinct rearing sites, located only 5-30 km apart, even though pairing occurred more than 3,000 km away from the breeding grounds. In addition, we show that individuals segregated into different rearing sites are in fact spatially mixed during nesting and we found no evidence of structure among groups of nests dispersed in the nesting colony. When favourable nesting conditions allow birds to nest away from the colony, those that did so are a non-random sample of individuals as they segregate spatially according to their membership to the nearest rearing site. We thus show that looking for a fine scale genetic structure based on nesting sites rather than on rearing sites may be misleading in precocial birds, possibly because nest site fidelity is a more flexible strategy than rearing site fidelity.

Introduction

The spatial structure of natural populations has major consequences both for contemporary population dynamics and long-term evolutionary changes. Dynamically, the rate of dispersal among different sites will determine to what extent local populations may fluctuate independently or as units of a meta-population (Hanski & Gaggiotti, 2004). Evolutionarily, the level of gene flow will determine how local populations are bound together as cohesive units, and at what scale evolutionary trajectories may diverge (Ross, 2001; Waples & Gaggiotti, 2006). Assuming a causal relationship between dispersal, gene flow and genetic structure, high rates of dispersal are often considered as a proxy of low genetic structure, especially when selection is thought to be similar across environments (Bohonak, 1999). However, two recent studies on blue tits (*Parus major*) showed that, when dispersal is directional, genetic differentiation can occur at a very fine spatial scale (1-8 km) in natural populations even under a regime of frequent and constant gene flow (Garant *et al.*, 2005; Postma & vanNoordwijk, 2005). Empirical evidence of such processes is still rare, partially due to the shortage of fine-scale studies of population structure linking genetic and demographic data (Ross, 2001), and thus their generality remains an open question.

There is a growing interest for the determination of fine-scale spatial structure in wild populations using genetic techniques (Shorey *et al.*, 2000; Nussey *et al.*, 2005). Fine-scale spatial structuring is often believed to result from non-random, and/or sex-biased dispersal (Sugg *et al.*, 1996; Coltman, Pilkington & Pemberton, 2003). Kin selection, site familiarity, inbreeding avoidance and outbreeding may all reinforce or disrupt fine-scale genetic structure (Chesser, 1991; Queller, 1994). At larger spatial scales, these mechanisms have profound consequences for population differentiation and dynamic (Chesser, 1991; Sugg *et al.*, 1996; Lambin & Yoccoz, 1998). However, how dispersal affect the fine-scale genetic structure is poorly known, especially in species with weakly developed social systems (Coltman, Pilkington & Pemberton, 2003).

In birds, female-biased dispersal and male philopatry to the nesting territory is common, the opposite of what is found in mammals (Greenwood, 1980; Greenwood & Harvey, 1982).

Waterfowl, and especially geese, represent an exception to this pattern as they show the pattern typical of mammals, i.e. male-biased dispersal and female philopatry. Mate choice is thought to occur in mixed flocks during winter or spring migration, away from the breeding ground, and usually result in permanent pair bonds in geese (Cooke, MacInnes & Prevett, 1975; Robertson & Cooke, 1999; Ganter *et al.*, 2005). In that context, the flow of nuclear genes is expected to be high and mostly male-mediated, as mated males will follow their female returning to its natal site. In accordance to that, lack of large scale genetic structure has been documented in several waterfowl species, even with maternally inherited markers (Avisé *et al.*, 1992). Nonetheless, non-random pattern of genetic relatedness have recently been detected among neighbouring nests in colonies of both Canada and greater white-fronted geese (*Branta canadensis* and *Anser albifrons*) as a result of female philopatry (Fowler, Eadie & Ely, 2004; Fowler, 2005). These results suggest the existence of possible fine-scale structuring in these birds despite possible random dispersal.

In precocial birds, there is commonly a spatial segregation between nesting and rearing sites, as families move from the nest shortly after hatch to sites where young grow and fledge (Erikstad, 1985; Rotella & Ratti, 1992). In large body size birds such as geese, families can travel several kilometres away from nesting colonies to reach rearing sites with high-quality resources (Cooch *et al.*, 1993; Sedinger *et al.*, 2001; Mainguy *et al.*, 2006). Although these sites are physically segregated, geese show some fidelity to both their nesting and rearing sites (Abraham, 1980; Lindberg & Sedinger, 1998 and references therein). Therefore, this raises the possibility that fine-scale genetic structuring may occur at the scale of either the nesting site, the rearing site, or both.

The snow goose (*Anser caerulescens*) is considered a classical example of contemporary male-biased dispersal in birds (Greenwood, 1980). Previous genetic investigations at the whole species range nourished a paradigm of low genetic structure within and among spatially segregated colonies at the scale of the North American continent, and even between the two sub-species of snow geese, the lesser and the greater (*A. c. caerulescens* and *A. c. atlanticus*) (Avisé *et al.*, 1992 and references therein). Using a much larger numbers of polymorphic markers than in previous studies, we challenge this idea by testing the hypothesis that fidelity to specific nesting and/or rearing sites can promote genetic

structuring of geese and a higher relatedness within than among sites in a local breeding population, even at a small (tens of km) spatial scale.

Methods

Study population and sampling procedures

The study was conducted on Bylot Island, Nunavut, Canada (72°53'N, 79°54'W), the most important breeding site for greater snow geese with about 20,000 breeding pairs (Reed, Hughes & Boyd, 2002). The local breeding population was defined as birds nesting and rearing their brood over an area of ca 800 km², which included the largest goose colony and the best rearing habitats on the island (Figure 1). Within this area, there is one large colony where most (>95%) of the birds nest, the remaining birds nesting in small, loose colonies in various areas. In years where snowy owls (*Bubo scandiacus*) nest, many geese will nest in small colonies around the owl nests (especially in the Qarlikturvik valley) in a protective association against egg predators (Bêty et al. 2001). Good brood-rearing areas are centred on dense patches of wetlands and occur at several sites within the study area (Figure 1). Data were collected in 2003, 2004 and 2005.

During the period of moulting when the birds are flightless, adults with their young are captured on their rearing sites in individual catches of several hundreds to band them (Reed *et al.*, 2003a). In 2004, we randomly sampled adult females in one to eight catches/site at three distinct rearing sites (Qarlikturvik valley, main colony and Dufour; Figure 1; Annexe 2). In 2005, we sampled both females and males at the same three sites and at a fourth site (Camp 3 site; Figure 1) to increase the spatial coverage (Annexe 2). Overall, 241 females (99 in 2004 and 142 in 2005) and 139 adult males were sampled for genetic analyses. An additional sample of 12 females was obtained from birds similarly captured at Akimiski Island (53°12'N, 81°24'W; Figure 1) during the rearing period. These birds were lesser snow geese and were used for between sub-species comparisons.

Since adults are difficult to catch at the nest, we had to sample their embryos. In 2003, we sampled 140 hatching embryos in nests (1 embryo per nest) at the main goose colony.

Samples were about equally split among three clusters of nests located as far apart as possible within the colony (average distance between clusters: 4.27 km; average diameter of clusters: 0.38 km). These nest clusters will be hereafter referred to as nesting sites. In 2004, due to the presence of snowy owls, a few hundred goose nests were distributed in small colonies around owls in the Qarlikturvik valley area, ca 30 km away from the main colony (Figure 1), which allowed us to compare birds that nest inside and outside the main colony. Thus, in that year we sampled 150 embryos randomly located within the main colony and 32 embryos in the Qarlikturvik valley.

For adults captured on rearing sites, we collected blood from the quill of a growing secondary flight feather, whereas for hatching embryos, blood sampling followed the procedure of Lecomte *et al* (2006). Blood samples collected in the field were stored in Queen's lysis buffer (Seutin, White & Boag, 1991) and kept at cool temperature for two to nine weeks before long term storage at -20°C in the laboratory. All methods described in the paper were approved by the Animal Care Committee of Université Laval following guidelines of the Canadian Animal Care Council.

DNA Isolation and Amplified Fragment Length Polymorphism Procedure

We extracted DNA using QIAamp DNA Mini kit for blood samples (QIAGEN), following the manufacturer protocol. The diluted DNA samples were run on 2 % agarose gels to determine the DNA quality and quantity. DNA was re-suspended in 100 µL of double distilled water for storage.

The Amplified Fragment Length Polymorphisms (AFLPs) technique was used to document the fine-scale genetic structure among nesting and rearing sites. Even though AFLPs is an underused technique in birds (Bensch & Åkesson, 2005), this choice was motivated by previous studies showing that, given a comparable analytical effort, AFLP were much more efficient than other markers such as microsatellite loci in discriminating weakly differentiated populations (Campbell, Duchesne & Bernatchez, 2003). The general mode of inheritance of AFLPs is biparental and dominant (Bensch & Åkesson, 2005).

Our AFLP procedure was based on the original protocol of Vos *et al.* (1995), with the following minor modifications. We digested 15 ng of high molecular weight DNA with restriction enzymes *EcoRI* and *MseI* and we ligated the resulting fragments with adaptors. We PCR amplified these fragments using the pre-selective primers *EcoRI*-A and *MseI*-C. We then re-amplified a subset of the fragments obtained from the first PCR using 6 combinations of selective primers (Table 1), which provided clear and variable profiles in preliminary tests on 18 different individuals. The AFLP denaturated fragments were separated on an ABI 3100 DNA sequencer using a ROX (red) labelled size standard. The digital gel data was collected by the Applied Biosystem GeneScan analysis software (ver. 3.7). Each lane file was scored by eye for the presence and absence of AFLP fragments at approximately 1-bp intervals using Applied Biosystem Genotyper software (ver. 3.7). We replicated 30% of our samples to test for repeatability of AFLP fragments scoring (see Results).

Homoplasy and genetic diversity

We tested for size homoplasy in the AFLP data set with the AFLP-SURV shareware (Vekemans *et al.*, 2002). If size homoplasy occurs, a negative and significant correlation between fragment size and frequency should be observed (Vekemans *et al.*, 2002). If the hypothesis of size homoplasy is rejected, one can then compute AFLP score in a data matrix assuming one locus for each amplified band (Wang *et al.*, 2003). We used the Transformer shareware (Caujapé-Castells & Baccarani-Rosas, 2005) to prepare our data matrix into the appropriate format for each software used below. Because AFLP markers must be analyzed as dominant loci, we analysed our data assuming a Hardy-Weinberg equilibrium within a given sampling location (Wang *et al.*, 2003).

Genetic diversity was first determined as the percentage of polymorphic loci, excluding loci shared by less than 5% or more than 95% of all individuals (95% criterion). Secondly, we calculated nearly unbiased estimates of heterozygosity using the method of Zhivotovsky (1999) with non-uniform prior allelic distribution.

Population structure and relatedness

The AFLPOP v 1.1 shareware (Duchesne & Bernatchez, 2002) was used in subsequent analyses to filter loci that were the most informative for population structure. This shareware allowed us to delete possible linked loci and loci with a frequency differential of less than 0.10 between the highest and lowest frequency observed at any sampling location for a given marker. We then used four complementary approaches to determine the genetic structuring of breeding geese. First, we applied the Bayesian approach of the STRUCTURE shareware to infer population structure patterns and to assign individuals to inferred clusters (Pritchard, Stephens & Donnelly, 2000). As in other log-likelihood approaches, cluster inference is subject to problem of convergence and local minima. We therefore ran 20 independent simulations, averaged values obtained from these runs and checked for slope variations in the log-likelihood function. All simulations used a no-admixture model without using prior information on the origin of individuals. The no-admixture model performs well for dominant markers when we do not study co-ancestry and gave similar results than the STRUCTURE version (unpublished) allowing for dominant markers (D. Falush *pers. com.*). For each simulation, we used 30,000 iterations of burn-in periods and collected data after 10^6 iterations.

Second, we used the allocation procedure of the AFLPOP v 1.1 shareware (Duchesne & Bernatchez, 2002) to determine the origin of nesting individuals among putative rearing site groups in 2004. We defined a log-likelihood threshold value of 1.3 for assignment (analogue to an $\alpha = 0.05$).

Third, we performed an Analysis of Molecular Variance (AMOVA. Excoffier, Smouse & Quattro, 1992) with the ARLEQUIN v. 3.0 shareware (Excoffier, Laval & Schneider, 2005) in order to apportion the total genetic variance into hierarchical components (within and among breeding groups) and computes Wright 's fixation index F_{ST} between all sampling locations. The significance of the overall F -statistic was derived from null distributions generated from 5000 random individual permutations among breeding groups. To add further evidence of a significant departure from $F_{ST} = 0$, we used the GENETIX shareware

(Belkhir *et al.*, 2004), and ran 50000 permutation tests on individual genotypes among the four rearing sites.

Finally, the degree of relatedness (r) between birds within and among sites was calculated using the unbiased estimates of the MER software (Wang, 2004) using 1000 bootstraps over loci. Due to the interdependence of pairwise estimates (Danforth & Freeman-Gallant, 1996), mean r comparisons among groups cannot be analysed using standard parametric statistics but require permutation approaches. Consequently, we performed two-tailed distribution-free permutation tests with 1000 repetitions using a SAS-based macro (see McKinnon, Gilchrist & Scribner, 2006 for details on the method).

Simulations

We performed individual-based simulations to distinguish between possible demographic causes for the patterns of genetic differentiation observed among sites of Bylot Island, following guidelines of Petit *et al.* (2001). Using the shareware EASYPOP (Balloux, 2001), we defined five distinct scenarios, with the first used as a null model and the others as tests of specific hypotheses: (1) random dispersal for both sexes; (2) random male dispersal and no dispersal for female; (3) no dispersal for male and random female dispersal; (4) limited dispersal for both sexes using an island model of dispersal (Wright, 1931), where among-site dispersal is equal; (5) limited dispersal for both sexes using a stepping-stone model of dispersal, where only neighbouring populations exchange dispersers. We tested an island-model of dispersal because no isolation by distance was previously detected with mitochondrial markers in this species (Avisé *et al.*, 1992; Quinn, 1992; Cooke, Rockwell & Lank, 1995). The linear stepping-stone model of dispersal, which predicts that neighbouring populations would be less differentiated than non-neighbouring ones, was used as an alternative to the previous model.

For each scenario, we used the following rules. The number of populations was fixed to four virtual sites. We specified a 1:1 effective sex-ratio (Gauthier, G. unpublished data. Cooke, MacInnes & Prevett, 1975) with a monogamous mating system (Cooke, Bousfield & Sadura, 1981) but allowing a 2% rate of extra-pair copulations (Dunn *et al.*, 1999). Each

individual was characterized by 44 loci, as in the real dataset (see Results). We set a mutation rate compatible with AFLP loci (i.e. 10^{-4} per generation. Campbell & Bernatchez, 2004) following a random model of mutation for unlinked loci (Bensch & Åkesson, 2005). The number of possible allelic states was restricted to 2 (with AFLP, state 1 for presence and state 0 for absence). We replicated each scenario 100 times and analyzed genotypes after 100 generations, computing the mean and the upper and lower quartiles of the 100 replicates. For each replication in each scenario, reference samples of $n = 30$ genotypes were randomly picked in each of the four sites. We then used ARLEQUIN v.3.0 (Excoffier, Laval & Schneider, 2005) to estimate F_{ST} values and P -values.

To determine values of dispersal rate per generation to include in the model, we needed to differentiate between natal and breeding dispersal. As recruitment of geese starts at two years and is completed at four (Reed *et al.*, 2003b), we assumed that natal dispersal occurred at 2-3 years and breeding dispersal at 4+ year of age. According to the model of Gauthier & Brault (1998), the stable age distribution in the population should be 13.1 % for the second and third age class and 49.2 % for the 4+ age class (the remaining 37.7 % for the 1st age class does not participate to dispersal). Therefore, the 2-3 and 4+ year individuals compose 21% and 79% of the potentially dispersing population, respectively. In addition, given a similar and high annual adult survival probability for both sexes (83 %. Gauthier *et al.*, 2001) and monogamous long term pair bonds, breeding dispersal of males should be low and driven either by dispersal of its own mate or by repairing following death of its mate. Based on these rules, we used values of dispersal rate per generation that ranged from 0 to 0.5 for males and from 0.04 to 0.08 for females. These ranges include the only available estimates for natal dispersal across distant colonies of lesser snow geese, i.e. 30 to 50 % for males and 4 to 5% for females (Rockwell & Cooke, 1977). Finally, 100 model replications were run to determine the variance around F_{ST} estimates measured as a function of different values of dispersal.

Results

Homoplasmy and genetic diversity

The scoring of AFLP fragments in whole-cell DNA extracts was highly repeatable as 99.2% of them (n = 190) were identical in replicate DNA samples. So scoring error was lower than reported in previous studies with values ranging from 1.9% to 2.5% (Busch *et al.*, 2000; Miller, Blinn & Keim, 2002; Mock *et al.*, 2002). Non-repeatable bands were mainly faint bands that showed up in some PCRs, but not in others. Size homoplasmy should not be a source of bias in our results since fragment size was not correlated with its frequency ($r = -0.09$; $P = 0.61$, n = 44 loci). The genetic diversity for each primer combination and each rearing site sampled is summarized in Table 1. In the size range of 50 to 500 bp, the six primer combinations generated a total of 191 clear and reproducible bands across the 701 individuals analyzed (Table 1A). The primer pair ACA/CCC generated the largest number of polymorphic bands (n = 15) whereas the primer pair AAC/CGC generated the smallest (n = 2). Average heterozygosity was relatively similar among rearing sites, ranging from 0.08 to 0.11 (Table 1B).

Population structure and relatedness

For population structure analyses, we retained the 44 loci that were the most informative among the 191 previously found. Without using prior information on the geographical origin of individuals, the model-based Bayesian approach of the STRUCTURE shareware indicated that individuals most likely belonged to 4 distinct groups, both for individuals sampled on the rearing sites in 2004-2005 and for those sampled within the nesting colony in 2003 (Table 2). When we mapped the origin of individuals sampled on rearing sites over the groups identified by STRUCTURE, the 4 inferred groups corresponded very well to the four rearing sites; 90.4 % of the individuals were correctly assigned to the 4 inferred groups (Figure 2) and differed from random expectation ($\chi^2_7 = 21.4$; $P = 0.003$). In contrast, no such relationship was found for the 3 nesting sites sampled in the colony as their assignment among the 4 inferred groups did not differ from random expectation ($\chi^2_6 = 5.7$;

$P = 0.44$). Interestingly, when we examined the embryos sampled inside and outside the main colony in 2004 with respect to the four rearing sites identified by STRUCTURE, we found that 96.8 % ($n = 31$) of those sampled in nests of the Qarlikturvik valley were allocated by AFLPOP to this rearing site, a pattern that differed from random expectation ($\chi^2_3 = 18.9$; $P < 0.001$). Conversely, those from nests located inside the main colony were nearly equally distributed among the 4 rearing-site groups ($\chi^2_3 = 2.6$; $P = 0.45$).

We detected a low but significant population structure among rearing sites for females, and this structure was stable over the two years (Table 3A). This stability is not an artefact of sampling the same individuals in both years because all individuals sampled in 2004 were banded and none of them were sampled again in 2005. This analysis reveals that, of the total molecular variance measured, up to 1.4 % was attributed to divergence between rearing sites (Table 3A; $F_{ST} = 0.014$, $P < 0.001$). To put this value into a wider context, this differentiation was 14 times less than the one measured between the two snow goose subspecies (20.7 %; $df = 1$; $P < 0.001$). We also found a significant structure among rearing sites for males, although the mean F_{ST} value was low (0.008), that is almost half of the mean value detected in females (Tables 3 A-B), in accordance with a more pronounced dispersal of males than females. Permutation tests of individuals among the four rearing sites added further evidence of non-random population structure during the rearing period of geese. Thus, only 12 random simulations out of 50,000 generated F_{ST} equal or higher than F_{ST} measured with the AMOVA approach (mean of these 12 simulations: 0.016 vs. 0.014). In contrast, we did not find evidence of genetic structure corresponding to the three geographic clusters of embryos sampled in the main nesting colony in 2003 ($F_{ST} = 0.001$, $df = 2$, $P = 0.95$; Table 3C). In 2004, when we could compare birds nesting in the main colony with those nesting outside the colony, i.e. at the Qarlikturvik valley rearing site, F_{ST} increased to 0.008 but was still not significant (Table 3C).

For females, the mean estimate of pairwise relatedness on rearing sites was greater within ($r = 0.013$; $SE = 0.002$) than among rearing sites ($r = -0.015$; $SE = 0.004$; $n = 1000$ permutations; $P = 0.04$). However, this was not the case for males, which showed similar

pairwise relatedness values within ($r = -0.015$; SE = 0.002) and among rearing sites ($r = -0.016$; SE = 0.003; $n = 1000$ permutations; $P = 0.66$).

Simulations

Individual-based scenarios indicated possible dispersal patterns that could have generated the observed population structure. First, scenarios where one or both sexes dispersed randomly (scenarios 1 to 3) never yielded F_{ST} significantly different from 0 regardless of the value of other parameters in the simulation. Significant F_{ST} values were obtained for a range of limited dispersal values for both sexes, using either the model of isolation with or without distance (scenarios 4 and 5). F_{ST} values similar to those measured were obtained when male dispersal rates per generation ranged from 0.1 to 0.4, and a low rate of dispersal by females (0.04 to 0.08; Fig 3). These results, however, were conditional upon using an effective population size (N_e) below or equal to 1,500, as simulations did not yield a significant F_{ST} above this value.

Discussion

Our study documents a genetic clustering between spatially distinct rearing sites located only ~10 km apart, though no concordance exists between genetic and geographic clusters within the main nesting colony. Detecting a genetic structure at such a fine-scale is surprising because previous results in geese suggested a high regime of dispersal and gene flow at large spatial scales. Wide-ranging male dispersal was advanced as the primary vector of genetic mixing because pairing occurs on the wintering ground, far away from the breeding colonies. It has also been suggested that females could play a role in gene exchange among colonies when bottlenecks occur, such as during glacial episodes (Avisé *et al.*, 1992) or after major perturbations, such as habitat degradation at some colonies (Jefferies, Rockwell & Abraham, 2004). Contrary to these arguments, our results imply that the classic paradigm of large and widespread genetic mixing in this species should be reconsidered and the pattern that we report must be linked to particular life-history traits of the species.

Simulations suggested that significant local genetic structure can arise even with levels of dispersal of the same magnitude as those reported in the literature (e.g. Rockwell & Cooke, 1977). Among the assumptions made by these simulation models, we emphasize the critical role of genetic drift in generating genetic differentiation among rearing sites as shown by the effective population size required in the simulations ($N_e < 1,500$) to obtain patterns compatible with those observed. This level represents about 6 % of the total census size of the greater snow goose breeding population surveyed on Bylot Island in recent years (Reed, Hughes & Boyd, 2002). This ratio of effective vs. total size is also than the average value of 11% reported for many animal species (Frankham, 1995). Also, one has to consider that only the most informative loci were used to estimate F_{ST} , such that values are likely to be over-estimated. Thus, gene flow in our simulations should be higher than values presented in Figure 3, which also means that N_e values compatible with the extent of population divergence observed among rearing sites should actually be less than 1,500. On the other hand, $N_e < 1,500$ may be possible, considering the fact that the current large census population size is very recent. Indeed, 100 years ago the entire population of this subspecies may have been as low as 4,000 individuals (Gauthier *et al.*, 2005), which is indicative of a much reduced effective size of this population in the recent past. Since long-term N_e is often closest to the size of the generation with the smallest single generation N_e (Frankham, 1995), the Bylot Island N_e could actually still be lower than 400.

In sex-biased dispersal systems, social associations among single-sex groups can drive the formation of genetic clusters (Coltman, Pilkington & Pemberton, 2003 and references therein). In our study, the adequacy between spatial and genetic structure is likely driven by high female philopatry at the rearing site scale, increasing the probability of higher relatedness within than among rearing sites. Under this model, females recruiting into the breeding population should rear their goslings where they were reared themselves. Although males show also significant clustering during rearing, their genetic differentiation was less important than for females. This result is consistent with the general pattern of male-biased dispersal reported before (Greenwood, 1980). However, the presence of a recognizable fine-scale structuring in both sexes is surprising and can only occur if males also show a relatively higher level of philopatry than reported until now, including some level of natal philopatry.

Until now, male natal philopatry in long-distant migrants such as geese was thought to be negligible because pairing occurs mainly in wintering grounds where birds from distant colonies are extensively mixed (Cooke et al. 1995). With long term pair bonds and high adult survival, natal dispersal should play a more important role in goose genetic structure through first-time pairing than breeding dispersal. Several lines of evidence suggest that pairing in geese is assortative and could contribute to reduce gene flow among colonies. First, hitherto unrecognized aggregations of birds born on the same rearing sites may persist away from the breeding ground, including on the wintering or staging areas. For instance, spatially distinct breeding groups of Pacific white-fronted goose (*Anser albifrons frontalis*) use exactly the same wintering grounds, though not at the same time (Ely & Takekawa, 1996). Second, individual recognition may allow preferential mating of individuals born in the same area (van der Jeugd, van der Veen & Larsson, 2002). Such assortative pairing is likely based on individual characteristics, such as plumage colour (Cooke, 1983; Cooke, Rockwell & Lank, 1995), size (Choudhury & Black, 1993) and familiarity (i.e. individuals paired with whom they have associated intermittently during early life. Choudhury & Black, 1994). Despite evidence for assortative mating, we still know too little on the pairing mechanism in these birds, as some pairing may even occur away from the wintering ground, close to breeding grounds. Indeed, Demers *et al.* (2003) found that some female greater snow geese that were unpaired in spring had a mate and laid eggs in the same summer. Clearly, more studies on pairing to uncover mechanisms that promote natal philopatry in males are needed to clarify this issue.

In addition to dispersal, three other potential sources of genetic mixing in snow geese are possible: extra-pair copulations (EPCs), nest parasitism and adoption of unrelated goslings during brooding. EPCs and nest parasitism are likely to act as homogenizing forces but given their low rate of occurrence reported, our simulations suggest that they do not prevent the establishment of fine-scale population structure. Adoption of unrelated offspring is a common feature in waterfowl (Prevett & MacInnes, 1980; Kalmbach, 2006), including snow geese. This behaviour occurs throughout the rearing period but up to 50 % of adoption occur after goslings reach 15 days of age (Williams, 1994). In our system, movements of families from the nesting to the brood-rearing is rapid and usually takes place within 6 days of hatch (Mainguy *et al.*, 2006), with little movements thereafter. Many

adoptions are thus likely to occur once families have reached their rearing sites, thereby restricting genetic flow among rearing sites through adoption.

Most studies looking at fine scale genetic structure in breeding bird populations have focused on nesting sites. We have shown here that in a precocial bird this may be misleading as we found no genetic structure within a large nesting colony, yet when the same individuals segregated according to their rearing sites, a clear genetic structure emerged. These novel findings call for an evolutionary explanation as to why a population may be structured more according to its brood-rearing sites rather than its nesting sites. In the Arctic, the availability of good nesting sites is often more temporally variable than the availability of good rearing sites, for instance due to unpredictable snow-melt pattern in spring or the occasional presence of “protector” species like raptors (Bêty *et al.*, 2001; Quinn *et al.*, 2003). These factors could contribute to reduced nest site fidelity (Chapter 3) and more easily promote the evolution of structure based on the rearing sites. In addition, as families leave their nesting site shortly after hatch, the environment experienced by young are primarily their rearing site and not the nesting site of their parents. In that context, the primary mechanism of philopatry in geese may be fidelity to a familiar rearing site, with fidelity to a specific nesting site a by-product of the latter (Abraham, 1980). Given the relatively low costs of movements to brood-rearing area after hatch (Mainguy *et al.*, 2006), benefits associated with colonial nesting (e.g. reduced egg predation) may indeed promote the mixing of geese that are segregated in genetically distinct rearing sites. This mechanism is supported by our observations of occasional nesting associations between geese and snowy owls, with owls providing the same benefits than a large colony, i.e. reduced egg predation rate due to their active exclusion of predators such as the arctic fox (*Alopex lagopus*) from their territory (Bêty *et al.*, 2001). When nesting owls provide such predator refuges, our results show that geese taking advantage of them are not a random sample of individuals but are primarily birds using the nearby rearing site. In doing so, these birds have the double benefit of nesting in a safe site and avoiding any potential cost associated with movements. In this context, nest site fidelity appears a more flexible strategy than rearing site fidelity in this species.

TABLE 1. Summary of AFLP polymorphisms according to primer combination (A) or rearing sites (B) for 701 greater snow geese sampled in the breeding population of Bylot Island (NU, CA).

A.

<i>EcoRI</i> primer ¹	<i>MseI</i> primer ²	Number of amplified loci ³	Number of polymorphic loci	% polymorphic loci ⁴	Average heterozygosity ⁵
ACA	CCC	36	15	20	0.19 ± 0.03
AAG	CGC	34	5	16	0.13 ± 0.06
AAC	CCC	35	6	31	0.18 ± 0.08
ACA	CCG	30	12	15	0.13 ± 0.02
AAG	CGG	35	4	11	0.03 ± 0.02
AAC	CGC	21	2	10	0.05 ± 0.04
TOTAL		191	44	17	0.12 ± 0.03

B.

Rearing Population	% polymorphic loci ⁴	Average heterozygosity ⁵
Quarlikturvik valley	14	0.10 ± 0.04
Main colony	18	0.09 ± 0.07
Camp3	20	0.08 ± 0.08
Dufour	16	0.11 ± 0.04
TOTAL	17	0.10 ± 0.04

¹ 5' CACGACGTTGTAACGACTGCGTACCAATTC-NNN3'

² 5' GATGAGTCCTGAGTAACG-NNN3'

³ Fragments in the size range of 50 -500 bp

⁴ 95% criterion

⁵ Average estimates ± SE based on the Bayesian method of Zhivotovsky (1999) for non-uniform prior distribution of loci

TABLE 2. Estimated mean likelihoods of data [$\ln \Pr(X | K)$] and posterior probabilities [$P(K | X)$] for different numbers of genetic clusters (K). The number of genetic clusters corresponds to the number of groups in the study population estimated by the STRUCTURE shareware (Pritchard, Stephens & Donnelly, 2000) without using any a priori information. Note that ~ 0 and ~ 1 refer to probability < 0.001 and > 0.999 , respectively.

K	$\ln \Pr(X K)$		$P(K X)$	
	Rearing sites	Nesting clusters	Rearing sites	Nesting clusters
1	- 3594.22	- 1920.10	~ 0	~ 0
2	- 3450.71	- 1286.71	~ 0	~ 0
3	- 3315.54	- 1266.64	~ 0	~ 0
4	- 3274.25	- 1241.00	~ 1	~ 1
5	- 3297.79	- 1267.71	~ 0	~ 0
6	- 3448.61	- 1838.82	~ 0	~ 0
7	- 3464.71	- 1848.70	~ 0	~ 0

TABLE 3. Hierarchical partitioning of genetic variance (AMOVA- Arlequin Software v.3.0) based on 44 AFLP loci showing percentage of total variance (%V) depending on the grouping in greater snow geese.

A. Comparison among 3 rearing sites, Qarlikturvik valley (QV), Main colony (MC) and DUFOUR, females only, 2004-2005

Variance component	d.f.	% V	<i>P</i>						
Among sites	2	1.42	< 0.001						
Between 2004-2005 within sites	1	0.05	0.41						
Within sites in each year	208	98.53	< 0.001						
Rearing sites									
	QV			MC			DUFOUR		
Variance component	d.f.	%V	<i>P</i>	d.f.	%V	<i>P</i>	d.f.	%V	<i>P</i>
Between 2004-2005	1	0.26	0.29	1	0.24	0.26	1	0.50	0.23
Within each year	92	99.74	< 0.001	59	99.16	< 0.001	57	99.50	< 0.001

B. Comparison among 4 rearing sites, Qarlikturvik valley (QV), Main colony (MC), DUFOUR and Camp-3, females and males 2005 sites

Variance component	Females			Males		
	d.f.	% V	<i>P</i>	d.f.	% V	<i>P</i>
Among sites	3	1.2	0.04	3	0.8	0.04
Within sites	138	98.8	< 0.001	135	99.2	< 0.001

C. Embryos in nests in 2003-2004

Variance component	Within main colony ¹			Among colonies ²		
	d.f.	% V	<i>P</i>	d.f.	% V	<i>P</i>
Among sites	2	0.01	0.95	1	0.8	0.12
Within sites	137	99.99	<0.001	180	99.2	<0.001

¹ 3 clusters of nests spaced out within the colony

² Qarlikturvik valley and Main colony

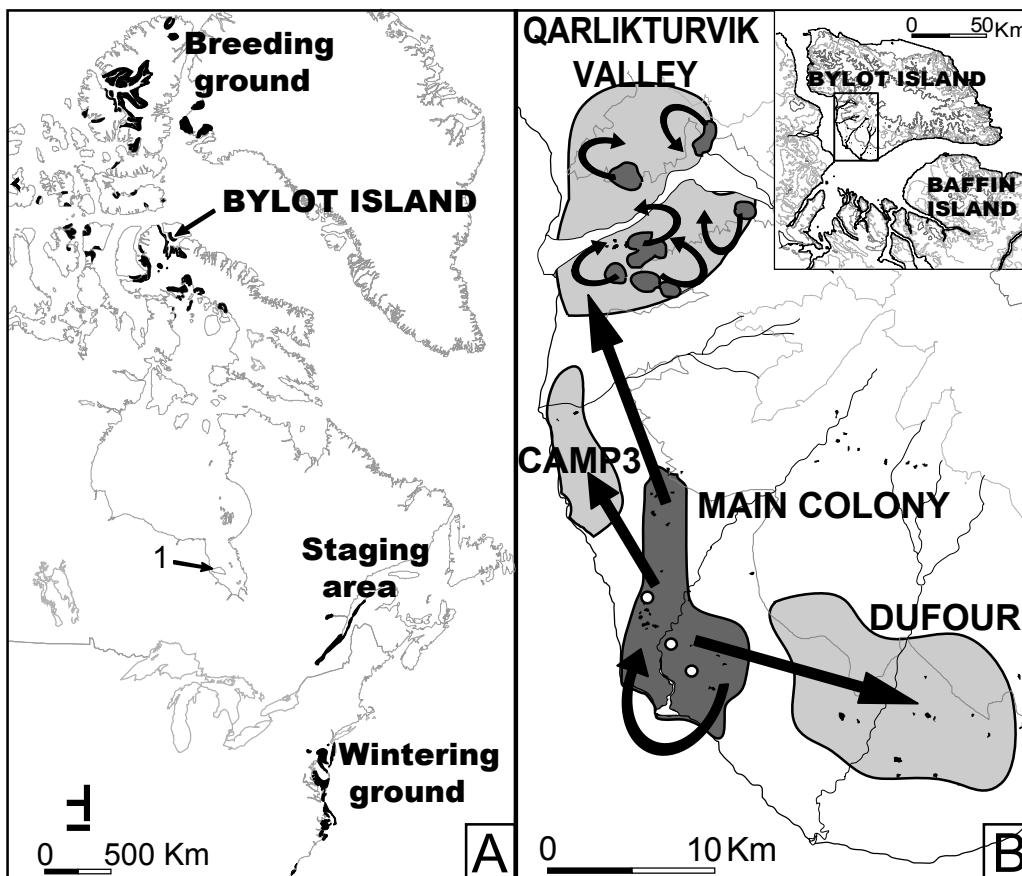


FIGURE 1. A. Geographical locations of the wintering, staging and breeding areas of greater snow geese (*Chen caerulescens atlantica*) in North America, including the locations of genetic sampling on Bylot Island and on Akimiski Island (1; breeding area of lesser snow geese (*Chen caerulescens caerulescens*)). B. Location of major nesting (dark gray) and brood-rearing (light gray) areas of greater snow geese on Bylot Island (drawn from information in Reed *et al.* (2002) and G. Gauthier, unpubl. data). The main colony is also used as a brood-rearing area by some birds. Geese nesting in the Qarlikturvik valley typically nest in association with snowy owls (*Bubo scandiacus*) only in years of peak lemming abundance. The black arrows show movements of birds between their nesting and brood-rearing areas as inferred by our genetic analyses of birds sampled both on the nesting and brood-rearing sites (see Results). White circles indicated locations of the three sampling nesting sites.

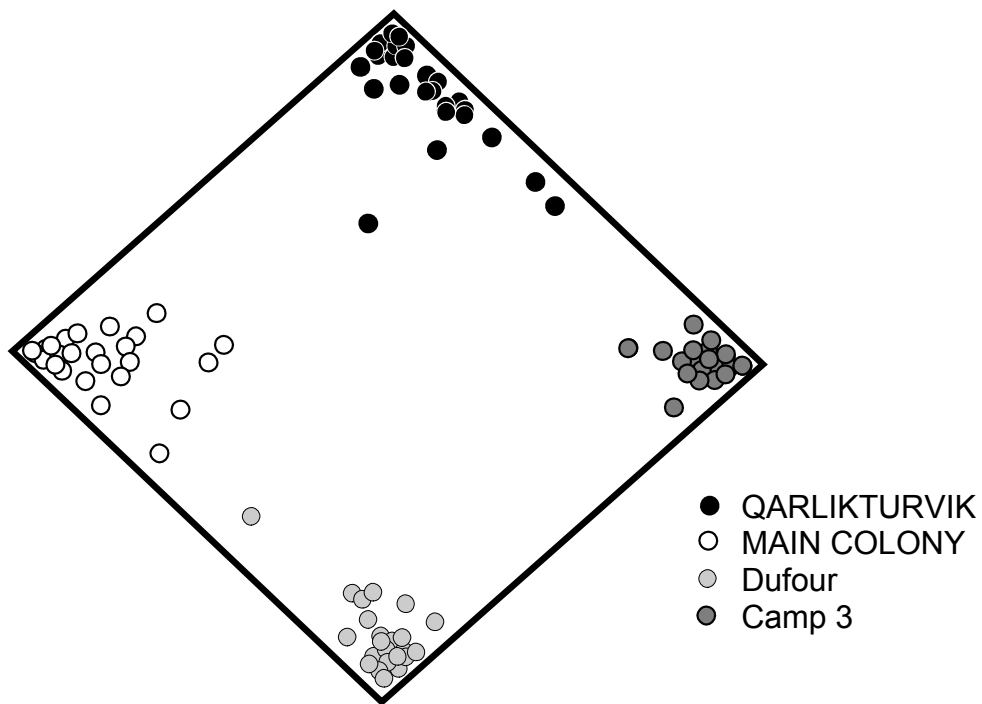


Figure 2. Relative membership of each individual greater snow geese sampled on the 4 different rearing sites within the genetic structure based on four groups inferred by the shareware STRUCTURE (Pritchard, Stephens & Donnelly, 2000). Each point is a sampled individual and the number of individuals shown is less than reality because of overlapping points.

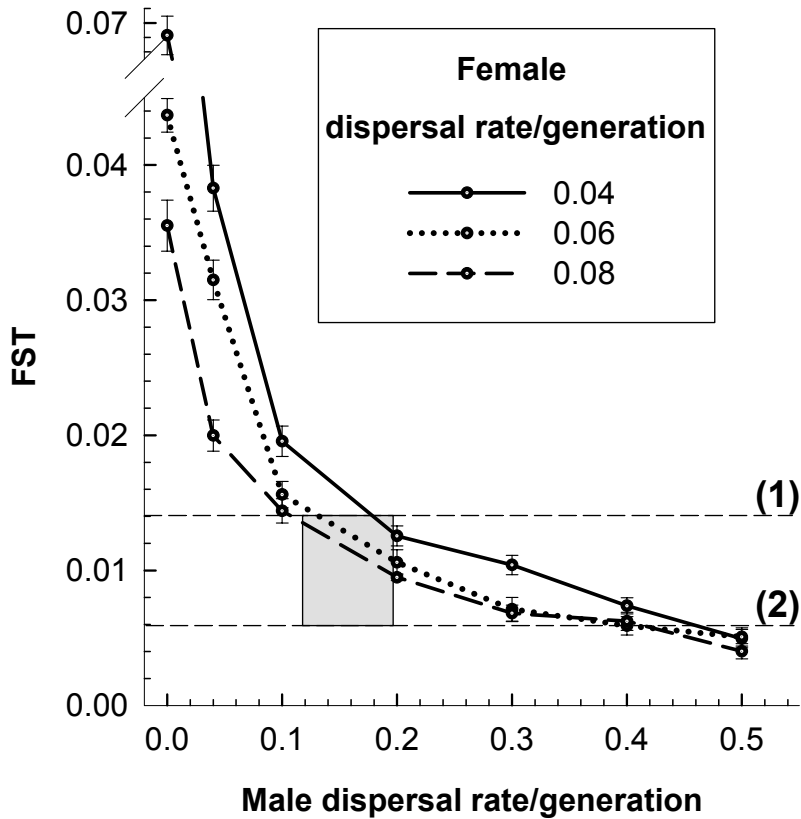


FIGURE 3. F_{ST} variation as a function of dispersal rates in both sexes for simulations with $N_e = 1500$. Mean values \pm SE of F_{ST} are obtained after 100 simulations in the software EASYPOP (Balloux, 2001). The dotted line (1) indicates the level of F_{ST} measured for females in our system and (2) the level where F_{ST} is not significantly different from 0 with an alpha threshold of 5%. The shaded square shows the range of dispersal values for males of this species reported in the literature (Rockwell & Cooke, 1977).

Chapitre 5

A NEW NONDAMAGING BLOOD SAMPLING TECHNIQUE FOR WATERFOWL EMBRYOS

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Résumé

Pour des raisons éthiques et de conservation, il est important de favoriser le développement de techniques les moins invasives possibles. Dans ce chapitre, nous décrivons une nouvelle technique, très simple à reproduire, qui permet de prélever des échantillons sanguins sur les jeunes en éclosion chez la sauvagine. Pour ce faire, il suffit de récolter le sang produit lorsque l'on perfore la coquille d'œufs en l'éclosion. Cette technique nous permet d'obtenir un grand nombre d'échantillons sanguins sans recourir au sacrifice ou à la contention d'aucun individu, minimisant ainsi le stress normalement produit lors d'une capture. De plus, le sang récolté est de très bonne qualité pour des analyses génétiques. Enfin, nous n'avons pas mesuré d'effet néfaste de cette technique sur la survie des embryons ou des oisons marqués de la Grande Oie des neiges.

Abstract

Development of minimally invasive techniques to collect blood in free-living birds is desirable for both ethical and conservation reasons. We describe a new, simple technique for collecting blood samples in hatching waterfowl eggs. It consists in recovering blood from a small hemorrhage after puncturing the shell of early hatching eggs. The technique allowed us to obtain a large number of blood samples and did not require the sacrifice or even the retention in place of any individuals, thus minimizing stress. It yielded high quality blood samples for genetic studies and had no adverse effects on embryos in the eggs or the post-hatched survival of young tagged in the egg in greater snow geese.

Introduction

Blood samples are routinely collected in genetic or ecophysiological studies to analyze a wide range of parameters in wild birds such as molecular markers, hormones or stable isotopes (Colwell *et al.*, 1988; Hoysak & Weatherhead, 1991; Schmoll *et al.*, 2004). The most common method for the collection of blood in birds is venipuncture (American Ornithologists' Union 1988; Standards for Components of British Columbia's Biodiversity 1998), a method described in details by Hoysak and Weatherhead (1991). However, some training and skill is required to be proficient with this method. Smith *et al.* (2003) advocated feather blood sampling rather than venipuncture to minimize negative impacts on individuals, but both techniques require the handling of birds, leading to some levels of stress (Cockrem & Silverin, 2002). Despite widespread utilization of those blood-collection techniques, few studies have examined how much they could negatively affect the behavior and survival of free-living birds (Stangel, 1986; Smith *et al.*, 2003; Schmoll *et al.*, 2004). Ethical committees encourage alternative methods that minimize impacts on the studied individuals (e.g. American Ornithologists' Union 1988). In species with special conservation status, such as those endangered, requirements to use methods that have no adverse effect on populations are very stringent (e.g. Gaunt *et al.* 1997). Those reasons led (Dutton & Tieber, 2001) to describe a technique to collect blood without manipulation of individuals, i.e. from incubating eggs using small syringes and fluorescent lamps. However, the success was variable depending of the species studied, and it was not tested in the field.

Our main objective is to report a new method for blood collection from hatching goose eggs with minimal handling and stress on the birds. We describe how the technique is simple to use in the field, we examine the quality of recovered blood samples for genetic analyses, and we evaluated if the technique affected the survival of tagged goslings.

Methods

The study was conducted on Greater Snow Geese (*Chen caerulescens atlantica*) breeding on Bylot Island (73°N, 80°W; Sirmilik National Park, Nunavut, Canada). We conducted field work during the hatching period in 2003-2004 (5 July - 15 July).

Our method is adapted from the technique developed by Alliston (1975) to web-tag young Anatidae in hatching eggs. His method entails making a small hole in the eggshell (directly below the opening made by the hatching young) to access the hatchling's leg and place a tag in its foot webbing. In doing so, one has to break through the extra-embryonic membrane, the chorio-allantois membrane, which is rich in capillaries filled with blood from the embryo (Deeming & Ferguson, 1991). This causes a small hemorrhage from which a few drops of blood can be collected. We recovered the blood by leaning the egg hole over a 1.5 mL Eppendorf collection tube already filled with 0.5 mL solution of Queen's Lysis Buffer (Seutin, White & Boag, 1991), allowing the blood to drip in. Immediately after collection, we closed the tube and shook it several times to homogenize the sample with the buffer solution. Samples were kept at ~4°C for several weeks before analysis in the laboratory. The sampled volume was calculated as the total volume in the tube minus the volume of Queen's Lysis Buffer.

We examined if blood sampling at an early stage of hatching had an effect on the survival of tagged young. We web-tagged 235 goslings in the egg at the same time that we took a blood sample. We also had a control group of goslings ($n=647$) not sampled for blood that were tagged following the procedure outlined by Alliston (1975). In both groups, we used only one gosling tagged per nest to insure independence of the data. We revisited many nests shortly after tagging (3 days later, on average) to check for the presence of dead embryos in eggs or dead young in the nest. Approximately 5 weeks after hatch, goose families were captured at their rearing sites during mass banding drives (Menu, Gauthier & Reed, 2001), and captured goslings were checked for the presence of web-tags. Our study followed the rules of the Canadian Council for the Animal Protection and was approved by the Comity for Animal Protection of the Université Laval (permit number 2003-010 and 2004-017).

We examined the quality of genomic DNA in the blood samples with restriction ligation followed by agarose gel electrophoresis (Quiagen Inc., 2004). We used the following criteria to assess DNA quality: a smear during the migration in the gel was an indication that low quality DNA containing impurities and/or degraded DNA had hindered migration out of the wells and caused non-uniform electrophoretic mobility.

Results

We were able to collect between 1 and 5 drops of blood from a single egg for a mean volume of 0.4 mL per sampling (SE = 0.1; N = 98). Blood coagulation occurred very rapidly (less than a minute), making it essential to quickly mix it with the buffer solution. After puncturing the egg, blood sampling took on average 15 s (SE = 4; N = 79). We were able to recover blood from 215 hatchlings that showed the first signs of hatching (small cracks in the eggshell, i.e. star-pipped egg) but from only 20 hatchlings that had fully ruptured shell membranes.

We never found dead embryos or goslings during nest visits shortly after web-tagging in either the blood sample (N = 103) or the control groups (N = 151). During banding, we caught 12 goslings out of 235 that were blood sampled in their eggs (5.1%) and 25 goslings from the control group (N = 647; 3.9%). Thus, we found no significant difference between the survival of tagged goslings that were blood sampled and web-tagged in the egg and those that were only web-tagged in the egg ($\chi_1^2 = 1.69$; P = 0.19).

All blood samples that were not in direct contact with the eggshell surface during collection showed high quality DNA (N = 78). However, all blood samples that ran over the eggshell (N = 20) showed low DNA quality during genetic analyses.

Discussion

Our blood sampling technique offers several advantages. First, the technique is easy to use in the field, is not time-consuming, and requires little material beyond what is routinely used for nest surveys. Second, sampled individuals are still in their eggs and thus

experience little effects of handling, thus reducing stress and possible injury due to physical restraint. Third, our technique is compatible with most behavioral and ecological research because of its low invasive level resulting from the absence of direct manipulation of individuals, as required by other blood sampled techniques (Colwell *et al.*, 1988). The volume of blood obtained with our technique was <7% of the total blood volume of individuals which represents about 8% of the total body mass in birds (Sturkie 1986), a proportion well below the limit established by ethical committees (e. g. American Ornithologists' Union 1988; Gaunt *et al.* 1997, Live Animal Capture and Handling Guidelines for Wild Mammals, Birds, Amphibians & Reptiles 1998). The sampled blood volume is comparable to that obtained with other sampling protocols: e. g. ~ 0.5 mL from the jugular vein of several passerine birds (in Hoysak and Weatherhead (1991); 0.4 mL from the brachial vein of shorebirds (in Colwell *et al.* 1998); 0.05 mL (SE=0.02; N=90) per quill of growing wing coverts in the Greater Snow Geese (N. Lecomte, unpubl. data). This volume is also above the minimum volumes usually required for DNA extraction (0.1 mL; Quiagen Inc. 2004), hormonal assays (0.25 mL; Lipar *et al.* 1999), or stable isotopes analyses (0.1-0.2 mL; Herrera *et al.* 2003). Finally, risk of injury for the handler should be minimal during the sampling.

Our technique is adapted from the web-tagging method described by Alliston (1975). Web-tagging is a widely used marking technique in waterfowl research nowadays (Seguin & Cooke, 1985; Blums, Mednis & Nichols, 1994; Blums *et al.*, 1999; Davis, Leopold & Kaminski, 2001). Alliston (1975) tested his egg-marking method in seven species of Anatidae and found no adverse effect on duckling survival and hatching success. We have web-tagged Snow Goose goslings in the egg for more than 12 years with no observed detrimental effect on their survival (Lepage, Gauthier & Menu, 2000); G. Gauthier unpubl. data). Alliston (1975) recommended that hatchlings should have completely ruptured their shell membranes themselves prior to puncturing a second hole in the egg. However, we found it difficult to obtain sufficient blood at this stage, presumably because the chorio-allantois membrane had begun to dry as the embryo resorbs much of the blood flowing in that membrane prior to hatching. In contrast, the hemorrhage was larger when the hole was made at the first evidence of hatching activity, which made easier blood collection, and thus we favored this stage in our sampling. Nonetheless, our results indicate that the sampling of

small amount of blood at an early hatching stage had no detrimental effects on the survival of sampled birds web-tagged in the egg. However, sampling should not be attempted in the absence of physical signs of hatching (e.g. small cracks) because breaking of the membranes or blood sampling at this stage may lead to desiccation of the embryo and eventually its death (Alliston 1975).

Although our method generally yielded high quality blood samples for genetic analyses, we found that this was dependent upon conditions during the collection procedure. In particular, blood spilling over the eggshell should be avoided during the sampling, as all blood samples that ran over the eggshell showed low DNA quality during genetic analyses, presumably due to contamination from soiled eggshell. The potential for blood contamination with our method may thus be higher than with other techniques such as venipuncture due to the higher risk of contact with the eggshell or human fingers during the sampling process. Moreover, instruments used to open the egg-shells (e.g. tongs) should be cleaned between uses (e.g. with ethanol) to prevent contamination of samples by the blood of other individuals. An additional limitation of our method is that knowledge of the precise hatching date is necessary to apply this technique successfully, as nests should be visited at the early hatching stage.

Our method should be especially useful for species with highly synchronized hatching or in colonial nesters. To our knowledge, marking of young inside the egg has only been applied in waterfowl. Although other non-waterfowl species have been web-tagged (e. g. Sabine's Gulls, *Xema sabini*, Abraham 1986; American White Pelicans, *Pelecanus erythrorhynchos*, Evans and McMahon 1987; Common Loon, *Gavia immer*, Fournier et al. 2002), we did not find any evidence of web-tagging in the egg. Therefore, we do not know to what extent our blood sampling technique can be applied safely to other groups of birds, especially for species with very small eggs (Deeming & Ferguson, 1991). To our knowledge, the smallest eggs that have been used for web-tagging in the eggs is about 53 x 36 mm (Bufflehead, *Bucephala albeola*, G Gauthier, unpubl. data).

Although web-tagging in the egg has been proposed 3 decades ago Alliston (1975), we could not find evidence, based on an extensive search of the literature (> 500 papers

consulted), that somebody used the small haemorrhage resulting from this marking to collect blood samples before. Our study therefore offers a new, simple blood sampling technique that can provide high quality samples with minimal stress on individuals and no detrimental effects on the survival of sampled birds. Our technique may be widely used in species where web-tagging already occurs because it requires little effort and no additional training or skill for the worker.

Conclusion générale

À travers cette thèse, j'ai intégré des concepts de risque de prédation, d'utilisation d'habitat et de structure de populations, et ceci afin de mieux comprendre les variations dans des paramètres fondamentaux en dynamique de population comme le succès reproducteur et la dispersion (Tableau 1). J'ai d'abord voulu comprendre l'influence de l'habitat sur le comportement de quête alimentaire des prédateurs et d'approvisionnement en eau de leur proie. Ces résultats ont permis de montrer une dynamique spatiale et temporelle des interactions trophiques directes et indirectes dans la toundra arctique. J'ai tenté alors d'examiner les liens entre l'hétérogénéité de l'habitat et les taux de dispersion à travers des modèles d'utilisation d'habitat et de capture-recapture. Enfin, j'ai examiné l'adéquation entre la structure spatiale des reproducteurs et leurs liens génétiques. Mon approche se veut ainsi intégratrice de concepts et de méthodes habituellement séparés, et ce, dans le but de détecter des mécanismes de dispersion liés à la productivité et à la distribution d'un herbivore clé dans l'écosystème arctique.

Habitat et relation prédateurs-proies

Il existe un consensus très fort sur l'importance de la structure de l'habitat dans l'équilibre des relations trophiques mais l'étude des mécanismes qui sous-tendent cette relation présente encore beaucoup d'incertitudes (McCoy & Bell, 1991). C'est dans cette recherche des mécanismes impliqués qu'il faut placer le chapitre 1. Ce chapitre m'a entre autre permis de montrer que la structure des milieux humides de la toundra affectait la vitesse et le succès d'attaque du renard arctique face à une espèce qui est capable de défendre son nid. De plus, l'abondance de lemmings, la principale proie des prédateurs, influençait indirectement les gradients de succès de nidification entre les refuges que constituent les milieux humides et les milieux mésiques. La force des interactions trophiques directes et

indirectes de ce système peut ainsi varier dans l'espace (voir Figure 1), à une échelle correspondant aux parcelles d'habitats.

Les milieux humides présentent un grand intérêt en termes de conservation et de biodiversité (Weller, 1999; Keddy, Birks & Wiens, 2000). Dans l'Arctique, ces milieux sont souvent les plus productifs et offrent les plantes préférées notamment par les oies durant leur reproduction (e.g. Kerbes, Kotanen & Jefferies, 1990; Gauthier, Rochefort & Reed, 1996). Dans les deux premiers chapitres, je présente des évidences de l'importance des milieux humides durant la nidification qui ne seraient pas dû uniquement à leur productivité primaire mais aussi à leur rôle de refuge et à leur haute disponibilité en eau. Ces résultats ajoutent donc une dimension supplémentaire à l'importance de ces milieux qui offriraient des habitats propices aux succès de nidification dans un contexte de limitation par la prédation. À mon avis, il serait pertinent de déterminer à quel point ces résultats peuvent s'exporter à d'autres espèces d'oiseaux arctiques. La faible disponibilité des milieux humides dans le paysage et une préférence des oies pour ces milieux lors de l'installation des nids génèrent également des hypothèses de limitation de ces milieux pour la productivité des oies.

De façon générale, les précipitations peuvent affecter le niveau des étendues d'eau mais aussi la structure des milieux humides (e.g. Weller, 1999), modifiant à la fois la disponibilité en eau et les contraintes au déplacement des prédateurs terrestres. Dans le système étudié, les précipitations n'affectent peu ou pas la structure en labyrinthe des polygones humides (décrite en détail dans le chapitre 1). Cette caractéristique me permet ainsi de distinguer nettement les effets de structure (constants entre les années) des effets d'abondance en eau due à la pluviométrie (variables selon les années). Par contre, les résultats des deux premiers chapitres ne permettent pas de conclure directement sur l'importance relative de ces deux effets.

Ressource, prédation et relations trophiques

Le rôle des interactions trophiques dans la structure des communautés est au cœur d'un débat opposant deux grandes hypothèses de régulation (Guitierrez *et al.*, 1994; Meserve *et*

al., 2003; Moore *et al.*, 2003; Gauthier *et al.*, 2004). Le premier type de régulation s'effectuerait par les ressources biotiques et/ou abiotiques (bottom-up) (e.g. Polis & Strong, 1996) alors que le deuxième serait par les consommateurs (top-down). (e.g. Hairston, Smith & Slobodkin, 1960). Chez beaucoup d'oiseaux, la prédation serait la cause principale d'échec au nid (contrôle top-down) (voir Martin, 1995 et les références citées dans le texte), bien que la littérature scientifique a davantage porté attention à l'abondance de nourriture comme moteur des variations de succès reproducteur (contrôle bottom-up) (e.g. Martin, 1987; Nagy & Holmes, 2005). Dans le chapitre 2, je contribue de façon originale à ce débat en soulignant comment l'utilisation d'une ressource par une proie peut mener à un contrôle top-down. Ainsi, je montre un effet positif de la ressource « eau » sur le succès reproducteur s'exprimant via la relation prédateur-proie (réduction du risque de prédation; voir Figure 1).

Le débat top-down/bottom-up rejoint un autre débat important en écologie, soit celui sur l'importance relative des effets biotiques et abiotiques dans les systèmes naturels, notamment dans ce qui a trait aux variations d'abondance et de productivité des populations (Newton, 1998; Begon, Harper & Townsend, 2005). Plusieurs accordent un rôle prépondérant à la nourriture et aux partenaires sexuels à travers les processus de compétition et de prédation. Un autre point de vue met plutôt l'accent sur l'impact de variables physico-chimiques et climatiques. Jusqu'à récemment, l'interaction entre ces deux types d'effets a été assez peu considérée mais semble de plus en plus une caractéristique importante des écosystèmes (Martin, 2001). De plus, l'effort actuel placé dans la compréhension des changements climatiques offre un contexte favorable à l'intégration des effets biotiques et abiotiques dans la compréhension du fonctionnement des écosystèmes (Root *et al.*, 2003). Le Chapitre 2 contribue ainsi à cet effort en montrant qu'un facteur abiotique (précipitation) et ses variations temporelles d'abondance influencent le succès de nidification des oies à travers une réponse comportementale de la proie face à un risque de prédation latent.

Les systèmes présentant des alternances d'abondance et de pénurie de ressources fournissent de bons exemples de limitation bottom-up de la productivité des écosystèmes (Polis *et al.*, 1997). Dans les milieux arides, de fortes précipitations induisent ainsi une

explosion de la disponibilité de nourriture et une explosion concomitante de l'abondance de nombreux consommateurs (Rotenberry & Wiens, 1991; Lima, Keymer & Jaksic, 1999; Coe & Rotenberry, 2003). Pourtant, les ressources abiotiques peuvent également influencer la réponse de proies en modifiant le risque de prédation. Malgré l'importance de ce mécanisme, les exemples suggérant que le comportement d'approvisionnement des prédateurs s'ajuste en fonction de l'abondance des précipitations sont encore rares (Post *et al.*, 1999; Fletcher & Koford, 2004). Le chapitre 2 fournit ainsi une démonstration additionnelle de tels mécanismes, à savoir une modulation du risque de prédation en fonction des précipitations par le comportement de la proie.

Malgré l'importance de l'eau dans la régulation physiologique des êtres vivants, nous connaissons très peu son rôle dans les stratégies individuelles. Ce manque de connaissance est d'autant plus important quand il est comparé au corpus de connaissances théoriques et empiriques sur les comportements d'approvisionnement en nourriture. Les effets limitant de la ressource « eau » dans le chapitre 2 suggèrent l'existence d'un compromis entre les besoins hydriques des oies durant le jeûne d'incubation et la reproduction dans un contexte de présence de prédateurs. Ce compromis peut être vu comme un analogue au compromis entre l'alimentation des adultes et les soins aux jeunes chez de nombreuses espèces soumis à un régime de prédation. Williams & Tieleman (2001) ont suggéré la création de modèles énergétiques incluant une régulation par les stratégies d'approvisionnement en eau chez les oiseaux vivants dans les déserts chauds. Je suggère d'étendre de tels modèles à d'autres systèmes. En effet, mes résultats démontrent l'importance de l'abondance en eau pour le succès de nidification alors qu'a priori le milieu Arctique n'est pas reconnu pour être limitant dans sa disponibilité en eau. Cette avenue serait ainsi une extension intéressante de ces résultats.

Risque de prédation et rapport de forces prédateurs/proies

Le risque de prédation est une force sélective importante, jouant un rôle clé dans l'évolution d'adaptations morphologiques et comportementales (Lima & Dill, 1990). Les modèles dérivés de la théorie des composantes biodémographiques prédisent un accroissement des risques pris par les adultes pour diminuer ceux de leurs jeunes chez des

espèces avec un fort potentiel reproducteur et une faible survie adulte, et l'inverse chez les espèces longévives à faible potentiel reproducteur (e.g. Ghalambor & Martin, 2001). De façon générale, peu d'études différencient risque de prédation pour les adultes et leurs jeunes, en particulier chez les oiseaux (Stoleson & Beissinger, 2001). Mais ces résultats ne font pas exception à cet égard en ne différenciant pas les effets combinés du risque de prédation sur les adultes et les œufs aux Chapitres 1 et 2. Toutefois, ce biais est probablement négligeable dans mon étude car il existe plusieurs évidences que le risque de prédation pour les adultes durant l'incubation est faible. Le seul prédateur potentiel des adultes dans le système étudié est le renard arctique (Reed, Hughes & Gauthier, 1995), avec une masse assez similaire à celle des oies durant l'incubation (renards: 3.18 kg, $SE = 0.09$, $n = 16$, D. Berteaux et A. Tarroux, données non publiées oies: 2.16 kg, $SE = 0.31$, $n = 45$, (Reed, Hughes & Gauthier, 1995). Il faut de plus noter ici que cette valeur de la masse des oies correspond aux femelles en fin d'incubation, au plus bas du cycle annuel de masse. Les renards sont donc au maximum 32 % plus lourds que les oies alors que les carnivores terrestres de moins de 25 kg s'alimentent en général sur des proies dont la masse est inférieure ou égale à 45 % de leur propre masse (Vézina, 1985; Carbone *et al.*, 1999). Enfin, de 1996 à 2005, J. Bêty, V. Careau et moi-même avons accumulé près de 1148 heures d'observations durant la nidification des oies et nous avons rapporté seulement 2 attaques mortelles sur un échantillon de près de 1500 attaques de renards sur des nids défendus par les oies.

À ce jour, les approches utilisées pour éviter les biais d'interprétation entre risque de prédation pour les adultes vs les jeunes ont été soit des études comparatives entre espèces avec un gradient d'effort reproducteur (Fontaine & Martin, 2006), soit des études manipulant le risque de prédation, notamment à l'aide de mannequins simulant des prédateurs ciblant les parents ou les jeunes uniquement (Ghalambor & Martin, 2001). Une alternative intéressante serait de comparer le comportement chez une même espèce où le rapport de masse avec le prédateur principal pourrait varier. Par exemple, je note que, sur 89 observations d'attaques de nids par les renards chez la Petite Oie des neiges sur l'Île Banks, deux ont causé la mort des femelles incubatrices (Samelius & Alisauskas, 2005) contre près de 1500 observations à Bylot pour la Grande Oie des neiges avec 2 mortalités (Bêty, Careau et Lecomte, obs. pers.). Cette comparaison tient en prenant en compte que

ces observations correspondent à tous les types d'attaques au nid (en présence ou non des parents, avec ou pas de succès de prédation sur les œufs). Ainsi, pour un même prédateur et des observations effectuées de façon similaire, le risque de prédation adulte au nid semblerait plus important pour la Petite que la Grande Oie des neiges, dont les masses diffèrent de près de 25-30%.

Dispersion et effets combinés

La prédation au nid et son évitement jouent un rôle déterminant pour la valeur sélective des individus. En théorie, le comportement des prédateurs peut affecter l'utilisation de l'habitat de reproduction par les proies qui tendront à éviter les parcelles d'habitats avec les risques de prédation les plus élevés (Rosenzweig, 1981; Martin, 1995; Fontaine & Martin, 2006). Les chapitres 1 et 2 montrent en effet un risque de prédation plus élevé en milieux humides qu'en mésiques et le chapitre 3 suggère que les oies montrent une dispersion préférentielle vers ces mêmes milieux humides même si les individus ne semblent pas répondre à leur succès de nidification précédent. De plus, les distances de dispersion les plus grandes (donc potentiellement plus coûteuses) correspondent à des individus qui nichent en association avec des Harfangs des neiges, une stratégie favorisant le succès de nidification.

De tels patrons de dispersion pourraient indiquer l'utilisation par les oies de signaux fournis par les caractéristiques intrinsèques des milieux et liées à la prédation (e.g. présence/absence d'hétérogénéité topographique) et/ou à l'information publique (e.g. succès des voisins, présences de conspécifiques), un signal pour lequel les évidences semblent de plus en plus répandues chez les oiseaux (Boulinier *et al.*, 1996; Danchin, Boulinier & Massot, 1998; Valone & Templeton, 2002; Doligez *et al.*, 2003). Au cours de la thèse, j'ai tenté de mesurer le succès de nidification moyen dans le voisinage de chaque nid de femelles à colliers afin de vérifier si les individus pouvaient utiliser l'information publique dans leur processus de dispersion. Malheureusement, vu le faible échantillon récolté malgré un effort important sur le terrain, je n'ai pas été en mesure de mesurer l'influence du succès de nidification des conspécifiques sur les stratégies individuelles de dispersion dans mon système.

Bien que les patrons de dispersion semblent cohérents avec les prédictions théoriques de maximisation de la valeur sélective, le mécanisme de cette dispersion pourrait être également dû à un facteur confondu au risque de prédation, comme la meilleure qualité des milieux humides en terme de nourriture disponible. En effet, même si la prédation peut être la cause principale d'échec au nid chez beaucoup d'oiseaux (voir Martin, 1995 et les références citées dans le texte), il existe peu d'évidence expérimentale de son effet sur les stratégies reproductrices, notamment en terme de dispersion. Classiquement, les approches expérimentales qui prouvent l'existence d'un mécanisme lié à la prédation utilisent des méthodes d'exclusion de prédateurs via des exclos, du trappage de prédateurs (Krebs *et al.*, 1995) ou l'utilisation d'îles avec ou sans prédateurs (Terborgh *et al.*, 2001). Je vois difficilement comment utiliser une telle approche dans mon système d'étude compte tenu des contraintes logistiques. Par contre, j'envisagerais une expérience couplant l'utilisation de bacs d'eau (cf. chapitre 2 – réduction du risque de prédation) et l'apport de nourriture *ad libitum* aux nids de femelles marquées une année t et la mesure de leur dispersion entre les années t et t+1.

Structure de population et dispersion

Les études génétiques utilisant les approches à fines échelles spatiales sont en pleine ébullition et montrent un lien étroit entre structure génétique et systèmes d'appariement et de dispersion (e.g. Sugg *et al.*, 1996; Shorey *et al.*, 2000; Coltman, Pilkington & Pemberton, 2003; Nussey *et al.*, 2005). Une dispersion incomplète ou différente entre les sexes sont ainsi les mécanismes proximaux d'une structuration de populations à fine échelle spatiale (Sugg *et al.*, 1996; Coltman, Pilkington & Pemberton, 2003). D'un point de vue évolutif, plusieurs causes de cette structure seraient possibles, soit la familiarité avec un site et la sélection de parentèle (Chesser, 1991; Queller, 1994). Dans le chapitre 4, je présente des évidences d'une structure génétique à fine échelle basée sur les sites d'élevages des jeunes mais pas sur les sites de nidification. Bien que le même patron ait été trouvé durant deux années différentes d'échantillonnage, ce n'est pas pour autant une preuve que celui-ci est stable à une échelle de temps plus large. Plusieurs études avec différentes approches spatiales ont en effet montré un changement de la structure génétique des populations

naturelles avec les années (e.g. Viard, Justy & Jarne, 1997; Garant, Dodson & Bernatchez, 2000; Nussey *et al.*, 2005). Par exemple, Nussey *et al.* (2005) ont montré pour la première fois chez un mammifère sauvage un déclin du F_{ST} à fine-échelle spatiale de près de 75 % en 20 ans, conséquence d'un changement de la taille effective de la population et du système d'appariement. Ce résultat suggère que les études de génétique de populations ne doivent pas assumer une stabilité dans le temps des structures mais plutôt considérer une possible variabilité spatio-temporelle de la structure et des mécanismes sous-jacents.

Dans cette thèse, j'ai utilisé une approche de génétique des populations afin de décrire des patrons de structure basés sur l'apparentement. Afin de comprendre les causes de ces patrons, des études complémentaires seront nécessaires, notamment sur le mécanisme d'appariement (e.g. reconnaissance d'apparentés ou de voisins, date de mise en place des couples, etc.) et les bénéfices d'élevage des jeunes entre apparentés chez la Grande Oie des neiges. À l'instar d'autres espèces d'oiseaux, il serait intéressant de déterminer si la reconnaissance d'apparentés peut être basée sur le phénotype (Choudhury & Black, 1993; Komdeur & Hatchwell, 1999) et/ou sur la familiarité (Choudhury & Black, 1994; van der Jeugd, van der Veen & Larsson, 2002). Il serait pertinent aussi de vérifier si le fait d'élever des jeunes entre apparentés résulte des bénéfices à vivre à proximité d'apparentés (e.g. aide dans l'élevage et l'évitement de la prédation. McKinnon, Gilchrist & Scribner, 2006), des bénéfices dus seulement à la philopatrie (e.g. familiarité avec les lieux. Schjørring, 2001) ou bien des deux. Des approches expérimentales comme celle utilisée par Choudhury & Black (1994) seront à explorer pour tester les hypothèses de reconnaissance et de date de mise en place des couples chez la Grande Oie des neiges. De plus, il serait pertinent d'associer des approches de capture-marquage-recapture avec la génétique moléculaire afin de déterminer en nature l'ampleur et les périodes de mélange des groupes d'oies durant leur cycle de vie. Une intégration de ces deux types d'approches est une avenue encore peu utilisée, bien que prometteuse car elle pourrait augmenter les chances de détecter des événements de dispersion à différentes échelles spatiales et temporelles (Tallmon *et al.*, 2002). Ainsi, la mesure des taux de dispersion dans le chapitre 3 est limitée par le sexe (femelles seulement), par la taille de la zone de recherche des nids et par une échelle de temps de l'ordre de 16 ans. Par contre, notre approche génétique nous permet de proposer des scénarios de dispersion pour les deux sexes, incluant des événements de dispersion qui

ont pu avoir lieu sur des échelles spatiales et temporelles plus grandes. Il reste encore à valider ces scénarios avec des études futures, visant notamment la période d'appariement où le brassage génétique s'effectue.

Récemment, Excoffier et Heckel (2006) ont fait le bilan des logiciels utilisés en génétique des populations en montrant leurs points forts, les précautions à prendre lors de leur utilisation et les combinaisons possibles de plusieurs logiciels. Par contre, ils n'ont pas abordé la question de la comparaison des résultats obtenus entre les logiciels pour des paramètres similaires (e.g. calcul de diversité génétique, F_{ST} , coefficient d'apparentement, etc...). Or, je m'aperçois que des logiciels différents ne donnent pas exactement les mêmes estimations de paramètres génétiques pour un même jeu de données, ce qui limite la comparaison des études entre elles. Ce problème peut venir des algorithmes des programmes, des prémisses de base utilisées par défaut (mais que l'utilisateur ne peut pas toujours modifier) mais aussi de problèmes de convergence des modèles, surtout lorsqu'ils utilisent des approches de maximum de vraisemblance. Une solution intéressante à ce problème serait d'unifier les approches, notamment via le programme R (<http://www.r-project.org/>) qui inclut déjà des modules d'analyses de génétiques des populations (e.g. Guillot, Mortier & Estoup, 2005), avec la possibilité de contrôler les paramètres par défaut des modèles. De plus, il serait intéressant que les programmes génétiques qui fonctionnent avec des procédures de maximum de vraisemblance s'inspirent des programmes de capture-marquage-recapture qui permettent d'ajuster les modèles tout en contrôlant pour les problèmes de minimum locaux, très fréquent avec ces procédures (e.g. Choquet *et al.*, 2003).

Message final et apport de la thèse

Pour conclure, cette thèse présente des résultats contribuant à la compréhension de mécanismes des relations prédateurs-proies et de la dispersion, où les échelles spatiales et temporelles jouent un rôle prépondérant. En intégrant différentes approches issues de la théorie de l'approvisionnement, des composantes biodémographiques et des interactions trophiques, j'ai apporté différentes perspectives sur le comportement de dispersion chez un herbivore important dans la toundra arctique. Au-delà de ces résultats, mon travail ouvre

des portes pour de futures études sur le lien entre l'utilisation de l'habitat et la prédation mais aussi sur les causes des patrons de dispersion observés et ses conséquences en termes de structure et de dynamique de populations. Dans cette perspective, l'étude de la dispersion souffre d'un manque de données empiriques (Ronce *et al.*, 2001). Je souhaite que mon travail et ses développements futurs contribuent à combler ce manque.

Ce travail est le fruit d'efforts déployés à la fois sur le long terme (depuis 1989) et durant mon doctorat. C'est pour moi un bel exemple de collaboration scientifique entre chercheurs et montre à quel point un effort conjoint favorise une synergie d'idées. J'ai construit mon projet à cette image, en mariant différentes approches, techniques et jeux de données et en développant des relations étroites entre les projets en cours. C'est dans cet état d'esprit que je souhaite continuer et encourager les futurs projets. L'Année Polaire Internationale qui s'amorce en 2007 a comme fondement l'échange des idées et la collaboration des chercheurs, et j'espère y contribuer par cette thèse et mon projet de post-doctorat.

TABLEAU 1. Synthèse des résultats les plus marquants et des approches utilisées au cours de la thèse.

CONCEPTS INTÉGRÉS		
<i>Risque de prédation</i>	<i>Utilisation de l'habitat</i>	<i>Structure de populations</i>
	→	→
RÉSULTATS PRINCIPAUX		
Milieus humides: refuges contre la prédation	Fidélité à l'échelle d'habitats particuliers	Structure génétique selon sites d'élevage plutôt que sites de nidification
Eau: ressource limitant le succès reproducteur	Dispersion : préférence des milieux humides	Philopatrie natale des mâles non-négligeable
APPROCHES GÉNÉRALES UTILISÉES		
Comportement des prédateurs et des proies	Comportement de dispersion des oies	Marqueurs génétiques
Approches empiriques et expérimentales	Capture marquage-recapture	Simulations basées sur les individus et sur le ré-échantillonnage
	Système d'Information Géographique	

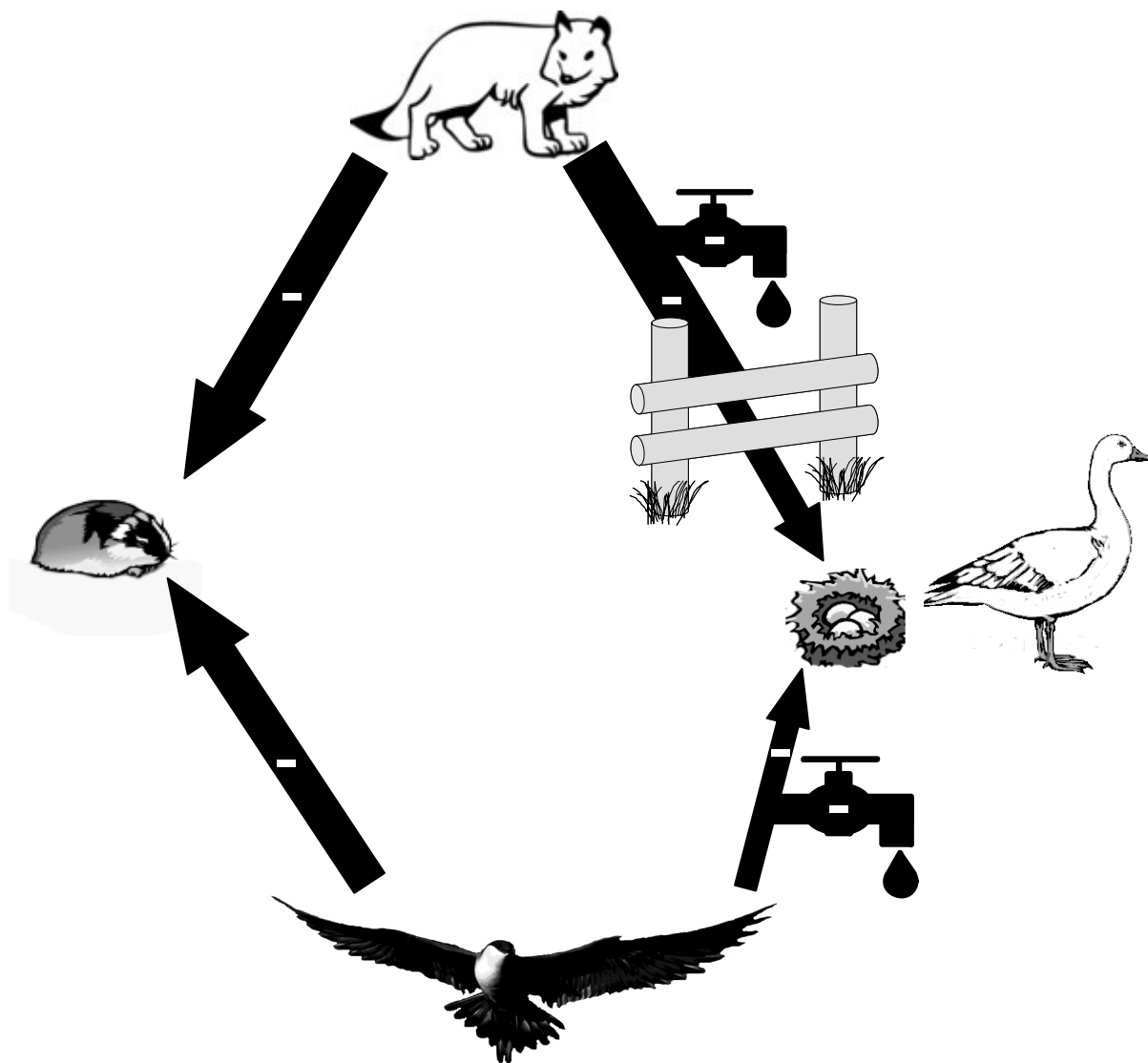


FIGURE 1. Schéma conceptuel simplifié représentant l'effet de refuge résultant de la complexité de l'habitat (barrière) sur la prédation du renard arctique ainsi que l'effet limitant de l'eau sur le succès reproducteur des oies, bénéficiant tant au renard qu'aux prédateurs aviaires (e.g. labbe parasite). On suppose ici que l'habitat n'affecte pas la prédation sur le lemming.

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ANNEXE 1

ANODEV ET r^2_{DEV}

ANODEV

L'ANODEV ou Analyse de Déviance est une application de l'analyse de variance dans un contexte de déviance; elle fournit un moyen d'évaluer l'impact d'une covariable dans un modèle. L'ANODEV compare ainsi la somme des déviances (DEV) expliqué par la covariable en question à celle des déviances qui ne sont pas expliquées par cette covariable. Voici la formule de calcul :

$$\text{ANODEV} = \frac{\text{DEV}(S_{\bullet}) - \text{DEV}(S_{b_0+b_1(x)}) / \text{np}(S_{b_0+b_1(x)}) - \text{np}(S_{\bullet})}{\text{DEV}(S_{b_0+b_1(x)}) - \text{DEV}(S_t) / \text{np}(S_t) - \text{np}(S_{b_0+b_1(x)})}$$

où S_t est le modèle dépendant du temps, $S_{b_0+b_1(x)}$ le modèle avec la covariable, (S_{\bullet}) le modèle où S est constant et np est le nombre de paramètres dans le modèle (Agresti, 2002). La statistique de l'ANODEV suit une distribution de F de Fisher où les degrés de liberté sont calculés ainsi : $\text{df1} = \text{np}(S_{b_0+b_1(x)}) - \text{np}(S_{\bullet})$ et $\text{df2} = \text{np}(S_t) - \text{np}(S_{b_0+b_1(x)})$.

r_{DEV}^2

Le r_{DEV}^2 est un indice analogue à un r^2 classique qui permet de donner un estimé du pouvoir explicatif d'une covariable au sein de différents modèles. Voici la formule :

$$r_{DEV}^2 = \frac{\text{DEV}(S_{\bullet}) - \text{DEV}(S_{b_0+b_1(x)})}{\text{DEV}(S_{\bullet}) - \text{DEV}(t)}$$

où tous les symboles utilisés sont identiques à ceux décrit pour l'ANODEV (Agresti, 2002).

ANNEXE 2

LOCALISATION DES PRÉLÈVEMENTS GÉNÉTIQUES

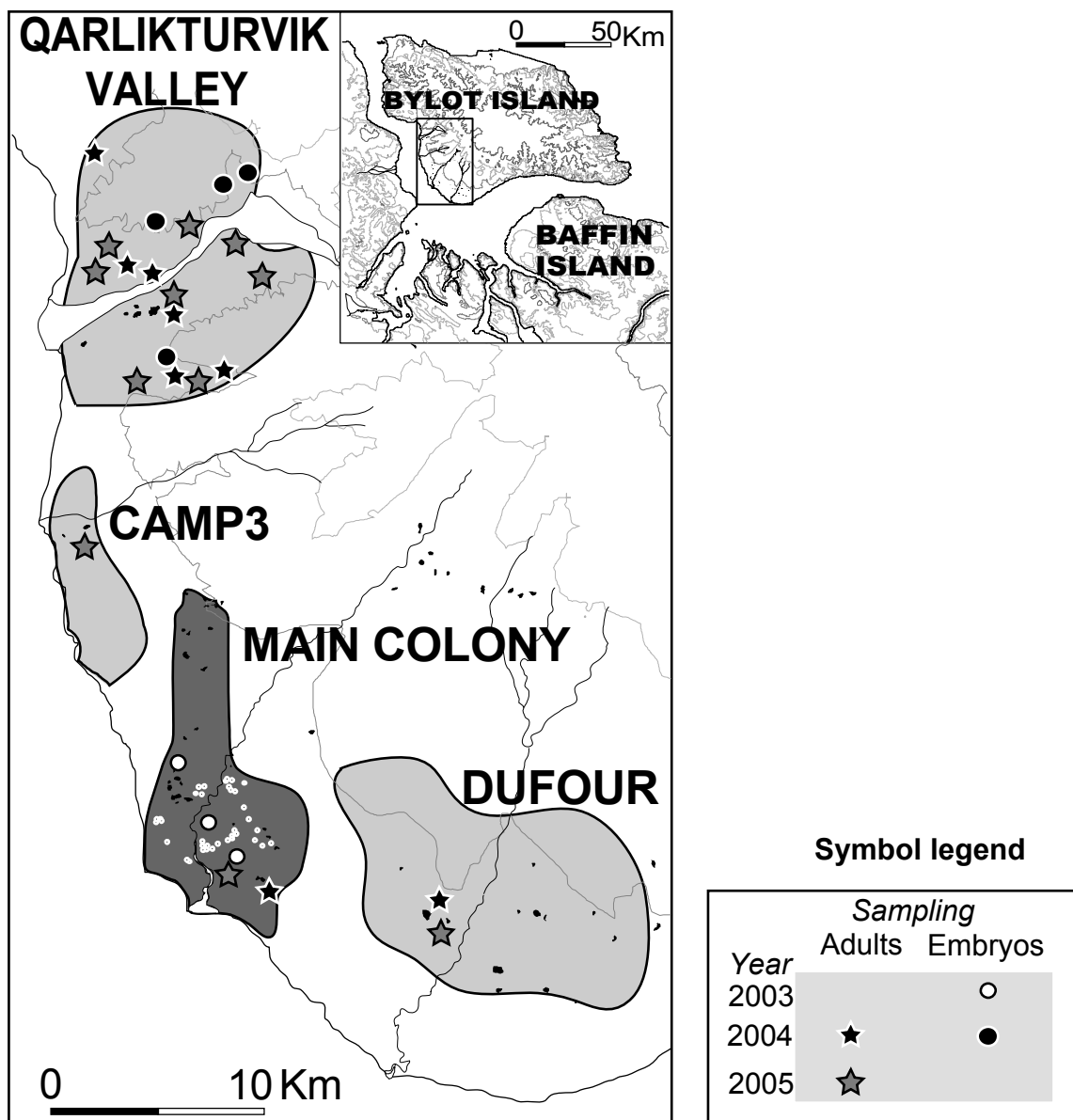


FIGURE 1. Localisations des sessions de baguages et des sites de nidification où nous avons effectué les prélèvements sanguins respectivement d'adultes et d'embryons.