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DÉPLACEMENTS DES FAMILLES DE LA GRANDE OIE DES NEIGES DURANT LA PÉRIODE D'ÉLEVAGE, ÎLE BYLOT, NUNAVUT.

Mémoire
présenté
à la Faculté des études supérieures
de l'Université Laval
pour l'obtention
du grade de Maître ès Sciences (M.Sc.)

Département de Biologie
FACULTÉ DES SCIENCES ET DE GÉNIE
UNIVERSITÉ LAVAL
Québec

Février 2003

RÉSUMÉ

Le déplacement des familles chez les oiseaux nidifuges a été associé à des coûts au niveau de la croissance et de la survie des jeunes. Dans cette étude, nous avons examiné les déplacements effectués par la Grande Oie des neiges nichant à l'Île Bylot, Nunavut, afin de quantifier ces coûts. Pour ce faire, nous avons suivi les déplacements de femelles munies de radio-émetteur entre leur site de nidification et d'élevage, et utilisé l'information provenant de la recapture de couvées marquées à l'éclosion. Les familles se sont déplacées sur des distances très variables allant de 2 à plus de 50 km. Les femelles se déplaçaient surtout le long de la mer (< 2 km) lors du mouvement entre les sites de nidification et d'élevage. Une fois établies dans le site d'élevage, les oies se déplaçaient peu. Les femelles ont également montré une certaine fidélité inter-annuelle envers leur site d'élevage. Aucun coût lié à la survie des oisons n'a été trouvé en relation avec la distance parcourue entre le site d'éclosion et d'élevage. Cependant, la croissance des oisons était affectée de façon différente selon la stratégie de reproduction adoptée. Les jeunes nés près du site d'élevage principal (< 5 km) ont eu une meilleure croissance que ceux ayant dû parcourir 30 km ou plus pour s'y rendre. Ceci s'expliquerait en partie par le temps passé dans des habitats de pauvre qualité durant le déplacement qui dure environ une semaine. Cependant, les jeunes qui ont accompli ce long déplacement ont eu une meilleure croissance que ceux qui sont demeurés à la colonie principale de nidification pour l'élevage. Nous proposons qu'un compromis dans la sélection des sites de nidification et d'élevage puisse expliquer pourquoi la majorité des oies nichant à l'Île Bylot réalisent de longs déplacements vers le site d'élevage. Les coûts de ce déplacement seraient en effet contrebalancés par un risque de prédation réduit sur les nids pour les oies nichant à haute densité dans la colonie.

ABSTRACT

Overland brood movements in precocial birds are thought to be costly in terms of growth and survival of young. In this study, we examined brood movement in Greater Snow Geese nesting on Bylot Island, Nunavut, to assess these potential costs. To achieve this, we monitored movements of radio-marked females from their nest to their brood-rearing sites and used information from the recapture of broods marked at hatch. Brood movements were highly variable, ranging from 2 to more than 50 km. Females tended to follow the seashore (< 2 km) during brood movement. Once in the rearing area, brood movements were considerably shorter. Females showed some inter-annual fidelity toward their brood-rearing area. We found no cost in terms of gosling survival in relation to distance moved between nesting and brood-rearing areas. However, gosling growth was affected differently by brood movement according to the breeding strategy. Goslings hatched near the main brood-rearing area (< 5 km) grew better than those moving 30 km or more. This could be partly explained by the time spent in low quality habitat during overland movements that lasted one week on average. However, goslings that made long overland movements grew better than those that stayed at the main nesting colony for brood-rearing. We suggest that a trade-off between nest and brood-rearing site selection may explain why the majority of nesting geese on Bylot Island make long movements toward their brood-rearing site. The costs of these movements could be balanced by a lower risk of nest predation for geese nesting at high density at the colony.

AVANT-PROPOS

Ce mémoire de maîtrise comprend deux chapitres rédigés dans la langue de Shakespeare, sous forme d'articles, dans le but d'être soumis à des revues scientifiques portant sur l'écologie animale. Le mode de présentation général comprend, dans l'ordre: le résumé, l'introduction servant de mise en contexte et l'étude même. Les déplacements réalisés entre les sites de nidification et d'élevage par les familles de la Grande Oie des neiges, à l'Île Bylot, Nunavut, font l'objet de ce mémoire. Plus spécifiquement, nous nous sommes attardés aux coûts et bénéfices potentiels associés aux déplacements par les oiseaux nidifuges en utilisant l'Oie des neiges comme modèle. Le premier article porte sur l'étude des déplacements des familles en utilisant des femelles munies de radio-émetteur et dans lequel les coûts associés à la croissance et à la survie des jeunes sont examinés. Cet article, dont je suis le premier auteur, rassemble un important jeu de données récoltées pendant une étude à long terme menée par Gilles Gauthier (Université Laval) et Jean-François Giroux (Université du Québec à Montréal), qui sont à la fois co-auteurs de cet article, de même que directeur et co-directeur, respectivement. Joël Bêty, confrère de laboratoire, a également contribué à cet article en y incorporant des données obtenues durant ses études doctorales, et est également co-auteur de cet article. Le second chapitre porte sur les coûts potentiels d'utiliser des milieux de pauvre qualité durant les déplacements en comparant l'utilisation de l'habitat et sa sélection, ainsi que le comportement des familles en déplacement comparativement à des familles bien installées dans un bon site d'élevage. Gilles Gauthier, Jean-François Giroux et Isabelle Duclos, collègue de l'Université du Québec à Trois-Rivières qui a contribué à cette étude en partageant une partie de ses données de maîtrise, sont co-auteurs sur cet article. Une conclusion relève les points importants de ce projet de maîtrise et offre des suggestions de recherche futures.

REMERCIEMENTS

La réalisation de ce projet d'étude est grandement attribuable à la participation de nombreuses personnes et différents organismes permettant des études dans le Haut-Arctique canadien.

Je tiens d'abord à remercier mon directeur, Gilles Gauthier, qui a porté une attention particulière à la bonne marche de mon projet, de par sa supervision sans reproche et ses vastes connaissances sur l'espèce étudiée. Malgré sa charge de travail considérable, il a su m'allouer le temps nécessaire pour répondre à mes questions et inquiétudes relativement aux opérations de terrain réalisées à l'Île Bylot, ainsi qu'à la rédaction de cet ouvrage par ses commentaires constructifs. Il en va de même pour mon co-directeur, Jean-François Giroux, qui a également apporté une contribution notable à ce projet d'étude, de par son sens critique et ses nombreuses heures de patience pour la capture d'oies au nid et de télémétrie en hélicoptère. Je leur suis reconnaissant de m'avoir donné une formation de chercheur de qualité dans un milieu unique et sur une espèce que j'ai bien aimé étudier. Jean Huot (Université Laval) a contribué à cet ouvrage par ses commentaires constructifs en tant que membre du comité d'évaluation et je tiens à le remercier également.

Je tiens également à remercier tous les gens qui ont contribué, de près ou de loin, à la récolte des données sur le terrain. Principalement Eric T. Reed et Joël Bêty qui, par leur expérience, m'ont guidé autant sur le terrain que dans mes analyses statistiques, afin de réaliser, du moins j'espère, un projet de recherche bien étoffé. À eux deux, ainsi qu'aux autres Bylotien(nes), spécialement: Marie-Christine Cadieux, Anna Calvert, Isabelle Duclos, Mathieu Dumas, Catherine Gagnon, Nikolas Lecomte, Ariane Massé, Olivier Mathieu, Daniel Munro, Joassie et Amos Ootovak, Gérald Picard (technicien, responsable des opérations de baguage, qui a contribué à une bonne partie des données récoltées), Vincent Préfontaine, Austin Reed (à qui plusieurs doivent leur passage à Bylot), et Jean-François Savard, un gros merci pour leur compagnie durant les mois passés là-haut.

Un gros merci aussi à mes collègues de laboratoire du 2040, Joël Bêty, Grégory Bourguelat, Marie-Christine Cadieux, Anna Calvert, Matthieu Féret, Nikolas

Lecomte, Hélène Sénéchal et Eric Reed pour leur camaraderie à l'intérieur et l'extérieur des murs du campus. Je remercie également les autres étudiants du Département de biologie, surtout ceux des groupes de recherche de Jean Huot et de Steeve Côté, pour leur partage d'idées. Merci aussi à ma petite sœur Marie pour son expertise lors de la réalisation des cartes trouvées dans cet ouvrage.

Merci également aux organismes suivants qui ont permis la réalisation de ce projet: Plan Conjoint sur les Oies Arctiques (Service Canadien de la Faune), Centre d'Études Nordiques (CEN) de l'Université Laval, Conseil de Recherche en Sciences Naturelles et en Génie du Canada (CRSNG), Ministère des Affaires Indiennes et du Nord du Canada, Fonds pour la formation de Chercheurs et l'Aide à la Recherche du Québec (FCAR), l'Association des chasseurs et trappeurs de Pond Inlet au Nunavut et l'équipe de l'Étude du Plateau Continental Polaire (Ministère des Ressources Naturelles du Canada).

Finalement, un gros merci à ma famille, mes proches et Elisabeth, pour leur amour, amitié, soutien et appui durant mon projet de Maîtrise.

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CHAPTER II

INTRODUCTION GÉNÉRALE

La migration est un phénomène répandu dans le règne animal permettant d'assurer des conditions optimales durant tout le cycle de vie des individus (Dingle 1980). Les animaux migrent ainsi en réponse à des changements saisonniers au niveau de leurs habitats et de leurs besoins vitaux. Ces changements poussent plusieurs espèces, allant des insectes aux grands mammifères, à se déplacer sur des distances parfois considérables, certaines espèces d'oiseaux accomplissant des migrations de plusieurs milliers de kilomètres. Ces mouvements migratoires sont souvent associés aux déplacements annuels entre les aires d'hivernage et ceux de reproduction comme par l'exemple chez le Caribou (*Rangifer tarandus*; Bergerud et al. 1990). À chacun de ces sites, les animaux tentent de maximiser l'utilisation des habitats optimaux en regard de leurs besoins (Pyke 1983). Chez les grands herbivores, par exemple, les individus vont chercher à occuper les milieux caractérisés par des plantes aux qualités nutritives élevées (Wilmshurst et al. 2000).

En période de reproduction, la théorie de la sélection de l'habitat de Fretwell (1972) propose que les individus essaient d'augmenter leur succès reproducteur en utilisant les meilleurs habitats disponibles. Ainsi, à même le site de reproduction, les animaux vont parfois devoir se déplacer afin d'accéder à des habitats de plus haute qualité en réponse à différents facteurs biotiques et abiotiques. Certains compromis peuvent alors prévaloir lors du choix de ces habitats entre la présence de conspécifiques et de prédateurs d'une part, et la qualité de la ressource retrouvée (e.g. nourriture, abri) d'autre part (Grand 2002). Les individus réussissant à occuper les meilleures sites ont alors plus de chances d'augmenter leur fitness (Higginbottom 2000, Pettorelli et al. 2001, Pöysä 2001). Les longues migrations entre les aires d'hivernage et de reproduction ainsi que les déplacements à plus petite échelle à l'intérieur d'une aire donnée (e.g. aire de reproduction) obéiraient donc aux même pressions de sélection et constitueraient en quelque sorte un continuum dans la quête de conditions optimales.

Les déplacements d'individus sur les aires de reproduction ont été décrits chez plusieurs espèces incluant les oiseaux nidifuges (i.e. dont les jeunes quittent le nid après l'éclosion) tels le Lagopède des saules (*Lagopus lagopus*, Erikstad 1985), le

Canard noir (*Anas rubripes*, Ringelman et Longcore 1982a), le Canard pilet (*Anas acuta*, Duncan 1987) et le Canard colvert (*Anas platyrhynchos*, Rotella et Ratti 1992). Le mode de reproduction de ces oiseaux, contrairement à celui des oiseaux nidicoles (i.e. dont les jeunes restent au nid après l'éclosion), les oblige à se déplacer sur des distances parfois considérables après l'éclosion afin de permettre aux jeunes d'avoir accès à une nourriture qui répond à leurs exigences nutritionnelles. Ces déplacements seraient effectués en réponse à un changement dans les besoins vitaux durant le cycle reproducteur. En effet, la sélection d'un habitat optimal pour satisfaire à un besoin particulier peut ne pas convenir à un besoin qui se crée plus tard dans la saison. Par exemple, les parents vont favoriser les habitats qui minimisent les risques de prédation sur les œufs et la femelle qui incube à cause de leur grande vulnérabilité (Mickelson 1975). Par contre, après l'éclosion, les habitats qui sont les meilleurs pour l'alimentation des jeunes risquent de différer des précédents. Ceci peut donc poser un problème particulier aux familles qui devront se déplacer vers des sites d'élevage plus favorables à la croissance des jeunes, impliquant des coûts potentiels en dépit des bénéfices pour les familles une fois rendu sur ces sites. Ces oiseaux tentent ainsi de sélectionner les sites répondant le mieux à leurs exigences afin d'accroître le nombre de jeunes qui réussiront à survivre jusqu'à l'envol (Cody 1985).

Un exemple bien connu de déplacement post-éclosion est celui de l'Eider à duvet (*Somateria mollissima*) dont les individus nichent sur des îles au milieu de l'estuaire du Saint-Laurent mais doivent les quitter après l'éclosion afin d'atteindre les sites d'élevage situés le long des rives du fleuve (Munro et Bédard 1977). L'utilisation des îles pour la nidification permet de diminuer la prédation sur la femelle et les œufs, une stratégie commune chez les Anatidés (Tombre et al. 1998, Ebbinge et Spaans 2002). Cependant, le site d'alimentation principal (site d'élevage) étant situé à près de 10 km de ces îles le long de la rive sud du fleuve Saint-Laurent, les familles doivent alors franchir cette distance afin d'y avoir accès. La traversée du fleuve par les familles comporte des risques pour la survie des jeunes étant donné leur grande vulnérabilité à plusieurs prédateurs aériens comme les goélands (*Larus argentatus* et *L. marinus*; Munro et Bédard 1977). Ce type de déplacement post-éclosion est donc caractérisé par des coûts importants. Les individus doivent alors adopter certaines stratégies afin de minimiser les coûts associés aux déplacements.

Bénéfices des déplacements pour les jeunes

La qualité et la quantité de nourriture retrouvées dans un site ont une forte influence sur la croissance des jeunes, le nombre d'entre eux qui survivront jusqu'à l'envol et leur taille adulte finale (Larsson et Forslund 1991; Rotella et Ratti 1992). Cette situation est particulièrement vraie chez les oies qui sont des herbivores stricts incapables de digérer les fibres contenues dans les plantes (Mattocks 1971). Les oisons doivent donc avoir accès à des plantes ayant une teneur élevée en protéines afin de maximiser leur croissance avant l'envol étant donné la courte période estivale dans l'Arctique (Sedinger et Raveling 1984, Person et al. 1998). La sélection des plantes répondant le mieux à leurs exigences nutritionnelles s'avère donc cruciale à cette période de l'année (Manseau et Gauthier 1993, Gadallah et Jefferies 1995, Sedinger et al. 1995). Chez la Grande Oie des neiges (*Chen caerulescens atlantica*), la taille des jeunes à la fin de l'été est directement liée à la quantité de nourriture disponible durant la période d'élevage (Lepage et al. 1998).

Une étude chez la Petite Oie des neiges (*Chen c. caerulescens*) nichant à La Pérouse Bay a montré que les jeunes des familles qui se déplacent vers de nouveaux sites d'élevage où la qualité et la quantité de nourriture sont supérieures à celles des sites traditionnels d'élevage (milieux dégradés plus pauvres) ont de meilleurs taux de croissance et de survie (Cooch et al. 1993) puisqu'il existe une relation positive directe entre ces deux variables (Owen et Black 1989, van der Jeugd et Larsson 1998, Cooch et al. 2002, Reed et al. 2003). Eriksson (1978) a trouvé une relation entre la sélection d'un lac (site d'élevage) par des familles de Garrots à oeil d'or *(Bucephala clangula*) et la quantité de nourriture trouvée dans ce lac, montrant qu'une sélection s'opère durant l'élevage des jeunes.

Le site choisi doit également répondre à un autre besoin des familles, soit celui de diminuer le risque de prédation sur les jeunes. Ainsi, des sites d'alimentation de qualité inférieure peuvent être quand même choisis par les adultes s'ils offrent une meilleure protection contre les attaques de prédateurs sur les jeunes (Stahl et Loonen 1998). Chez ces espèces, cependant, l'accès aux sites fournissant les meilleures conditions d'alimentation et offrant des abris adéquats contre les prédateurs n'est souvent garanti que par le déplacement des familles.

Coûts des déplacements pour les jeunes

Diminution du taux de survie des jeunes

Les déplacements vers des habitats d'élevage sont parfois associés à une baisse dans la probabilité de survie des jeunes comparativement à ceux qui ne se déplacent peu ou pas. Plusieurs études portant sur les Anatidés supportent cette idée, dont celles de Ringelman et Longcore (1982b) chez le Canard noir, Leonard et al. (1996) chez le Fuligule à dos blanc (*Aythya valisineria*) ainsi que celles de Mauser et al. (1994) et de Rotella et Ratti (1992) chez le Canard colvert. Des résultats similaires sont rapportés pour d'autres familles d'oiseaux nidifuges tel le Vanneau huppé (*Vanellus vanellus*; Blomqvist et Johansson 1995) et le Lagopède des saules (Erikstad 1985). Ces études démontrent qu'il y a une mortalité plus élevée chez les couvées se déplaçant sur de longues distances versus celles qui ne le font pas, mais ces auteurs n'ont pas été en mesure de déterminer comment et quand exactement cette mortalité survient. Cette situation est en bonne partie attribuable à la difficulté de suivre les couvées en milieu naturel.

L'épuisement, l'exposition aux intempéries et la prédation seraient les agents responsables d'une baisse du taux de survie durant les déplacements (Ball et al. 1975). Ces auteurs ont également observé que la plus grande partie de la mortalité des jeunes s'opérait à l'intérieur des deux premières semaines de vie, soit la période où ils se déplacent le plus. Des observations suggèrent aussi que certains jeunes, peu de temps après l'éclosion, auraient de la difficulté à suivre la mère, une situation qui se solderait par la séparation et éventuellement la mort du jeune (Rotella et Ratti 1992). D'un autre côté, l'étude de Talent et al. (1983) sur des couvées de Canard colvert ne rapportent pas de baisse dans le taux de survie des jeunes due aux déplacements des familles sur de longues distances puisque seulement quelques jeunes ont été perdus lors des mouvements entre les sites (aucune perte de couvée totale), suggérant que les déplacements n'affectent pas toujours négativement les couvées. Dzus et Clark (1997) ont obtenu des résultats similaires chez cette même espèce, les familles parcourant de grandes distances ayant un taux de survie ne différant pas de celles qui demeuraient sur place.

La prédation pourrait être le principal facteur responsable de la mort des jeunes en déplacement (Dzubin et Gollop 1972). Une femelle Canard pilet a été suivie lorsqu'elle menait sa couvée en terrain découvert sur une distance de 5.2 km par Duncan (1983). Il a été témoin de tentatives successives de prédation de la part d'un Busard St-Martin (*Circus cyaneus*) et d'une Buse de Swainson (*Buteo swainsoni*) en l'espace de deux jours seulement. Bien qu'il n'y ait pas eu de jeunes capturés par un prédateur, on voit ici le risque de prédation associé aux mouvements entre des sites. Chez l'Eider à duvet, Munro et Bédard (1977) ont rapporté que les familles formaient des crèches afin de diminuer le taux de prédation sur les jeunes par les goélands. Ces auteurs ont néanmoins constaté un taux de prélèvement allant jusqu'à 37% des jeunes durant le déplacement entre les îles (site de nidification) et la berge (site d'élevage). Un dernier cas à titre d'exemple est celui observé par Glasgow (1977) rapportant l'attaque d'un coyote (*Canis latrans*) sur une famille de Bernache du Canada (*Branta canadensis*) lorsque cette dernière se déplaçait entre deux lacs, résultant en la perte de plusieurs jeunes. Ces événements soulignent les dangers potentiels se rapportant à des mouvements d'un site à l'autre, qui peuvent différer grandement selon le site d'étude. Cependant, les bénéfices associés au fait de se déplacer, telle l'augmentation des chances de survie par l'accès éventuel à des sites de meilleure qualité, devraient être plus grands que les coûts pour qu'il y ait maintien de ce type de comportement (Eriksson 1978).

Coût énergétique

Les déplacements des jeunes entre les sites de nidification et d'élevage peuvent entraîner un coût énergétique non-négligeable relié à la locomotion. Ce coût peut se répercuter sur la croissance des jeunes en fonction de la distance parcourue. Ainsi, chez le Harelde kakawi (*Clangula hyemalis*), Pehrsson et Kenneth Nyström (1987) ont démontré que la croissance des jeunes était négativement corrélée à la distance parcourue, les jeunes exécutant les plus longs déplacements ayant une masse moindre par rapport à ceux qui se déplacent peu entre le site de nidification et d'élevage. Cette même relation a été observée chez une population de Lagopède des saules (Erikstad 1985). Cependant, une étude menée par Duncan (1987) ne donne pas les mêmes résultats chez les jeunes du Canard pilet. Il a démontré que la croissance n'était pas affectée par une marche de 3 km chez des canetons âgés de 12 à 24 heures lorsque ces derniers étaient comparés à un groupe témoin ne s'étant pas déplacé. L'énergie dépensée durant les déplacements serait mineure, se limitant possiblement à une réduction des réserves de glycogène. La masse des jeunes ayant marché, lorsqu'ils ont atteint l'âge de 7 et 11 jours, tendait même à être supérieure à celui du groupe témoin. Cela suggère que la croissance n'est pas toujours affectée négativement par des déplacements de grande amplitude. De plus, les coûts associés à la locomotion dans un environnement froid seraient négligeables d'après les travaux d'Otis (2002) sur les oisons de la Grande Oie des neiges.

Un autre aspect important est que, lors des déplacements, il est possible que les familles allouent une plus grande partie de leur temps à la locomotion au détriment du temps voué à l'alimentation. Par exemple, Giroux (1980) a observé des familles de Bernache du Canada se déplacer, parfois en courant (vitesse moyenne de 2.3 km/h), sur de longues distances (8.3 km) avec quelques arrêts de courte durée en une seule journée. On peut supposer que le gain énergétique par l'alimentation lors de ces déplacements soit moindre que pour des familles installées dans les sites d'élevage, ce qui pourrait éventuellement nuire à la croissance des jeunes.

Utilisation de l'habitat durant la période d'élevage

Durant les mouvements, les familles devraient préférer utiliser des habitats qui leur permettent de se nourrir et de se cacher des prédateurs. Par exemple, chez une population de Canard branchu (*Aix sponsa*) se reproduisant dans le sud du Dakota, les femelles guident leurs petits dans les bandes de forêts le long des cours d'eau et dans les terres humides, ce qui leur procure un abri contre les prédateurs et leur fournit de la nourriture (Granfors et Flake 1999). Bien que la disponibilité de ces habitats soit plus faible, ils sont préférés pour les déplacements vers les sites d'élevage comparativement aux habitats ouverts qui comportent plus de risques. Chez la Bernache du Canada, Giroux (1980) a noté que des familles ont rallongé leurs déplacements de 2.3 km afin de profiter de l'abri que pouvait fournir la végétation le long des clôtures et des bords de route, diminuant ainsi le risque d'être détecté par un prédateur. On remarque encore ici la préférence pour un habitat dont la disponibilité est faible mais procurant des avantages. Cependant, les familles peuvent parfois être contraintes d'utiliser des habitats sous-optimaux durant leur déplacement comme les jeunes couvées d’eider traversant le fleuve St-Laurent (Munro et Bédard 1977). Il est alors concevable de penser que le temps passé dans ces habitats de pauvre qualité nutritive peut entraîner un délai dans la croissance des jeunes, particulièrement si le déplacement des familles se fait sur une période de plusieurs jours. En effet, il est probable que des individus ayant accès dès l’éclosion à des sites d’alimentation de qualité seraient favorisés comparativement à des individus devant passer un certain temps dans des habitats de qualité inférieure avant d’avoir accès à ceux de meilleure qualité.

Certains oiseaux nidifuges parcourent de longues distances afin d’avoir accès à des sites adéquats pour l’élevage de leurs jeunes malgré la présence de sites plus près du nid qui, en apparence, pourraient convenir. Cette situation a été observée chez la Petite Oie des neiges, avec des distances de déplacement allant jusqu’à 10 km, et chez le Canard branchu, le Canard noir, le Canard colvert, le Canard pilet et le Fuligule à dos blanc avec des distances moindres (Abraham 1980, Granfors et Flake 1999, Ringelman et Longcore 1982a, Rotella et Ratti 1992, Duncan 1987, Leonard et al. 1996). Pour certaines de ces espèces, les femelles amèneraient leur couvée vers leur propre site natal d’élevage ou un site où elles ont élevé leur couvée avec succès dans les années passées (Abraham 1980, Cooke et Abraham 1980, Smith et Flake 1985). Ceci suggère que la fidélité au site serait un phénomène important pour expliquer le choix du site. Les expériences de reproduction antérieures peuvent effectivement influencer le choix d’un site en conférant des avantages tels l’augmentation de l’efficacité d’alimentation par la connaissance des ressources ainsi que par la diminution du risque de prédation par la connaissance des refuges présents (Anderson et al. 1992).

Cas de la Grande Oie des neiges

La Grande Oie des neiges est l’une des espèces d’oies qui niche le plus au Nord (Gauthier et al. 1992). Son aire de reproduction est composée principalement de la Terre de Baffin et de l’Île Bylot dans le Nunavut. Approximativement 15% de la population totale de cette espèce niche sur l’île Bylot (Reed et al. 1992), faisant de cet endroit un site intéressant pour l’étude de cette espèce.

Chez cette oie, la période d'élevage est cruciale car les jeunes doivent atteindre la taille et la condition physique nécessaire pour accomplir la migration automnale sous la contrainte d'un été arctique court (Lesage et Gauthier 1997). Lors de cette période, les étangs, les lacs et les milieux humides qui les entourent représentent un habitat important pour les familles, tant pour la quantité et la qualité de la nourriture qu'on y retrouve que pour l'abri qu'ils procurent contre les prédateurs terrestres (e.g. Renard arctique; *Alopex lagopus*; Hughes et al. 1994b, Duclos 2002). En effet, durant cette période les jeunes sont incapables de voler, tout comme les adultes qui sont en période de mue (Giroux et al. 1984; Hughes et al. 1994a,b). La présence de plantes nutritives comme *Eriophorum schreuchzeri* et *Dupontia fisheri* dans les milieux humides et autour des lacs figure probablement parmi les conditions essentielles pour la croissance rapide des oisons durant cette brève période (Manseau et Gauthier 1993, Massé et al. 2001). L'importance de la qualité et de la disponibilité de la nourriture et ses effets sur la croissance des jeunes chez la Grande Oie des neiges a d'ailleurs été démontrée dans l'étude de Lepage et al. (1998).

Il existe trois stratégies principales utilisées par les oies lors de la période de reproduction sur l'Île Bylot. Tout d'abord, la majorité des oies nichent à haute densité (grande colonie) au centre de la plaine sud-ouest de l'île, près de la côte. Pour ces individus, deux types de stratégie sont possibles pour l'élevage des jeunes. La première est de demeurer à la colonie après l'éclosion et ce durant toute la période d'élevage. La seconde consiste à accomplir des déplacements considérables en quittant la zone de nidification principale afin de rejoindre des habitats offrant une nourriture de meilleure qualité (bons sites d'élevage). Une grande proportion de ces oies choisissent la vallée du camp-1 (Reed et al. 1992), l'un des meilleurs sites d'élevage retrouvé sur l'île mais situé à 30 km de la colonie principale. Une troisième stratégie adoptée est de nicher à faible densité (petites colonies éparses) près du site d'élevage principal (Bêty et al. 2001). Les oies adoptant cette stratégie évitent alors les inconvénients potentiels associés à de longs déplacements tout en ayant accès rapidement à une nourriture de qualité pour leurs jeunes. Une hypothèse pouvant expliquer pourquoi la majorité des oies semblent préférer nicher à forte densité loin du site d'élevage principal serait que ces individus bénéficient d'une diminution du risque de prédation sur les œufs, et donc d'un succès de nidification plus élevé, que les individus nichant à faible densité de façon isolée (Bêty et al.

2001). Un élément appuyant cette hypothèse est que les années où les oies nichent en grand nombre près des sites d'élevage sont celles où elles peuvent nicher en association avec des rapaces tels que le Harfang des neiges (*Nyctea scandiaca*) et la Buse pattue (*Buteo lagopus*) dont la nidification est occasionnelle et liée à la dynamique des populations de lemmings (Lepage et al. 1996, Bêty et al. 2001). Cette association permet alors de tirer profit de la protection des oiseaux de proie contre les prédateurs de nids tels que le Renard arctique, le Labbe parasite (*Stercorarius parasitus*), le Goéland bourgmestre (*Larus hyperboreus*) et le Grand Corbeau (*Corvus corax*) (Tremblay et al. 1997, Bêty et al. 2001).

La présence de ces trois stratégies de reproduction fait donc de la Grande Oie des neiges un modèle intéressant pour l'étude des coûts et des bénéfices associés aux déplacements du site de nidification vers les sites d'élevage. Dans cette étude, l'objectif principal était de quantifier et caractériser les mouvements faits par les familles entre les sites de nidification et d'élevage, et de déterminer si les déplacements engendraient des coûts pouvant affecter le succès reproducteur des oies. Plus spécifiquement, dans le premier chapitre, nous avons d'abord décrit les mouvements réalisés par les familles dont les femelles étaient munies de radio-émetteurs pour ensuite vérifier s'il y avait un effet de ces déplacements sur la survie et la croissance des oisons. Nous avons également examiné la fidélité des femelles au site d'élevage. Finalement, nous avons comparé le succès de nidification entre différents sites afin de mieux comprendre l'ensemble des coûts et bénéfices pour les oies qui nichent à haute et faible densité à l'Île Bylot. Dans un deuxième chapitre, nous avons comparé l'utilisation et la sélection de l'habitat, ainsi que le comportement des familles durant les déplacements à ceux de familles déjà installées au site d'élevage principal. L'objectif principal de cette comparaison était de déceler d'éventuelles différences (e.g. au niveau de l'utilisation de milieux sub-optimaux) pouvant affecter négativement la croissance des jeunes.

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CHAPITRE I

THE EFFECTS OF BROOD MOVEMENTS ON GOSLING GROWTH AND SURVIVAL IN GREATER SNOW GEESE

RÉSUMÉ

Nous avons examiné les coûts et bénéfices associés aux longs déplacements entre les sites de nidification et d'élevage chez la Grande Oie des neiges nichant à l'Île Bylot, Nunavut. Nous avons étudié ces mouvements en utilisant des femelles munies de radio-émetteurs (*n* = 51) entre 1997 et 2001. Nous avons également évalué si la distance parcourue affectait la survie et la croissance des oisons par la recapture de familles marquées juste avant l'envol. Les déplacements entre le site de nidification et d'élevage étaient très variables (étendue: 2.6 - 52.5 km; médiane = 28.3 km) mais assez rapides (en ≤ 6 jours pour 72% des femelles). Lors de ces déplacements, 56% des femelles étaient retrouvées près de la mer (< 2 km). Les déplacements étaient considérablement réduits une fois que les familles étaient établies dans l'aire d'élevage. Plus de la moitié (62%) des femelles marquées ont montré une fidélité inter-annuelle à leur site d'élevage précédent. La distance parcourue entre les sites de nidification et d'élevage n'affectait pas la survie des oisons. Cependant, la croissance des oisons différait selon le site de nidification et d'élevage sélectionné. Les oies nichant près du site d'élevage principal ont élevé des oisons de taille et de masse corporelle plus élevée que les oisons de celles qui ont niché à la colonie principale et qui ont franchi une longue distance pour atteindre le site d'élevage principal. Par contre, les oisons qui ont quitté la colonie ont obtenu une meilleure croissance que ceux qui y sont demeurés durant la période d'élevage pour une année sur deux. Ainsi, malgré certains coûts impliqués lors de ces déplacements, ils peuvent avoir été bénéfiques pour les oiseaux nichant dans la colonie principale. Le succès de nidification des oies à la colonie principale était plus élevé que celui des oies nichant au site d'élevage dans quatre années sur huit. Nous suggérons qu'il existe un compromis entre la sélection d'un site de nidification qui minimise les risques de prédation sur le nid et d'un site d'élevage qui maximise la croissance des jeunes.

ABSTRACT

We examined the long-distance movements between the nesting and brood-rearing areas and the associated costs and benefits in Greater Snow Geese breeding on Bylot Island, Nunavut. We studied these movements using radio-marked females (n = 59) between 1997 and 2001. We evaluated if distance moved affected gosling survival and growth by recapturing marked broods shortly before fledging. Movements from nesting to brood-rearing sites were highly variable among individuals (range: 2.6 - 52.5 km; median = 28.3 km) but were fairly rapid (in ≤ 6 d for 72% of the females). During these movements, 56% of females traveled near the seashore (< 2 km). Movements were considerably reduced once broods had settled on a brood-rearing area. More than half of the radio-marked females (62%) showed between-year fidelity to their previous brood-rearing area. Gosling survival was not related with distance moved between nesting and brood-rearing sites. However, gosling growth differed according to nesting and brood-rearing sites selected. Geese nesting close to the main brood-rearing area reared significantly heavier and larger goslings than those that nested at the main nesting colony and made extensive overland movement to their brood-rearing site. However, goslings leaving the main nesting colony had a better growth than those that stayed there through all brood rearing in one of two years. Therefore, even though brood movements entailed some costs, they may have been beneficial for birds nesting in a dense colony. Nesting success of geese at the main colony was higher than the one of geese nesting at the main brood-rearing site in four out of eight years. We suggest that a trade-off may exist between selecting a nesting area that minimizes the risk of egg predation and a brood-rearing area that maximizes gosling growth.

INTRODUCTION

Migration is a strategy used by animal species to ensure optimum conditions at all times when their life history requirements or the environment changes seasonally (Dingle 1980). In birds, long-distance migratory movements between wintering and breeding grounds are common. Once on the breeding grounds, birds should select the best habitats to optimize their reproductive success (Cody 1985). However, within the breeding area, shorter but still significant movements may be required in response to changes in vital needs. For instance, in precocial birds such as waterfowl, broods often make overland movements after hatch to reach suitable brood-rearing sites (Black Ducks, *Anas rubripes*, Ringelman and Longcore 1982, Mallards *Anas platyrhynchos*, Rotella and Ratti 1992, Northern Pintails *Anas acuta*, Duncan 1987). Habitat selection theory (Fretwell 1972, Pyke 1983) predicts that animals will move to habitat patches that maximize their fitness at each stage of the breeding cycle.

In ground-nesting birds such as geese and ducks, a major constraint when selecting a nest site is to minimize the risk of predation on eggs and incubating females (Mickelson 1975). For instance, Barnacle Geese (*Branta leucopsis*), Dark-bellied Brent Geese (*Branta bernicla bernicla*) nest on islands to avoid mammalian predation (Tombre et al. 1998, Ebbinge and Spaans 2002). Nesting in association with birds of preys may also reduce egg predation in some species (Bêty et al. 2001, Ebbinge and Spaans 2002). However, as soon as precocial young hatch, new requirements emerge as parents must bring them to suitable feeding areas. This is especially critical in geese as their goslings are strictly herbivorous and require high quality food plants to successfully complete growth. Access to the best feeding sites results in large and heavy goslings at fledging (Larsson and Forslund 1991, Lepage et al. 1998, Sedinger et al. 2001) that have high survival rate during the fall migration (Owen and Black 1989, Schmutz 1993, van der Jeugd and Larsson 1998, Cooch et al. 2002, Reed et al. 2003) and large final adult body size (Larsson and Forslund 1991). Other factors such as escape cover from predators may also affect juvenile survival and thus influence the choice of feeding sites by broods (Laing and Raveling 1993, Stahl and Loonen 1998). Parents selecting the best feeding sites with adequate refuges from predators should thus increase their chance of producing offspring.

Site fidelity is common in birds and has been reported in both nesting (Cooke and Abraham 1980, Lindberg and Sedinger 1997) and brood-rearing geese (Lindberg and Sedinger 1998). Previous experience may influence nesting and brood-rearing sites selection, conferring advantages that increase feeding efficiency or reduce predation risk from knowledge of local food resources or refuges (Anderson et al. 1992). However, site fidelity may become maladaptive when the habitat becomes severely degraded as reported in Lesser Snow Geese (*Chen caerulescens caerulescens*, Cooch et al. 1993, Williams et al. 1993).

In geese, large movements between nesting and brood-rearing areas (sometime up to 40 km) are common in order to have access to high quality resources (Cooch et al. 1993, Sedinger et al. 2001). Movements between nest and brood-rearing sites have been associated with high predation risk in precocial birds (Dzubin and Gollop 1972, Ball et al. 1975, Duncan 1983, Pöysä et al. 1999) and a negative relationship between overland travel distance and brood survival has been reported (Ball et al. 1975, Blomqvist and Johansson 1995, Leonard et al. 1996, but see Dzus and Clark 1997). However, Eriksson (1978) suggested that the benefits of selecting the best feeding areas for the juveniles should outweigh mortality risks during movements.

We examined the costs and benefits of long-distance movements between nesting and brood-rearing areas in Greater Snow Geese breeding on Bylot Island in the Canadian High Arctic. At this site, the most important brood-rearing area is located 30 km away from the main nesting colony. Although some broods stay around the main nesting colony during rearing, most parents move from the colony to this distant area shortly after hatch to rear their brood. A variable number of geese also nest at low density at this brood-rearing area and stay there to rear their brood (Hughes et al. 1994a, Lepage et al. 1996). This situation provided a unique opportunity to evaluate the potential costs of long-distance movements by comparing birds adopting these different strategies.

Our specific objectives were first to describe movements of radio-marked females that used areas distant from their nest site to rear their brood. Second, we determined if females showed fidelity to specific brood-rearing areas. Third, we examined whether distance moved was negatively associated with gosling survival. Fourth, we compared growth among goslings that 1) hatched near the main brood-rearing area and stayed there, 2) hatched at the main nesting colony and moved a long distance to the main brood-rearing area, or 3) hatched at the main nesting colony and stayed there. Finally, we compared nesting success between geese that established their nests in the main nesting colony and the main brood-rearing area to determine if there was a trade-off in site selection between the nesting and brood-rearing periods.

METHODS

Study area

We conducted our study on Bylot Island, Sirmilik National Park, Nunavut, Canada (73° N, 80° W), the most important breeding site of Greater Snow Geese (>20 000 pairs in 1993, Reed et al. 1998). Data were collected at three study sites (Fig. 1). Site-1 is the main brood-rearing area although some pairs also nest there in most years (Lepage et al. 1996). It is a large glacial valley (2-5 km wide, approximately 50 km^2) bordered by steep hills to the north and southeast, and rolling hills to the southwest. It is a good brood-rearing area due to high density of wetlands (Hughes et al. 1994b). Site-2 is located 30 km further south in the center of the main nesting colony on the Island (Bêty et al. 2001) but some broods also use this site during the rearing period. It covers approximately 16 km^2 around a narrow valley (0.5 km wide) with some wetlands and is surrounded by low hills with gentle slopes and extensive upland habitats. Site-3 covers about 10 km^2 and is along the way of geese moving between Site-2 and Site-1 (transit area). It is centered on a narrow valley (0.3 km wide) bordered by low hills to the northeast and southeast, high hills to the east, and along the seashore by a sandy beach to the northwest and wet polygons to the southwest. No birds nested in this area.

Nest monitoring and mass captures

We searched for goose nests during laying and early incubation at Site-1 and Site-2 from 1992 to 2001, except at Site-2 in 1993 (see Bêty et al. 2001 for details). We determined nesting success of all nests monitored at both sites. A nest was considered successful when at least one egg hatched and nesting success was calculated using the Mayfield method (Johnson 1979). During the hatching period, we marked newly-hatched goslings with uniquely numbered web tags.

About five weeks after hatch, broods were captured in mass banding drives during a 7-day period in early August when adults were molting and before the young could fly. Captures occurred at the brood-rearing area (Site-1) from 1990 to 2001 and at or

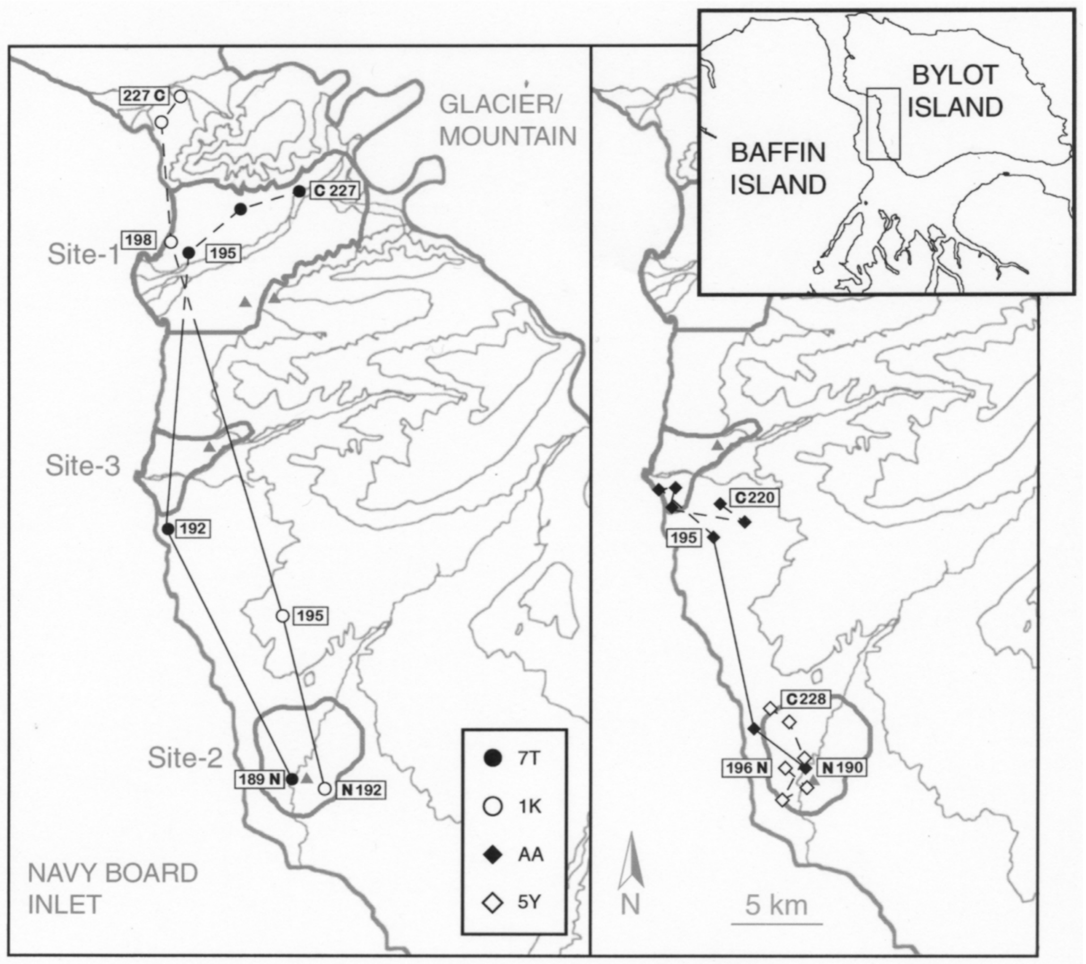


Figure 1. Location of the three study sites (thick solid lines) with examples of radio-tracked Greater Snow Goose females (neck–collar codes are shown in legend) moving to Site-1 (A), to Site-3 (B) or staying in Site-2 (B) on Bylot Island, Nunavut. Successive positions determined from the air between nest sites (N) and capture sites near the end of brood-rearing (C) are linked. Numbers indicate Julian dates (1 = January 1) associated with nest, capture and some positions. Thin solid lines represent *between-area* movements (i.e. movement between nest and brood-rearing sites) whereas dashed lines represent *within-area* movements (i.e. movements within the brood-rearing area; see methods). Ground receiving stations (▲) are shown for each study site.

near the main nesting colony (Site-2) in 1992, 1999 and 2001. Captured birds were classified as adult (≥ 1 year old) or young based on plumage, sexed by cloacal examination, and banded. A sample of adult females also received neck collars (see Menu et al. 2000 for details). Goslings were measured (culmen, head, tarsus, and ninth-primary length), weighed to the nearest 25 g (nearest 1 g since 1995), and checked for the presence of web tags.

Capture and tracking of radio-marked birds

A total of 305 females were marked with radio-transmitters affixed to neck collars from 1995 to 1999 (total weight 59 ± 9 g, < 3% of bird body mass). These birds were caught in a distinct banding operation conducted a few days before the main banding operation at Site-1 and, occasionally, between Site-1 and Site-2 (see Demers et al., in press). From 1997 to 2001, we searched for nests of these females through radio tracking by helicopter and on the ground (see Mainguy et al. 2002 for details). In 2000 and 2001, we also marked nesting females with radio-transmitters at Site-2 just before hatching. Females were captured with a bow trap triggered from a blind. Because we were interested in movements of females from their nest to distant brood-rearing areas, we targeted females that had been captured in previous years at Site-1 during brood rearing and marked with neck collars. Goslings of radio-marked females were also web-tagged.

After hatch, we conducted radio tracking by helicopter every two to three days from 16 to 20 July 2000 and 11 to 23 July 2001 to find radio-marked females and their brood during movements to rearing areas. Females were spotted with binoculars from the air and most of the time we were able to determine their brood size. We recorded their position with a GPS receiver although displacement of broods due to the helicopter approach decreased the positioning accuracy (± 200 m). Similar but less intense aerial radio-tracking was done in 1997-1998 (no visual contact was made). In all years, presence of radio-marked females was also monitored on the ground from two elevated blinds at Site-1 and one at Site-2. Ground tracking was carried out every 1 to 3 d until banding at Site-1 and daily at Site-2 during hatch and shortly after. Ground tracking was also done daily at the transit site (Site-3) from 17 to 21 July 2000 and 12 to 20 July 2001. This complemented aerial tracking and allowed us to precisely determine departure date of broods from the colony (Site-2) and arrival date at the main brood-rearing area (Site-1). Radio-marked females were located by helicopter once more prior to banding in August to determine if birds were still on the Island. Some females were recaptured with their brood during mass banding drives in all years, and in 2000-2001 we searched and captured individually all remaining radio-marked females and their broods.

We determined distance moved between successive aerial locations (including the nest and capture site) in 2000-2001. We divided brood movements in two categories: 1) movements from the nest to the rearing area (i.e. *between-area*) and 2) within the brood-rearing area (i.e. *within-area*). This was established by plotting travel route of each individual and determining when broods switched from long, clearly directional movements between successive locations to short, local movements without clear orientation or when families stayed in the same area for > 10 d based on ground-tracking (see Fig. 1). For females moving to Site-1, the southern limit of that study area was used to determine the end of the *between-area* movement. The southern limit corresponded approximately to the maximum detection range from the ground receiving stations. We calculated distance moved in a straight line between the nest site and first location in the brood-rearing area (*between-area* movement) and the longest distance between any pairs of locations once in the brood-rearing area (*within-area* movement). We also calculated minimum mean travel speed (m/h) between successive locations (spaced in time by ≤ 72 h only). Travel speed underestimates the walking speed because the actual route followed by broods may not be linear between successive locations. We evaluated duration of *between-area* movement as time elapsed between nest departure and first detection in the brood-rearing area. We also measured on maps the shortest distance of females to the seashore at each location during *between-area* movements.

We calculated total distance moved in a straight line between the nest and capture site in August (*total* movement) for all radio-marked females between 1997 and 2001. We evaluated fidelity to brood-rearing area by calculating the distance between capture sites of radio-marked birds in different years. Because some radio-marked females had been first banded before 1996 and the time elapsed between successive captures varied between one and eight years, we determined if distance between capture sites was related to the number of years. If a female was recaptured more than once, we only used the two most recent locations.

Survival and growth of goslings

In 2000-2001, we calculated gosling survival of radio-marked females as the ratio between the number of goslings recaptured near fledging (all goslings pooled) and the total number that left the nest in a given year. We also compared the proportion of females that had experienced total brood loss (i.e. no young at recapture) between years as radio-tracking allowed us to accurately determine females that lost all their young. We tested for a possible effect of total distance moved on gosling survival following the procedure of Rockwell et al. (1993), where the proportion (P) of hatched young surviving until recapture in August is calculated for each female by the ratio Brood Size near Fledging/Goslings Leaving Nest (*BSF/GLN*). Under the null hypothesis that *P does not depend of distance moved between nesting and brood-rearing areas*, we calculated the expected value of *BSF* for each year and individual i as:

$$E(BSF)_i = GLN_i \times \overline{P} \qquad \text{eqn 1}$$

We then calculated:

$$DevP_i = BSF_i - E(BSF)_i \qquad \text{eqn 2}$$

We used the deviation in P (*DevP*) to assess the effect of distance moved on gosling survival. A significant relationship between *DevP* and distance moved would indicate rejection of the null hypothesis.

We compared growth of goslings that stayed near their nesting area and those that moved to a distant rearing area using measurements of web-tagged goslings recaptured at banding. This analysis benefited from a much larger sample size spanning several years because it was not limited to radio-marked females. Unfortunately, we were unable to conduct all possible comparisons in the same year because of variations in sampling effort among years. The comparison between goslings that hatched at the main nesting colony (Site-2) and moved to Site-1 for brood-rearing vs. those that hatched and stayed at the main nesting colony for brood-rearing could be made in 1992 and 2001 only. Similarly, the comparison between goslings that hatched and stayed at the main brood-rearing area (Site-1) vs. those that hatched at the main nesting colony (Site-2) and moved to Site-1 for brood-rearing could only be made in 1996 and 2000.

Statistical analyses

All statistical tests were performed with SAS version 8.0 (SAS Institute Inc. 1999). As no significant differences were found among years in distance moved, minimal travel speed and duration (one-way ANOVA, all $P > 0.09$), all years were pooled. We used paired *t*-tests to compare *between-area* and *total* movements, and *between-area* and *within-area* movements. We used logistic regression to compare the proportion of females originally caught at Site-1 that returned to this site, and the proportion that stayed at Site-1 throughout the brood-rearing period among years. We used Spearman rank correlation to test if distance between successive captures was related to the number of years elapsed and if distance moved from the nest to the brood-rearing area was related to gosling survival. We used Fisher’s exact test to compare gosling survival between years. For all analyses, radio-marked females nesting in more than one year were included only once (first year of successful nesting) to avoid pseudo-replication.

We analyzed growth rate of gosling for each year because of high annual variation (Lepage et al. 1998). Sampling unit used was brood mean (range: 1-5 goslings per brood) to insure independence of our data. Because head, culmen and tarsus length are highly correlated within individuals (Lindholm et al. 1994), an index of body size was derived with a principal component analysis using all recaptured goslings. The first principal component (PC1) explained > 74% of the total variance and weightings were similar for the three morphometric measurements in all years. We compared body size (i.e. PC1) and body mass of goslings hatched or captured in different areas (depending on year) with ANCOVAs using gosling age as covariate. Because goslings require ~ 24 h to complete hatching, our estimates of gosling age had a precision of ± 1 d. The covariate age was highly significant (all $P < 0.001$) but the interaction terms between the covariate and the treatment (i.e. site) were not significant in any years (all $P > 0.07$) and were thus deleted from the models. Because we used brood means, we could not control for the effect of sex in our analyses. However, Lepage et al. (1998) found little effect of sex on growth from a large sample of goslings at our study area. Finally, we compared nesting success between Site-1 and Site-2 annually using z-tests (Johnson 1979).

Statistical tests were two-tailed and significance levels were set at 0.05. Inspection of residuals indicated no violation of the assumptions of normality and homogeneity of variance. All means are presented ± SE.

RESULTS

Brood movements

Fifty-two females marked in 1995-1999 during brood-rearing were found nesting in subsequent years (23 in 1997, 24 in 1998, two in 2000 and three in 2001). All these females nested in the main nesting colony (Site-2), except one in 2000 that nested 10 km further southeast. In addition, 12 females were marked on nests at the main nesting colony in 2000 and 21 in 2001. Once females nesting twice were excluded ($n = 6$), the total sample was reduced to 79 nests, of which 51 produced a brood (12 in 1997, 12 in 1998, 10 in 2000 and 17 in 2001).

A total of 42 radio-marked females were recaptured at the end of the summer. Females not found at banding had either left Bylot Island following an early brood loss to molt elsewhere (Reed et al., in press a; $n = 4$), died during brood-rearing ($n = 3$) or had a known radio failure ($n = 2$; female departure was potentially confounded with transmitter failure). At recapture, 28 females (66%) were located in or around the brood-rearing area of Site-1 including seven that were in a small valley 4 km north of Site-1, eight (19%) were between the main nesting colony and Site-1 (five of them near Site-3), four (10%) stayed at the main nesting colony (Site-2) and two (5%) moved elsewhere on the Island (one moved inland toward the glaciers and one moved south of the main nesting colony; Fig. 1).

Total distance moved by radio-marked birds between the nest and capture sites at the end of brood-rearing was similar to the distance measured during *between-area* movements shortly after hatch in 2000 and 2001 (25.9 ± 2.8 vs. 23.2 ± 1.8 km, respectively; paired *t*-test, $t = 2.06$, $P = 0.06$, df = 14). *Total* distance moved by all females (i.e. 1997 to 2001, $n = 41$) averaged 25.6 ± 1.7 km but varied considerably among individuals (range: 2.6 – 52.5 km, Fig. 2); the distance was greatest for individuals that moved to Site-1, intermediate for those that moved only to the transit area (Site-3) and shortest for those that stayed at the colony (Table 1, $F_{2,37} = 41.5$, $P < 0.001$). In contrast, *within-area* movements once broods had settled on a rearing site were much smaller than *between-area* movements (2000-2001;

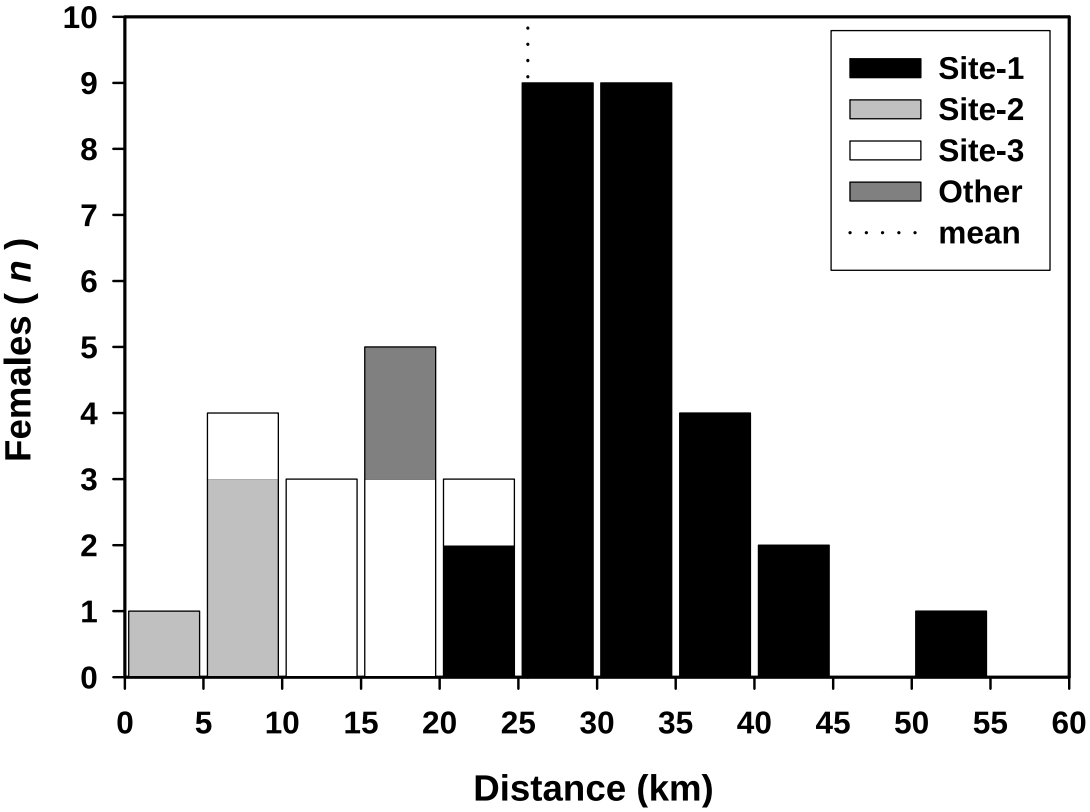


Figure. 2. Frequency distribution of total distance moved between nest and recapture sites by radio-marked females (n = 42) according to recapture site, 1997-2001. All females but one nested at Site-2. Site-1 = main brood-rearing area, Site-2 = main nesting colony, Site-3 = transit area between Site-1 and Site-2, and Other = elsewhere (see Fig. 1).

Table 1. Characteristics of movements of radio-marked Greater Snow Goose females between their nest and the brood-rearing area on Bylot Island, 2000-2001. All females nested in the main colony (Site-2). Mean ± SE (*n*).

	Brood-rearing area		
	Main area (Site-1)	Transit area (Site-3)	Nesting colony (Site-2)
Total distance moved (km) [a]	32.2 ± 1.2 (27)	15.2 ± 1.4 (8)	5.5 ± 1.0 (4)
Between-area movements [b]			
Distance (km)	27.7 ± 0.8 (14)	17.1 ± 1.2 (6)	7.6 (1)
Travel speed (m/h)	218 ± 13 (14)	164 ± 30 (6)	93.6 (1)
Distance to sea shore (km)	2.6 ± 0.5 (12)	1.2 ± 0.4 (4)	5.4 (1)
Within-area movements [c]			
Distance (km)	6.6 ± 1.0 (13)	4.6 ± 1.2 (6)	2.8 (1)
Travel speed (m/h)	37 ± 7 (7)	23 ± 7 (5)	20 ± 7 (2)

[a] Distance in a straight line between nest and capture sites at the end of brood-rearing. In this case, we incorporated data from 1997-1998.

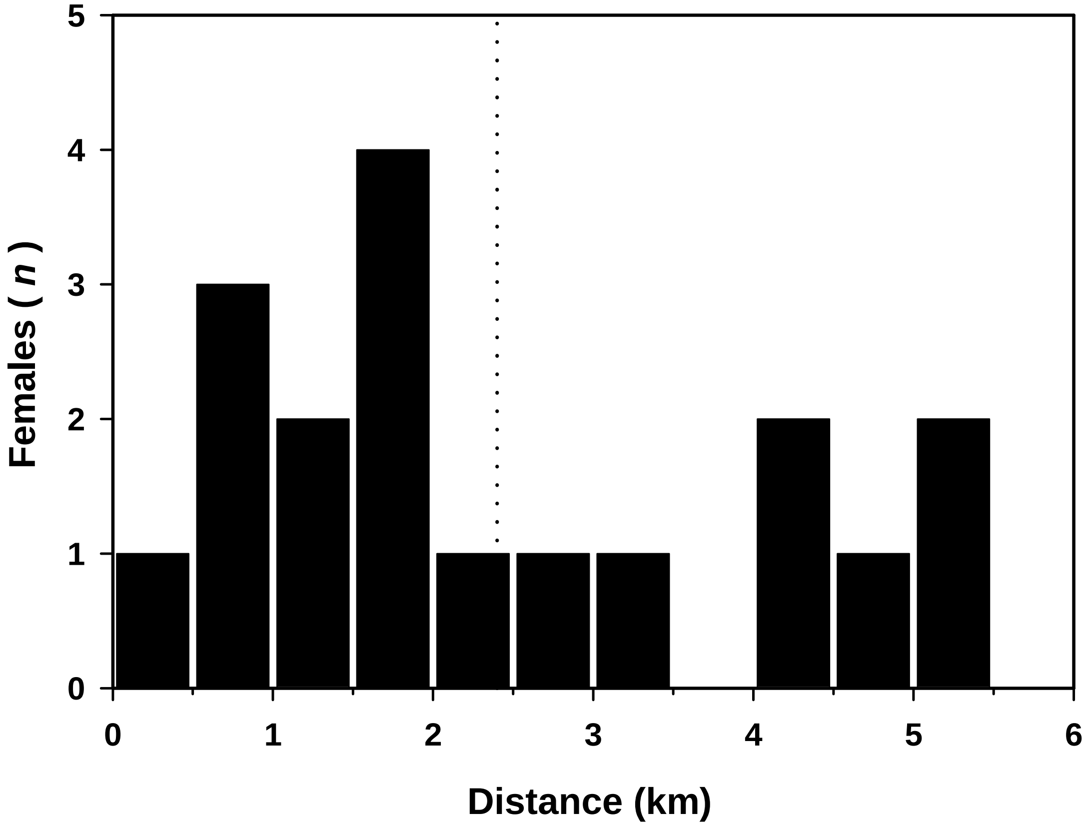
[b] Distance in a straight line between nest site and first location in the brood-rearing area.

[c] Longest distance in a straight line between any pairs of locations once settled on a brood-rearing area.

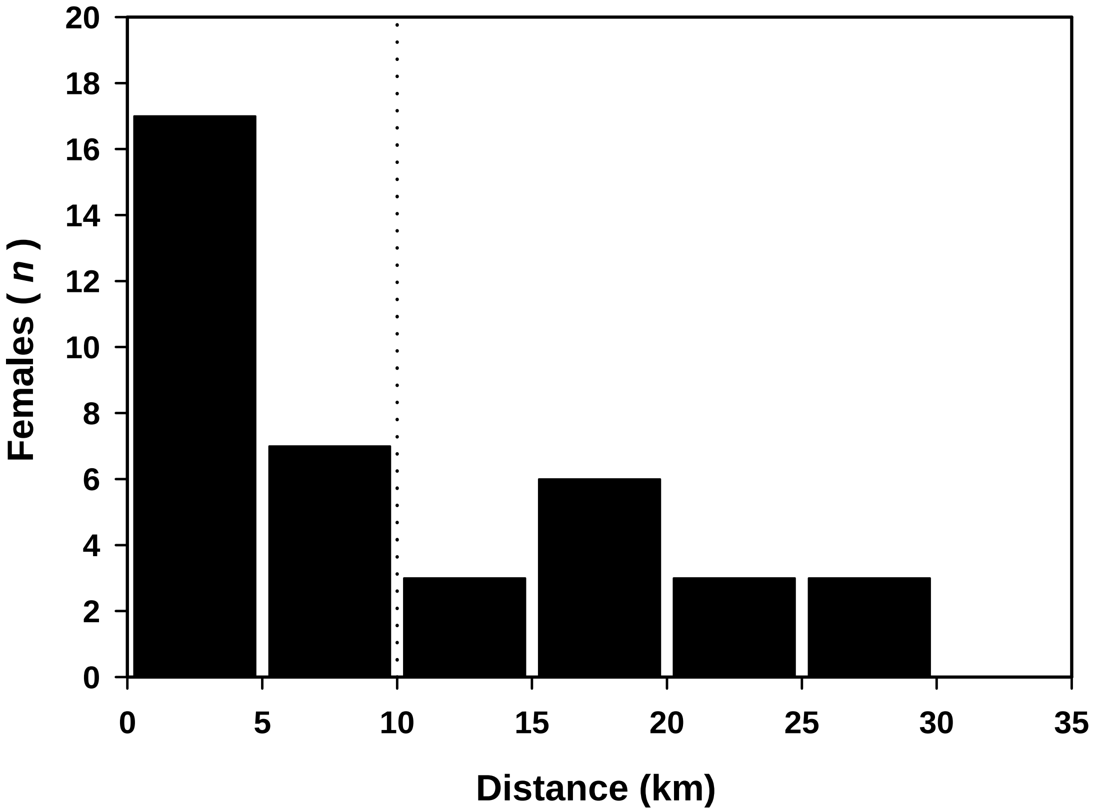
5.5 ± 1.0 vs. 23.2 ± 1.8 km, respectively; paired *t*-test, $t = -9.32$, $P < 0.001$, df = 14) and did not differ between Site-1 and Site-3 (Table 1, $F_{1,17} = 0.43$, $P = 0.52$). Similarly, minimal travel speed during *between-area* movements was greater for geese moving up to Site-1 (the farthest) than to Site-3 (Table 1, $F_{1,20} = 5.96$, $P = 0.025$). Minimal travel speed during *within-area* movements was much slower than during *between-area* movements (30 ± 5 vs. 191 ± 13 m/h, respectively; paired *t*-test, $t = -8.23$, $P < 0.001$, df = 12) and did not differ between areas (Table 1, $F_{1,12} = 2.74$, $P = 0.13$). Duration of *between-area* movements was only available for geese that moved to brood-rearing Site-1 and was fairly short (5.8 ± 0.5 d, $n = 32$). During *between-area* movements, broods traveled at an average distance of 2.4 ± 0.4 km from the seashore. However, the frequency distribution suggested a bimodal pattern during these movements with 56% of the broods ($n = 18$) located close to the coast (< 2 km from the sea shore) and the remainders traveling further inland (2 - 5.5 km, Fig. 3).

Fidelity to brood-rearing site

Among the 42 radio-marked females recaptured, 35 had been captured in previous years at Site-1 during brood rearing. The proportion of females that returned to Site-1 varied among years (1997-2001: $\chi^2_3 = 8.7$, $P = 0.03$) but was generally high (60 to 100%; overall mean: 71%). For females that returned to Site-1, the proportion that stayed in this area until the end of brood rearing did not differ among years (60-86%, $\chi^2_3 = 2.8$, $P = 0.42$). All females leaving the Site-1 area went further north to the next valley after staging 10 ± 3 d at Site-1 (see Fig. 1 A an example). Inter-annual distance between capture sites in August was not correlated with time elapsed since previous capture (time span: 1 to 8 years, $r_s = 0.07$, $P = 0.65$, $n = 39$). Average distance between captures was 10.0 ± 1.4 km with 62% of the females caught < 10 km from their previous location suggesting that Greater Snow Geese showed some philopatry toward their brood-rearing area on Bylot Island (Fig. 4).



<u>Figure 3.</u> Frequency distribution of distance to seashore of radio-marked females (*n* = 18) during movements between the nest and brood-rearing area in 2000-2001. Dotted line represents the mean.



<u>Figure 4.</u> Frequency distribution of inter-annual distances between successive captures of radio-marked Greater Snow Goose females (*n* = 39) during brood-rearing in early August, 1996 to 2001. Dotted line represents the mean.

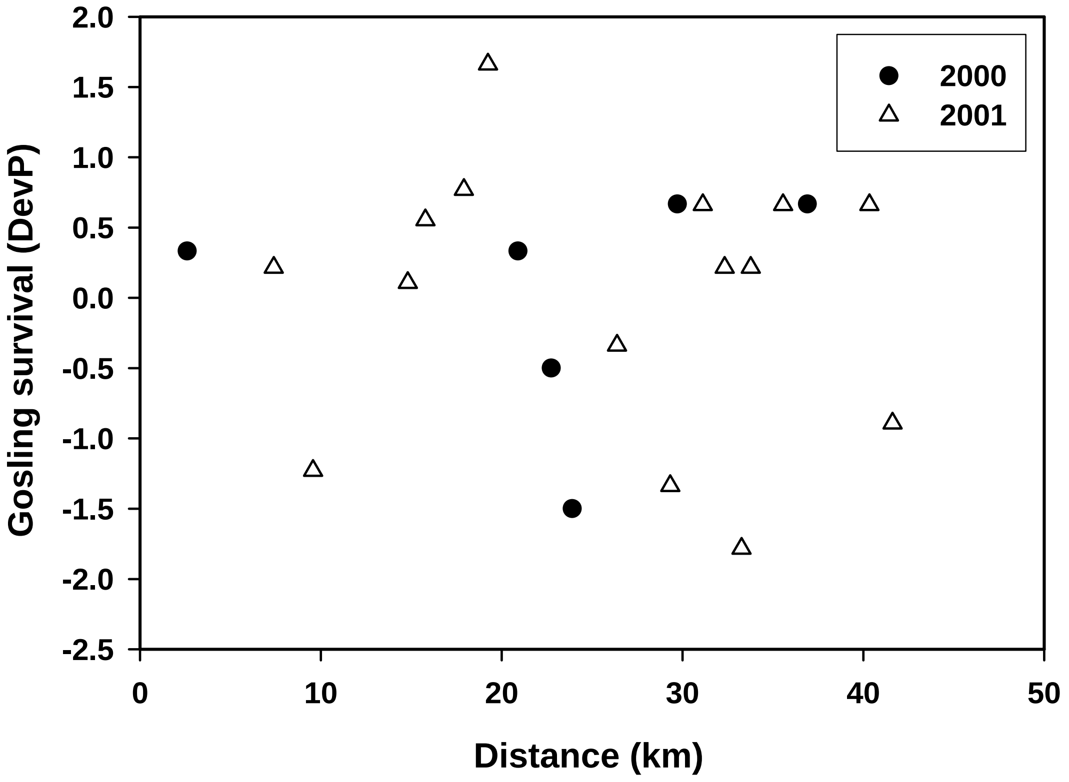
Gosling survival and growth

Gosling survival of radio-marked females was higher in 2000 than in 2001 (68%, n = 22 vs. 39%, n = 57, respectively, Fisher's exact test, P = 0.024). However, the proportion of females that experienced total brood loss did not differ between these two years (14%, n = 7 vs. 29%, n = 17, respectively, Fisher's exact test, P = 0.62). Brood survival was not affected by distance moved between the nest and brood-rearing area (Fig. 5).

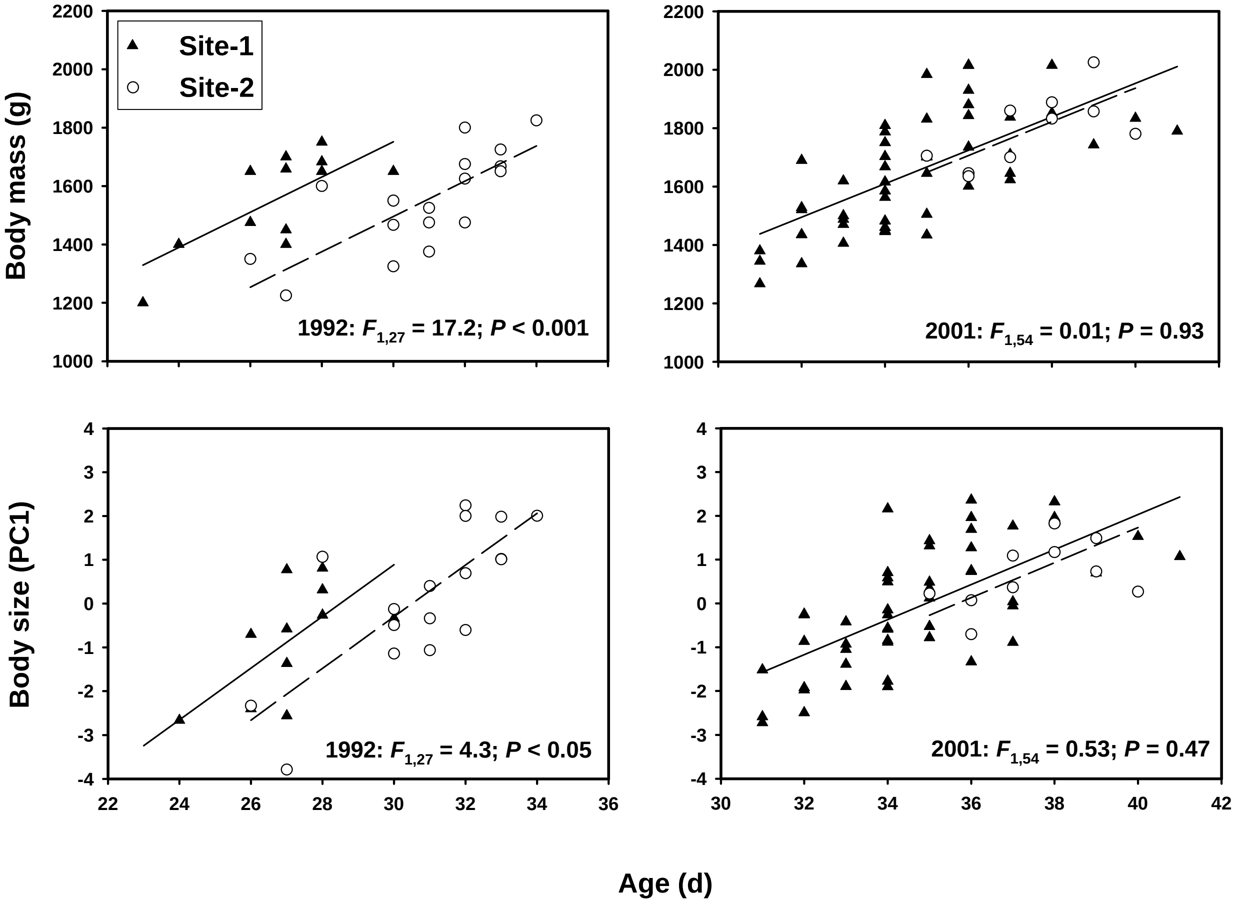
In 1992, 1996, 2000, and 2001, a total of 5801 young were web-tagged (annual range: 289 to 1860) and 467 young from 228 broods were recaptured near fledging (range: 46 to 162 from 29 to 75 broods). Goslings recaptured in 1996 and 2000 were of the same age (30.9 ± 0.2 d old, Tukey-Kramer test, P = 0.99) whereas those recaptured in 1992 were slightly younger (29.2 ± 0.5 d. old, P = 0.005), and those in 2001 older (35.1 ± 0.3 d. old, P < 0.001). Goslings that hatched at the main nesting colony (Site-2) and that were recaptured at Site-1 had moved a mean distance of 32.1 ± 0.6 km, (n = 27 broods) compared to only 4.9 ± 0.5 km (n = 15) for those hatched and recaptured at the main nesting colony. Goslings that moved to Site-1 were nonetheless heavier and larger than those that remained at the main nesting colony in 1992 but not in 2001 (Fig. 6). In contrast, goslings that hatched and were reared at Site-1 (total distance moved: 2.9 ± 0.3 km; n = 34 broods) were heavier (in 2000) and larger (in 1996 and 2000) than those that nested at the main nesting colony (Site-2) and moved to Site-1 (total distance moved: 29.8 ± 0.6 km; n = 24) (Fig. 7). Thus, goslings that hatched near the main brood-rearing area had a better growth than those that hatched farther away and had to move there.

Nesting success

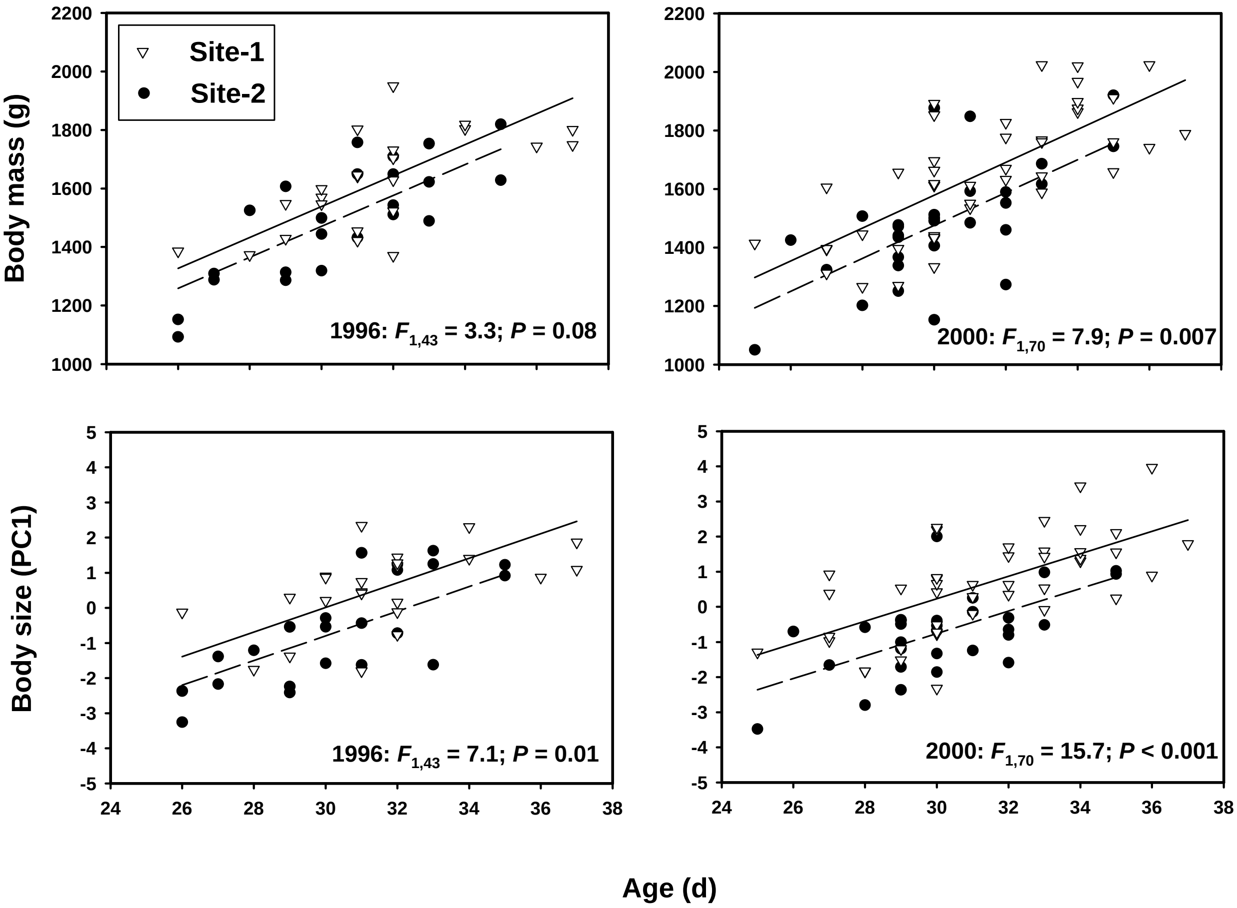
Nesting success of geese varied greatly among years and sites (range: 3 to 88%) but was significantly lower for geese nesting at low density at the brood-rearing site (Site-1) than for those nesting at high density at the main nesting colony (Site-2) in four out of eight years (Fig. 8). No significant difference was found in the four other years. In three of these years (1996, 2000, and 2001), most nests monitored at Site-1 were associated to raptor nests (Snowy Owls, *Nyctea scandiaca*, or Rough-legged Hawks, *Buteo lagopus*) that offer protection to goose nests against predators (Bêty et al. 2001).



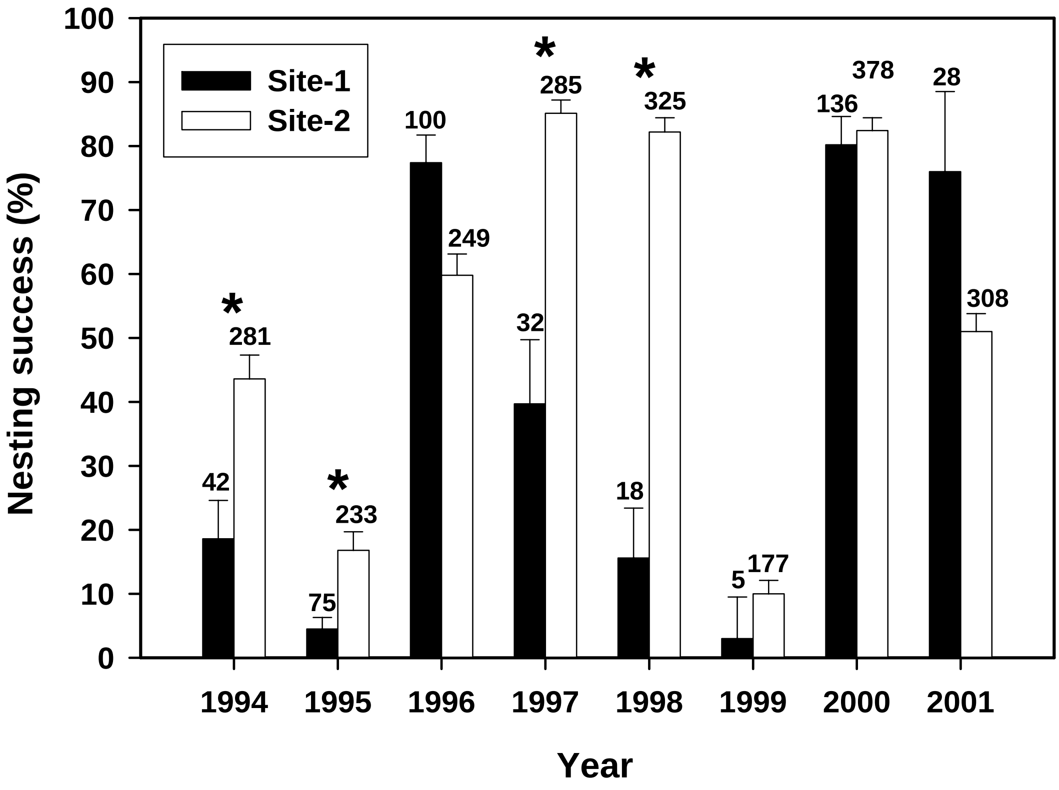
<u>Figure 5.</u> Relationship between gosling survival (expressed as deviations from expected mean, see method) and distance moved between the nest and brood-rearing area (i.e. recapture site in August) for radio-marked females in 2000-2001 ($r_s = 0.03$, $P = 0.89$).



<u>Figure 6.</u> Relationship between body mass (g) and body size (PC1 scores; see methods) of goslings hatched at the main nesting colony (Site-2) and age according to the brood-rearing area used, Site-1 (solid line) or Site-2 (dashed line). The *F* values presented are for the site effect. There was no interaction between age and site (*P* > 0.5 in all cases).



<u>Figure 7.</u> Relationship between mean brood mass (g) and body size (PC1 scores; see methods) of gosling reared at Site-1 and age according to the nesting area used, Site-1 (solid line) or Site-2 (dashed line). The *F* values presented are for the site effect. There was no interaction between age and site (*P* > 0.07 in all cases).



<u>Figure 8.</u> Nesting success of Greater Snow Geese at Site-1 (main brood-rearing area) and Site-2 (main nesting area) 1994-2001. Means ± SE; sample sizes are shown on top of bars. Asterisks indicate significant differences between sites (*P* < 0.05).

DISCUSSION

Brood movements

Many Greater Snow Geese using the main nesting area to breed on Bylot Island (Site-2) moved to a distant brood-rearing area (Site-1) where a high density of wetlands provides high quality habitat for broods (Hughes et al. 1994b, Massé et al. 2001). These movements could reach 30 km or more, occurred shortly after hatch and were completed within a week. Similar movements have been reported in other goose species (Emperor Geese *Chen canagica*, Laing and Raveling 1993; Barnacle Geese, Stahl and Loonen 1998). However, some females moved to a much lesser extent and reared their young close to their nesting area. Long-distance movements had not been reported by Hughes et al. (1994a) in their study of space use by broods on Bylot Island because all females that they marked were nesting in the brood-rearing area of Site-1. Movements between the nest and brood-rearing area were easy to distinguish from *within-area* movements once broods had settled on a rearing area because the latter movements were slower and without clear directional orientation. Despite the small size of newly-hatched goslings, our results indicate that parents try to get to specific feeding areas very early during the brood-rearing period.

More than half of radio-marked broods moving away from the colony were located close to the coast (< 2 km). The terrain near the coast is relatively flat with a large sandy beach and this may be easier to walk for small goslings than the more rugged terrain further inland. Wetland patches, which provide high quality feeding areas and potential refuge against attacks from terrestrial predators (Hughes et al. 1994a), are also more common along the coast than further inland where upland habitat predominates (Massé et al. 2001). In addition, proximity to the sea may provide a refuge against terrestrial predators such as foxes.

Once settled on a rearing site, broods of Greater Snow Geese tended to stay within a restricted area as reported for Barnacle Geese (Larsson and Forslund 1991) and Black Brant (Lindberg et al. 1998). *Within-area* movements were of the same magnitude (~ 5 km) than those described by Hughes et al. (1994a) for this population. However, some females made secondary movements later in the summer, sometimes up to 8 km, as also reported by Hughes et al. (1994a). These authors identified three space use strategies by broods (sedentary, shifter and wanderer). Sedentary females were thought to be more experienced, had young that hatched earlier and used a greater proportion of the best brood-rearing habitat than those of the two other groups. These patterns were documented for females that nested directly at the main brood-rearing area (i.e. Site-1). Because geese nesting at the main nesting colony and moving 30 km to Site-1 arrive later on the brood-rearing area than those that nested there, it is possible that the space use strategy of birds coming from far away was predominantly of the shifter or wanderer type. By settling first in the best habitats, birds nesting at or near the brood-rearing area may have limited access to these habitats for birds arriving later (Prop et al 1984, Hughes et al. 1994a, Stahl et al 2001). Unfortunately, we were unable to document habitat use of our females once on the brood-rearing area to ascertain this hypothesis.

Fidelity to brood-rearing site

Radio-marked females generally exhibited inter-annual fidelity to their brood-rearing sites, although several females apparently moved to sites different (> 10 km) from those used in previous years. Even though 10 km may appear a long distance between capture sites to establish that a bird was faithful or not, this is a short distance when considering that home-range size of broods can reach 20 km^2 once settled on a rearing site (Hughes et al. 1994a). It is thus conceivable that capture sites separated by 5 to 10 km between years may represent extreme locations of overlapping home ranges. In Lesser Snow Geese, Cooch et al. (2001) suggested that philopatry to the brood-rearing area may be a more plastic trait than fidelity to the nesting area. Unfortunately, we did not have enough data to adequately test fidelity to nesting site. Among 10 radio-marked females that nested twice on Bylot Island with a functioning radio-transmitter, seven nested within 500 m of their previous nest site, a proportion similar to the one found in Lesser Snow Geese (72%, Cooke and Abraham 1980). However, under some circumstances, fidelity to the nesting area may be much lower in Greater Snow Geese, especially in response to variable snowmelt patterns (Lepage et al. 1996).

Gosling survival and growth

Mortality observed during brood rearing was relatively high and particularly variable between years, but nonetheless comparable to what has been found in other goose species (Flint et al. 1995, Schmutz et al. 2001). We did not find evidence for a survival cost associated with distance moved during brood movements shortly after hatch as found in other precocial species (Ball et al. 1975, Blomqvist and Johansson 1995, Leonard et al. 1996, Pöysä et al. 1999). Therefore, predation risk during long-distance *between-area* movements may have been of similar magnitude to the one encountered after settling on a brood-rearing area even though dispersing broods may go through the territories of several different predators. However, movements between the nest and brood-rearing sites occurred during the first week after hatch whereas our recaptures were made five weeks later. Thus, other factors than distance moved may have influenced brood survival during the subsequent four-week period and this may have masked any potential effect of long-distance movement on survival. Our sample size was also relatively small, thus limiting our ability to detect small effects.

In contrast to survival, both the nesting and brood-rearing areas selected by breeding pairs influenced gosling growth. Parents that left the main nesting colony to settle on the main brood-rearing area of Site-1 reared heavier and larger gosling than those that stayed at the colony after hatch in one out of two years. In Ross Geese, Slattery (2000) showed that goslings from broods that moved the farthest from a dense nesting colony were largest and heaviest. Similarly, Lesser Snow Goose goslings that dispersed to alternate rearing areas showed better growth and survival than those remaining on the traditional feeding areas, which had been severely degraded due to overgrazing (Cooch et al. 1993, Williams et al. 1993). Greater Snow Goose density on Bylot Island is relatively high (Massé et al. 2001) and goose grazing reduces standing crop and plant production (Gauthier et al. 1995, 1996). Therefore, broods staying at the main nesting colony may be at a disadvantage compared to those moving to other brood-rearing areas due to the high density of geese nesting there (several thousands, Bêty et al. 2001) in relation to the amount of forage plant available (Massé et al. 2001). In many species of geese, including Greater Snow Geese, there is a direct link between feeding conditions encountered by growing goslings and body mass at fledging (Aubin et al. 1993, Cooch et al. 1993, Lindholm et al. 1994, Lepage et al. 1998, Sedinger et al. 2001).

Although moving out of the main nesting site accrued some benefits to goslings, we found that these goslings nonetheless had a lower growth than those hatched directly on the main brood-rearing area. This suggests that long-distance movements between nesting and brood-rearing areas entail some costs. Goslings hatched at the main brood-rearing area had immediate access to high quality forage plants in the extensive wetlands present there (Hughes et al. 1994b) whereas those hatched at the main nesting site had to make long overland movements in order to reach this site. In addition to the potential cost of walking 30 km or more, they had to cross extensive areas of upland habitat where food is of poor quality (Hughes et al. 1994b, Massé et al. 2001). Furthermore, broods arriving later in the main feeding site may have been forced to use a greater proportion of lower quality habitat (Hughes et al. 1994a, see above). Thus, a better access to high quality food for goslings hatched at the brood-rearing area may explain their better growth compared to those moving from a distant nesting site. It is important to note that in our study we were unable to compare the three strategies in a same year, which may lead to potential biases.

Rapid growth and large body mass at fledging is important for goslings growing in the Arctic. Indeed, survival of goslings during the fall migration is directly related to body mass at fledging (Owen and Black 1989, Schmutz 1993, van der Jeugd and Larsson 1998, Cooch et al. 2002, Reed et al. 2003). Therefore, differences in growth related to the selection of nest or brood-rearing site selection may have important fitness consequences for goslings.

Trade-off between brood-rearing and nest site selection

Our results suggest that the best strategy for breeding pairs could be to nest close to good brood-rearing areas. By nesting directly at or near the best feeding sites, parents avoid for their goslings the costs associated with long-distance movements such as time spent in poor feeding habitat, reduced access to the best rearing habitats due to competition, and reduced feeding time associated with walking long distances. However, few geese nest near the main brood-rearing area each year whereas a large proportion of geese uses the main nesting colony far away from the best rearing sites. We suggest that a high nest predation risk when geese are nesting at low density near the brood-rearing area may explain this situation. Indeed, the benefits of nesting close to good rearing sites may be counterbalanced by a high predation risk on nests as data on nest success suggests in our study. Birds nesting colonially at high density may benefit from a lower predation risk and thus obtain a higher breeding success than birds nesting at low density (Massaro et al. 2001). The predator swamping effect and anti-predator behaviour might explain partially the lowering of predation risk in colonial birds (Becker 1995). Breeding pairs must thus choose their nesting and brood-rearing sites according to those two opposite selective pressures. The fact that most of the breeding pairs nest at high density at the main nesting area suggests that low nest predation risk may overweigh the costs associated with long-distance movements.

Occasionally, geese nesting at the main brood-rearing area have access to predator refuge. Indeed, in peak lemming years, geese can benefit from a nesting association with Snowy Owls or Rough-legged Hawks that offer protection against predators (Bêty et al. 2001, Ebbinge and Spaans 2002). Thus, when birds of prey are nesting, more geese nest at the main brood-rearing area than in other years, and most of them are near raptor nests (Lepage et al. 1996, Bêty et al. 2001). Under these conditions, geese benefit of a low predation risk on their eggs and a quick access to feeding site, resulting in the best overall breeding strategy. However, the possibility to nest in association with birds of prey occurs only occasionally (once every three to four years due to the lemming cycle). Furthermore, density of raptor nests on Bylot Island is relatively low even in peak lemming years, and some raptor nests in areas unsuitable for goose nests (e.g. steep slopes). Therefore, this strategy can probably be used only by a minority of birds at the population level (Bêty et al. 2001).

In conclusion, we suggest that a trade-off may exist between selecting a nesting area that minimizes predation risk on nest and a brood-rearing area that maximizes gosling growth. Decision made by breeding birds, influenced by their previous experience, will directly affect their reproductive success through egg survival, gosling growth and subsequent survival during the fall migration. Moreover, biotic factors (e.g. lemming abundance) can directly affect the best annual combination of nest and brood-rearing sites.

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CHAPITRE II

HABITAT SELECTION AND BEHAVIOUR OF GREATER SNOW GEESE DURING MOVEMENTS FROM NESTING TO BROOD-REARING SITES

RÉSUMÉ

Chez la Grande Oie des neiges se reproduisant à l’Île Bylot, une grande proportion des familles parcourent de longues distances (~ 30 km) entre le site de nidification et le site d’élevage principal. Nous avons comparé l’utilisation et la sélection de l’habitat, et le comportement de ces oies durant ces déplacements à celui des familles déjà rendues au site d’élevage. Nous avons déterminé l’utilisation de l’habitat et le comportement à l’aide de décomptes (14 au 20 juillet 2001) faits à deux sites: le site d’élevage principal (*n* = 6 décomptes) et un site de transit (*n* = 9) situé à mi-chemin entre le site de nidification et celui d’élevage. Les ruisseaux, polygones humides et lacs (tous des habitats de haute qualité) ont été sélectionnés aux deux sites tandis que les milieux mésiques (un habitat de pauvre qualité en terme de site d’alimentation et de refuges contre les prédateurs) a été évité. Cependant, les familles au site de transit ont été observées en proportion significativement plus grande dans les milieux mésiques que celles observées au site d’élevage principal (26% vs. 13%, respectivement). Le comportement des oies n’a pas différé entre les sites, les familles allouant la majorité de leur temps à l’alimentation (54%) et au repos (28%). Nous proposons que le déplacement des familles engendrent des coûts dus à une augmentation du temps passé dans des habitats de pauvre qualité, ce qui affecterait négativement la croissance des oisons.

ABSTRACT

In Greater Snow Geese breeding on Bylot Island, a high proportion of broods make long-distance overland movements (~ 30 km) between the main nesting and brood-rearing sites. We compared habitat use and selection, and behaviour of geese while moving to the main brood-rearing area with those of geese that had already reached the rearing area. We determined habitat use and behaviour during surveys (14 to 20 July 2001) conducted at the brood-rearing area (n = 6 surveys) and a transit site (n = 9) located between the nesting and rearing sites. Streams, Wet polygon, and Lake (all high quality habitats) were selected at both sites, whereas Upland (a low quality habitat in terms of feeding opportunities and predator refuge) was avoided. Broods at the transit site were nonetheless observed in a significantly greater proportion in Upland habitat than those observed at the rearing area (26% vs. 13%, respectively). The behaviour of geese did not differ between sites and they spent most of their time grazing (54%) and resting (28%). We suggest that brood movement may entail some costs in terms of increased time spent in low quality habitat and thus negatively affect gosling growth.

INTRODUCTION

Variation in food quality greatly affects habitat selection in herbivores (Wilmshurst et al. 2000, Kie et al. 2002). This is especially true for species like geese, which cannot digest plant fibre (Mattocks 1971) and must thus select high quality food plants (Ydenberg and Prins 1981, Gauthier and Bédard 1990, Sedinger 1997). Goslings, which are also herbivorous, face the additional challenge of growing and must therefore maximize their protein intake to sustain rapid growth (Sedinger and Raveling 1984, Lepage et al. 1998, Person et al. 1998). Because the Arctic summer is very short, goslings should concentrate their feeding in the best habitats to maximize their growth before the southward fall migration. Food choice is therefore critical at this time of the year (Manseau and Gauthier 1993, Gadallah and Jefferies 1995, Sedinger et al. 1995) as body size of goslings at fledging directly affects survival after departure from the breeding grounds (Owen and Black 1989, Schmutz 1993, van der Jeugd and Larsson 1998, Reed et al. 2003).

In many arctic-nesting geese, wetlands are the preferred habitats during brood rearing (Laing and Raveling 1993, Hughes et al. 1994a,b). These habitats are dominated by graminoid plants, a high quality food for growing goslings (Manseau and Gauthier 1993, Massé et al. 2001), and have a high density of ponds and small lakes, which provide refuges against terrestrial predators such as Arctic foxes (*Alopex lagopus*; Laing and Raveling 1993, Hughes et al. 1994a,b). However, broods must often cover long distances after hatch in order to reach these high quality brood-rearing sites (Cooch et al. 1993, Stahl and Loonen 1998, Slattery 2000, Sedinger et al. 2001, chapter 1). These movements between nesting and brood-rearing sites may force broods to spend some time in habitats that lack high quality food or where predation risk is high.

In Greater Snow Geese (*Chen caerulescens atlantica*) nesting on Bylot Island, Nunavut, long-distance movements between nesting and brood-rearing areas are frequent (chapter 1). Shortly after hatch, many broods move 30 km or more within a six-day period to reach high quality brood-rearing sites. These long overland movements occur over extensive areas of upland habitats characterized by low quality forage plants with scattered patches of more suitable habitats (Hughes et al.

1994b). However, broods may be expected to follow paths that will maximize the time spent in the best available habitat in terms of food resources and predator refuges for goslings.

Our objective was to determine to what extent geese moving between nesting and brood-rearing areas used low quality habitats. To address this question, we compared habitat use and selection, and behaviour of broods during these movements with those of broods that had already reached prime brood-rearing areas.

METHODS

Study area

The study was conducted in 2001 at the Bylot Island migratory bird sanctuary, Sirmilik National Park, Nunavut Territory, Canada (73° 08’ N, 80° 00’ W). The most important brood-rearing site for geese on the Island (Site-1, Reed et al. 1992) is located 30 km north of the main nesting colony (Site-2, Fig. 1). A large number of geese at the main nesting colony bring their brood to Site-1 within 1-week after hatch (chapter 1). Data were collected at two sites: the first one was a 14-km^2 portion of the main brood-rearing area (Site-1, ca. 50 km^2, Hughes et al. 1994b) and included large patches of wetland habitats with high quality plants. The second site (Site-3, ca. 10 km^2) was located halfway along the route used by broods moving from Site-2 to Site-1 (Fig. 1). Each site was delimited according to topographical features that limited observation of geese. Most broods observed at Site-3 were traveling from the main nesting colony to Site-1 although a small number may remain in that area for the whole brood-rearing period (chapter 1). Broods observed at Site-1 had either nested there or were among the first broods to arrive from the main nesting colony (Site-2).

Habitat types

We recognized six habitat types at Site-3 and four at Site-1 (Fig. 1) according to physical characteristics visible on 1:13 000 black and white aerial photographs. Habitats identified on photographs were later verified by ground-truthing. Upland, Wet polygon, Lake, and Stream habitats were found at both sites whereas Beach and River habitats were only found at Site-3. The Upland habitat was covered by a diversity of mesic plant communities dominated by *Salix arctica*, forbs, and a sparse cover of diverse graminoids (e.g. *Arctagrostis latifolia*) (Duclos 2002). The Wet polygon habitat was dominated by sedges (*Eriphorum* spp. and *Carex aquatilis*) and grasses (mostly *Dupontia fisheri*), the preferred plants of geese (Manseau and Gauthier 1993). Wet polygon included the wet meadow and polygon pond habitats

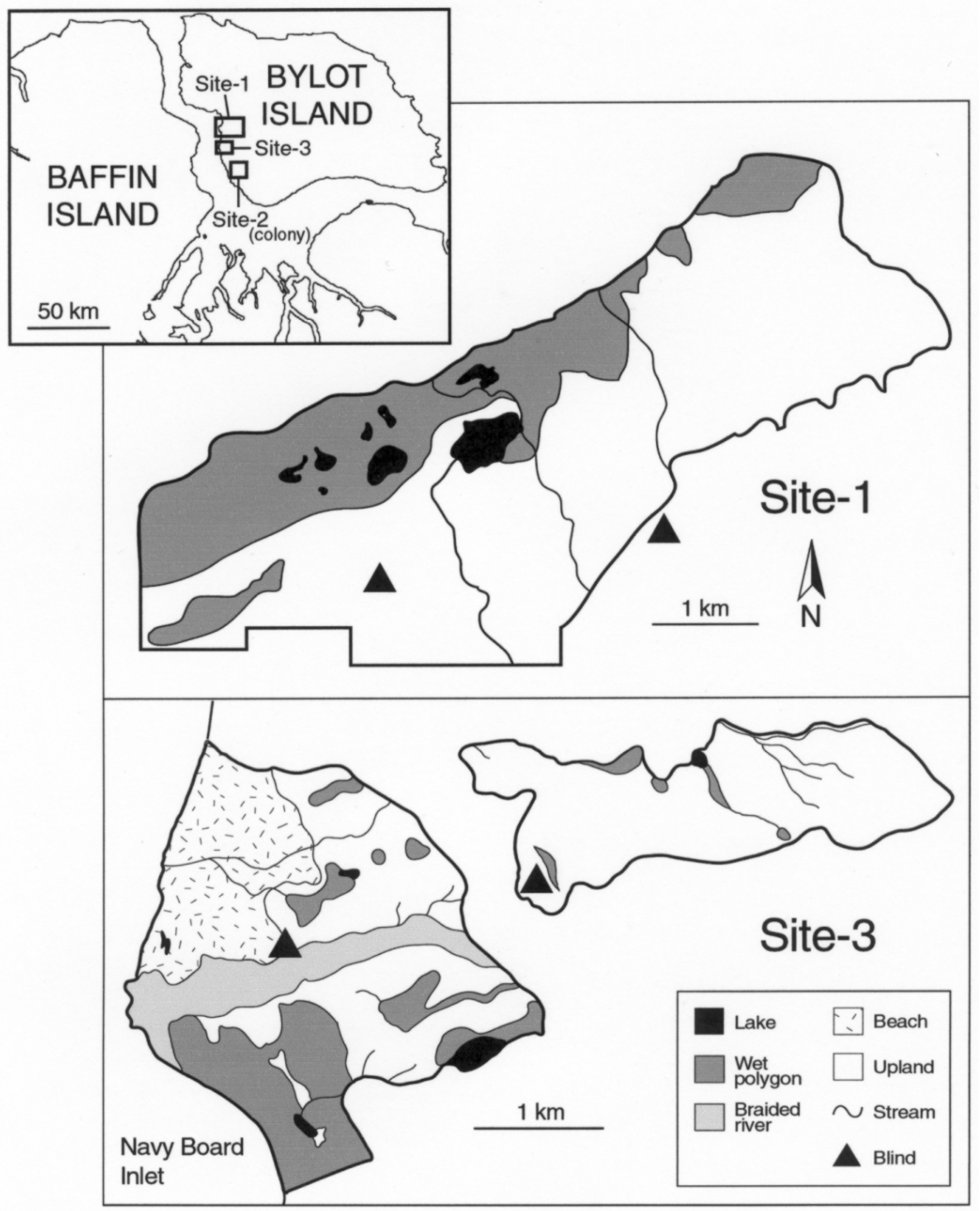

Figure 1. Location of the three study sites on Bylot Island, Nunavut, Canada. Site-1 is the main brood-rearing area, Site-2 the main nesting area, and Site-3 a transit area for broods during movements from Site-2 to Site-1. Observation areas at Site-1 and Site-3 are shown with their respective habitat.

categories of Hughes et al. (1994b). The Lake habitat included medium to large water bodies (> 3000 m^2) and lakeshores (i.e. a margin of ca 5 m around lakes). The Stream habitat was defined as stream beds (usually less than 2 m wide and running through Upland habitat) with a 5-m margin on each side covered by plants typical of wet habitats. The Beach habitat was the flat, sandy shore along the sea (average width: 1 km) and was mostly deprived of vegetation except for small patches of *Alopecurus alpinus*, *Carex maritima*, *Poa arctica*, and *Luzula confusa* (Duclos 2002). Finally, the River habitat was defined as the bed of large braided rivers; it was composed of rocks, sediments and fast-flowing water, and generally lacked vegetation. We evaluated the availability of each habitat type using maps drawn from the aerial photographs and a Koizumi digital planimeter (estimated error = 5-10%). Some parts of the study area not visible from the observation blinds at Site-3 were excluded in our evaluation of habitat availability.

Field observations

At each site, we conducted several surveys between 14 and 20 July (starting five days after the peak hatch recorded at Site-2). Observers occupied two elevated blinds simultaneously at each site and used spotting scopes (20 – 60 x; Fig. 1). The day was divided into four 6-h periods and survey start times were systematically distributed across the four periods independently at each site. One or two surveys separated in time by > 7 h were conducted daily for a total of nine surveys at Site-3 and six at Site-1. The whole study area was scanned, and habitat used and instantaneous behaviour of adults were recorded for all pairs encountered (scan sampling; Martin and Bateson 1993). Presence of young could not be determined for distant pairs but among geese observed at close range non-parental geese were rare, as most of them leave the Island before hatch (Reed et al. in press). Surveys lasted 20 to 60 min and between 102 and 493 broods per survey were observed. At Site-1, we could not distinguish between broods hatched there and those hatched at the main nesting colony (Site-2) because observations were made on unmarked birds.

We used the same behavioural categories than Hughes et al. (1994b) but considered the pair as the sampling unit rather than single adult because the behaviour of pair members was not independent. We could not accurately determine the behaviour of goslings due to their small size and grayish colour. However, preliminary observations indicate that behaviour of both adults and goslings was highly correlated. Behaviour categories included alert (both adults stationary with head up); grazing (at least one adult had the head below horizontal, either stationary or moving slowly); resting (both adults sitting and either sleeping, brooding young, or preening); walking (both adults moving on land with head up; swimming birds were also included in this category). Grazing was assigned whenever one of the adults was grazing even if the other was engaged in another activity. When broods were walking at the transit area (Site-3), we also determined if their general movement was oriented toward the north (i.e. the brood-rearing area), the south (toward the main nesting colony) or undetermined.

Statistical analyses

We first determined habitat selection by comparing habitat use and availability at each site using the selection ratio ($\hat{w}_i$) of Manly (1993):

$$\hat{w}_i = o_i / \pi_i \qquad \text{eqn 1}$$

where o_i is the habitat use (proportion of all broods observed in habitat i) and π_i is the availability of that habitat. We evaluated the significance of habitat selection with log-likelihood chi-squared tests and Bonferroni simultaneous confidence intervals:

$$\chi_L^2 = 2\sum_{i=1}^{k} u_i \ln\left\{ u_i \Big/ \left(\sum u_i\right)\pi_i \right\} \qquad \text{eqn 2}$$

where u_i is the observed number of broods in habitat i and $(\Sigma u_i)\pi_i$ is the expected number of broods in that habitat according to its availability.

In a second analysis, we compared the distribution of geese among habitats (i.e. habitat use) and their behaviour between the two study sites. We used principal component analysis (PCA), an ordination technique allowing the analysis of non-independent variables such as proportion of geese in different behavioural categories, to reduce the dimensions of the complete data set to fewer orthogonal axes (Côté et al. 1997). We did a first PCA on the proportion of geese observed in each habitat according to site (to test habitat use), and a second one on the proportion of geese observed in a particular behaviour in each habitat and site (to test behaviour). For habitat use, we compared the two sites with one-way ANOVAs using scores obtained on the three dominant axes of the first PCA as dependent variables. Similarly, for behaviour, we assessed the effect of site and habitat with two-way ANOVAs using scores obtained on the three dominant axes of the second PCA as dependent variables. Tukey-Kramer tests were used for *a posteriori* comparisons. The sampling unit used in these analyses was each survey. Because River and Beach habitats were only present at Site-3, they were pooled with Upland habitat. Even though data analyses were done on the PC scores, the original data (i.e. proportion of individuals in each habitat or behaviour) are presented in the figures for sake of clarity.

We used z-tests to compare proportion of geese heading toward the brood-rearing site or the breeding colony. All analyses were conducted using SAS version 8.0 (SAS Institute Inc. 1999). Statistical tests were two-tailed and significance levels were set at 0.05. Inspection of residuals indicated no violation of the assumptions of normality and homogeneity of variance.

RESULTS

Habitat use and selection by broods

Wet polygon was the most heavily used habitat by broods, both at the transit site and on the brood-rearing site (Table 1). Upland was the second most important habitat used on the brood-rearing site whereas the Beach and Lake habitats were ranked second and third at the transit site. When considering availability, broods significantly selected Stream, Lake and Wet polygon habitats, whereas Upland habitat was avoided at both sites. At the transit site, the Beach habitat was used in proportion to its availability whereas the River habitat was strongly avoided (Table 1).

The first PCA axis explained 52% of the total variation in the distribution of geese among habitats whereas the second and third axes accounted for only 28% and 20%, respectively. Loadings of the original variables on the first axis (Table 2) indicated that this axis discriminated between the use of Wet Polygon and Upland/Beach habitats. Average PC scores along this first axis differed between the two sites ($F_{1,14} = 4.92$; $P = 0.045$) as broods were more often observed in Wet polygon habitat (and thus less often in Upland habitat) at the brood-rearing site (Site-1) than at the transit site (Site-3, Fig. 2). No site differences were found when comparing scores along the second ($F_{1,14} = 3.5$; $P = 0.09$) and third ($F_{1,14} = 2.0$; $P = 0.18$) axes. When looking at the spatial distribution of broods within the transit site, most geese were observed within 1 km from the sea (75%, $n = 1416$) even though this coastal strip covered only about 38% of the total area surveyed at Site-3. This narrow coastal strip was mostly composed of the Beach and Wet polygon habitats (see Fig. 1).

Brood behaviour

The first axis of the PCA on behaviour data explained 45% of the total variation in the behaviour of broods, compared to 32% and 23% for the second and third axes, respectively. The first axis discriminated resting from other behaviours, especially grazing. The second axis discriminated between walking and grazing, whereas the third one discriminated alert from other behaviours (Table 3). There were no

Table 1. **Availability, use and selection of habitats by Greater Snow Goose broods during movements from nesting to brood-rearing sites, i.e. at a transit site (Site-3, n = 1416) and at the main brood-rearing area (Site-1, n = 2519) on Bylot Island, 14-20 July 2001. Signs (+, –, =) indicate habitats which are significantly more, less, or equally used according to their availability (critical P values: $P < 0.008$, Site-3, and $P < 0.01$, Site-1).**

Habitat type	Availability (π_i)	Number of broods observed (u_i)	Use (o_i)	Selection ratio ($\hat{w}_i$)	Standardized selection ratio (B_i)[b]	Selection
Site-3 (transit site)						
Upland	0.510	103	0.065	0.127	0.006	–
Lake	0.015	168	0.130	8.667	0.393	+
Wet Polygon	0.200	848	0.584	2.920	0.132	+
Stream	0.003	35	0.027	9.000	0.408	+
Beach[a]	0.144	261	0.193	1.340	0.061	=
River[a]	0.128	1	0.001	0.008	0.000	–
Site-1 (brood-rearing site)						
Upland	0.587	314	0.125	0.213	0.014	–
Lake	0.017	141	0.056	3.294	0.216	+
Wet Polygon	0.391	1941	0.770	1.969	0.129	+
Stream	0.005	123	0.049	9.800	0.641	+

[a] Habitats unique to Site-3

[b] $$B_i = \frac{\hat{w}_i}{\left(\sum_{i=1}^{k} \hat{w}_i\right)}$$

Table 2. **Loading of original variables along the three axes derived from the principal component analysis of the proportion of Greater Snow Goose broods observed in each habitat type.**

Habitat	Axis 1	Axis 2	Axis 3
Wet Polygon	-0.69	0.07	0.02
Upland[a]	0.60	0.15	-0.52
Lakes	0.27	-0.77	0.46
Streams	0.28	0.61	0.71

[a] includes Beach and River habitats at the transit area (Site-3)

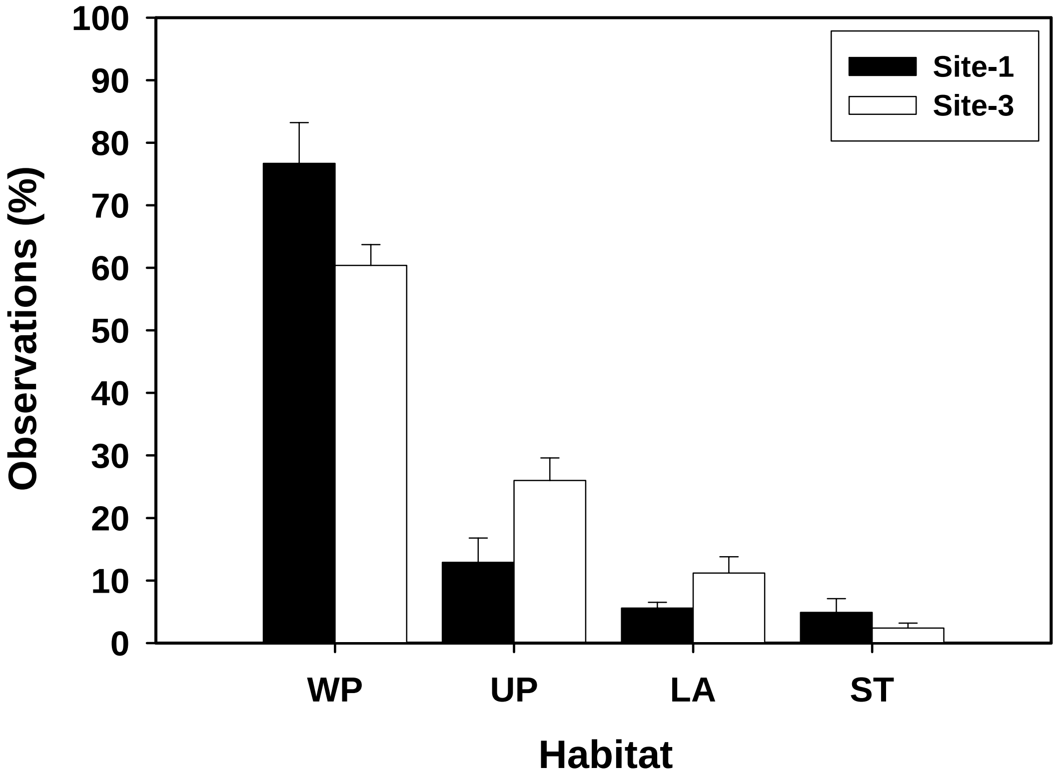

Figure 2. Percentage (Mean ± SE) of Greater Snow Goose broods observed in different habitats during movements from nesting to brood-rearing sites, i.e. at the transit site (Site-3, *n* = 9 surveys) and at the brood-rearing site (Site-1, *n* = 6 surveys) on Bylot Island, Nunavut, Canada. WP = Wet Polygon, UP = Upland, LA = Lake, ST = Stream. At Site-3, Upland habitat included River and Beach habitats.

<u>Table 3.</u> Loading of original variables along the three axes derived from the principal component analysis of the proportion of Greater Snow Goose broods observed in each behavioural category.

Behaviour	Axis 1	Axis 2	Axis 3
Grazing	0.56	-0.56	-0.20
Walking	0.18	0.78	-0.41
Resting	-0.73	-0.11	0.15
Alert	0.34	0.26	0.87

differences between sites in average PC scores (first axis: $F_{1,53} = 3.23$; $P = 0.079$, second axis: $F_{1,53} = 0.56$; $P = 0.46$, third axis: $F_{1,53} = 0.00$; $P = 0.96$) indicating that broods were generally behaving in the same way at the transit and brood-rearing sites (Fig. 3). However, PC scores along the first axis differed among habitats ($F_{3,51} = 7.2$; $P < 0.001$) because broods rested more often in Lake habitat than in other habitats (Fig. 3). Even though there was no interaction between site and habitat (all axes, $P > 0.44$), broods seemed to walk more and rest less in Upland and Stream habitats of Site-3 compared to Site-1. At the transit site (Site-3), broods that were walking and for which we could assign a direction were heading in greater proportion towards the brood-rearing area (Site-1) than towards the main nesting colony (77% vs. 23%, respectively, z-test, $P < 0.05$, $n = 115$).

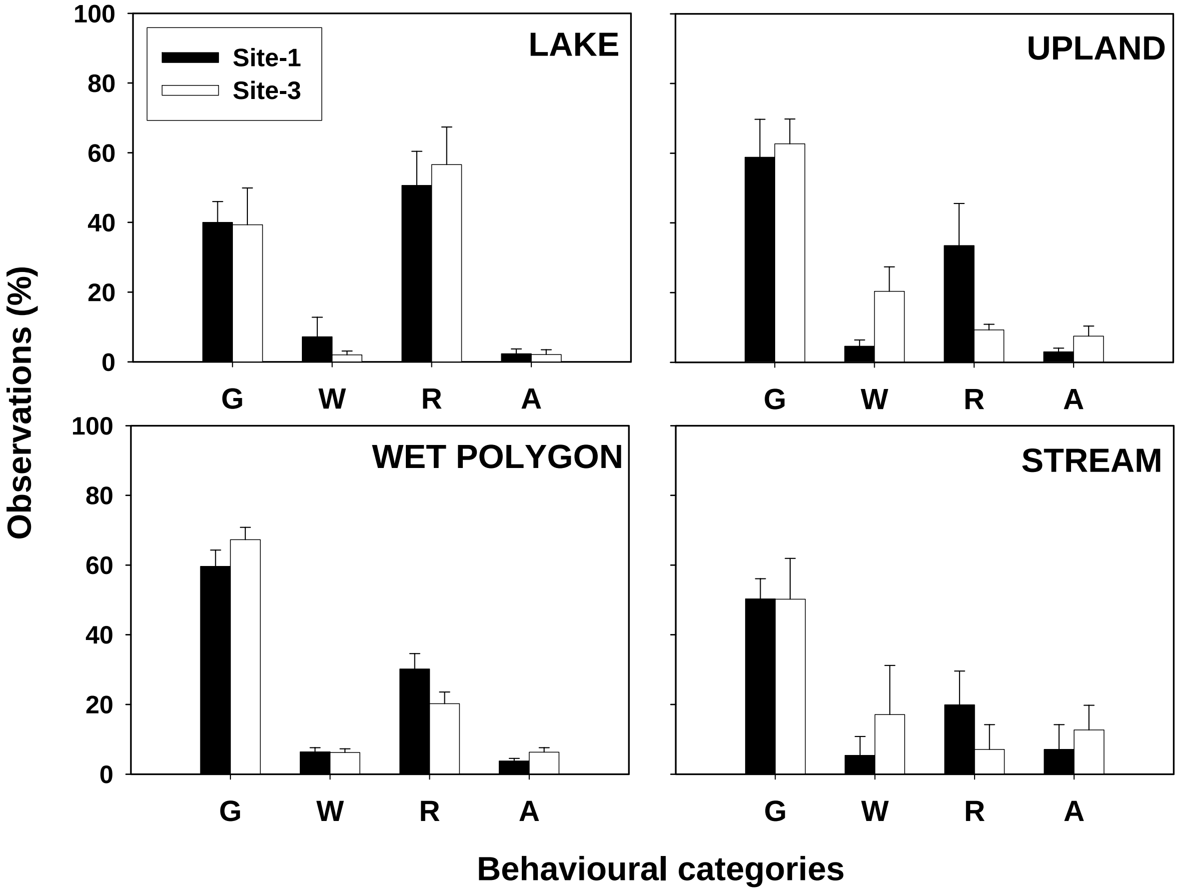

Figure 3. Behaviour of Greater Snow Goose broods observed in different habitats during movements from nesting to brood-rearing sites, i.e. at the transit site (Site-3, *n* = 9 surveys) and at the brood-rearing site (Site-1, *n* = 6) on Bylot Island, Nunavut, Canada (Mean ± SE). G = Grazing, W = Walking, R = Resting, A = Alert. At Site-3, Upland habitat included River and Beach habitats.

DISCUSSION

Habitat use and selection by broods

At both study sites, broods strongly selected Stream and Wet polygon habitats, which are those providing the highest amount of forage plants for geese on Bylot Island (Massé et al. 2001). The Lake habitat, as well as ponds found in Wet polygon habitat, provide refuges against terrestrial predators such as Arctic foxes (Giroux et al. 1984,1986, Hughes et al. 1994b, Duclos 2002) and Red foxes (J. Mainguy, personal observation) and this habitat was also selected at both sites. In contrast, the Upland habitat was significantly avoided at both sites despite being the most common habitat, covering approximately 90% of the southwest plain of Bylot Island (Massé et al. 2001). It thus appears that during overland movements, broods showed the same habitat preference as those that had already settled at the main rearing site.

Despite these similarities, broods observed at the transit area nonetheless spent more time in Upland habitat, a sub-optimal habitat, than at the main rearing site. This suggests that broods are forced to use sub-optimal habitat during part of their overland movement. Thus, even if broods always show a preference for wetland by selecting the same high quality habitat patches, they eventually have to leave them in order to reach the best feeding sites located at the main brood-rearing area. The Upland habitat is characterized by a low abundance of high quality forage plants for geese and lacks predator-safe areas such as lakes or ponds (Hughes et al. 1994b, Duclos 2002). This may explain why broods avoided it even though it was used in greater proportion during brood movements than after settling in the main rearing area.

A possible way for brood to minimize the time spent in the low quality Upland habitat during part of overland movement may be to use the Stream habitat as travel paths. Streams running through the Upland habitat were highly selected even though they cover a very small proportion of the study area. Broods may use them because stream banks provide high quality forage plants (Massé et al. 2001). Additionally, streams running in small gullies may be easier to walk for newly-hatched goslings because they offer a less rugged terrain than the Upland habitat, and they can offer some protection against terrestrial predators by hiding broods from sight better than the more exposed terrain of Upland habitat.

Most of the geese observed at the transit site used a narrow strip along the coast. The presence of a vast Wet polygon habitat patch located in the southern part of the coastal area may be a key reason to explain why geese were predominately observed in that part of the study area during brood movement. In contrast, other Wet polygon habitat patches were much smaller and sparsely distributed further inland through the Upland habitat (see Fig. 1). When leaving that coastal Wet polygon habitat patch, broods could use the Beach habitat to continue their movement. This may explain why the Beach habitat was used in proportion to its availability even though this habitat was mostly deprived of vegetation, and thus provided very few feeding opportunities (Duclos 2002). However, the sandy beach offered a very flat terrain, which may be an energetic advantage during movement. In addition, its proximity to the sea provides a good escape cover against attacks by terrestrial predator such as foxes. Overall, the coastal area allowed broods to have access to patches of high quality foraging plants and to continue their movement in a relatively safe habitat (i.e. the Beach) after leaving wet polygons. On the Beach, we often witnessed broods moving quickly in straight line between small patches of vegetation where they briefly stopped to peck at the plants.

Behaviour of brood-rearing geese

Behaviour of broods at the transit area did not differ from the one observed in the brood-rearing area, presumably because geese selected the same habitats and thus behaved in the same way. The higher frequency of resting in the Lake habitat compared to all other habitats may be explained by the need for a nearby refuge from terrestrial predator like foxes, as geese resting on lakeshores or in water may escape more easily from their attacks. Because most broods at the transit site were in movement to another brood-rearing area, we expected that walking should be more prevalent there than at the main brood-rearing site. Even though broods tended to walk more in the Upland and Stream habitats at the transit area, overall the proportion of broods observed walking did not differ from the one found in broods that had already settled at the main brood-rearing area. Broods of Greater Snow Geese have large home range and are known to range widely in search of food (Hughes et al. 1994a) and this may explain why walking activity remained the same after they have accomplished *between-area* movements. Another possibility is that broods may have been able to reconcile walking and grazing during their overland movement. In fact, many broods observed at the transit site were assigned to the grazing category even if they were moving slowly in a directional way.

Potential biases

In our study, we cannot exclude the possibility that observations of brood that differed slightly in age may have lead to biases. If broods observed at the brood-rearing area were composed in part of early-hatched gosling that had completed their movement from the main nesting colony, then these broods may have been older than the one observed at the transit site. However, hatching is highly synchronized in snow geese (~ 90% of nests hatch over an 8-day period, Lepage et al. 2000), and thus these possible age differences were probably small. Early-hatched broods may also be accompanied by more experienced adults (Hughes et al 1994a) and thus show different habitat use or behaviour than older ones. Another potential bias is that some broods actually selected the transit area to rear their young rather than simply passing through. Inclusion of broods in our analysis that had already settled in a rearing area with those that were still in movement may have masked differences in our between-sites comparisons. However, radio-tracking data showed that the number of geese that used the transit area to rear their goslings was probably small (chapter 1).

Costs and benefits of overland movement by broods

In geese, selection of brood-rearing habitats with high quality food plants is essential to enable goslings to complete their growth before the fall migration (Sedinger and Raveling 1984, Laing and Raveling 1993, Lepage et al. 1998, Person et al. 1998). In Greater Snow Geese, such as in other goose species, a large number of broods will make long-distance movements to get to high-quality feeding sites soon after hatch (Cooch et al. 1993, Slattery 2000, Sedinger et al. 2001, chapter 1).

However, potential cost of these movements may be increase time spent in poor habitat in term of quality of feeding sites and predator refuges, even though broods apparently attempt to maximize the time spent in high quality habitat. Reduce feeding opportunities during long-distance overland movements may in part explain why goslings hatched in large colonies far from their brood-rearing site (~30 km) had a lower growth than those that hatched very close to it (< 5 km, chapter 1). Movement may nonetheless provide a selective advantage as gosling growth is often better for broods leaving the main nesting colony for distant brood-rearing area than for those that stayed there to rear their brood (Cooch et al. 1993, Slattery 2000, chapter 1). In our study, we found no evidence for a cost in term of gosling survival related to long-distance movement (chapter 1), which suggest that reduced availability of predator refuge during overland movement may not be too severe. In addition, it is unlikely that broods moving long distances between nesting and rearing areas experienced a greater energetic cost than those that moved short distances as they all devote the same amount of time to locomotion (i.e. walking behaviour category). Moreover, the results of Otis (2002) suggest that the cost of walking in a cold environment may be negligible in goslings.

Overall, our results indicate that overland movements allow access to high quality brood-rearing sites but involve spending some amount of time in low quality habitats. Therefore, we suggest that even if negative consequences on gosling growth may be related to long distance movements, access to better feeding sites apparently outweigh these costs and may explain why this type of movement is maintained through time.

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CONCLUSION GÉNÉRALE

Ce projet avait comme objectif principal d’examiner les coûts et les bénéfices associés aux déplacements de familles entre différents sites suivant un changement dans les besoins vitaux. La Grande Oie des neiges nous a servi de modèle afin de tenter de comprendre quels sont les enjeux de ces déplacements ainsi que d’essayer de savoir s’il pouvait exister un compromis favorisant le maintien de ce comportement.

Tout d’abord, nous n’avons pas trouvé de coût en terme de probabilité de survie des oisons selon la distance parcourue entre les sites d’éclosion et d’élevage durant deux années d’étude. Ainsi, les oisons parcourant une grande distance (allant parfois à > 50 km) ne subissent pas un taux de mortalité plus élevé que ceux se déplaçant sur des distances plus courtes (< 5 km). Chez certaines espèces, cependant, une relation positive a été trouvée entre la distance parcourue et le taux de mortalité des jeunes. Par contre, chez une même espèce, soit le Canard colvert, Rotella et Ratti (1992) ainsi que Mauser et al. (1994) ont trouvé cette relation alors que les travaux de Talent et al. (1983) et de Dzus et Clark (1997) ne l’ont pas supportée. Ainsi, la situation semble très variable pour une même espèce, des conclusions opposées se dégageant de différentes études. On peut donc en retenir que la possibilité de coûts en termes de survie des jeunes est toujours présente mais qu’elle peut se manifester de manière plus prononcée selon le milieu. Par exemple, la présence de différents types de prédateurs selon le site d’étude ainsi que leur densité peuvent avoir une grande influence sur la survie des jeunes. Il est aussi plausible que les espèces qui franchissent de grandes distances durant leur déplacement inter-site se trouvent dans l’obligation de traverser le territoire d’un plus grand nombre de prédateurs, augmentant le risque de prédation. Dans notre étude, la survie ne semble pas avoir été affectée négativement, peut-être dû au fait que les familles ont su maximiser l’utilisation des milieux fournissant un refuge (i.e. lacs et étangs) contre l’attaque de prédateurs terrestres durant leur déplacement.

Nous avons cependant découvert un effet des déplacements des familles sur la croissance des jeunes, ceux se déplaçant sur une grande distance (de la colonie de nidification principale au site d’élevage, 30 km ou plus) ayant une croissance plus faible que ceux éclos près du site d'élevage. Nos résultats démontrent que ce coût serait en partie attribuable au temps passé dans des habitats de pauvre qualité pour l'alimentation lors des déplacements. Cependant, se déplacer pour accéder à des sites d'élevage offrant des plantes répondant mieux aux exigences nutritionnelles des jeunes (en quantité et qualité) a permis aux oisons d'avoir une meilleure croissance que ceux demeurant à la colonie principale malgré que ces derniers aient parcouru peu de distance après l'éclosion (~ 5 km). Le déplacement des familles sur une grande distance, malgré son coût, permet de bénéficier de ressources de bonne qualité et procure donc un avantage sur les familles demeurant à la colonie principale où la nourriture est plus pauvre. Ceci peut expliquer le maintien de ce comportement qui a été aussi rapporté chez d'autres espèces d'oies (Cooch et al. 1993, Slattery 2000).

Le succès de nidification plus élevé à la colonie principale comparativement à celui des oies nichant à faible densité près du site d'élevage principal pourrait expliquer l'existence du mouvement inter-sites. Au niveau individuel, nicher en colonie augmente les chances de produire des jeunes à l'éclosion tandis que les conduire au site d'élevage de qualité leur assure une meilleure croissance. Cette stratégie, utilisée par la majorité des oies nichant à l'Île Bylot, représente donc un bon compromis afin de maximiser le succès reproducteur. Le fait de passer du temps dans des habitats sub-optimaux lors des déplacements des sites de nidification aux sites d'élevage serait compensé largement par l'accès à des plantes de meilleure qualité nutritive. Eriksson (1978) propose que les mouvements des familles vers les sites d'alimentation doivent procurer des bénéfices supérieurs aux coûts encourus pour se maintenir. Les résultats de notre étude viennent appuyer cette idée. Il est important également de souligner que les individus utilisant répétitivement cette stratégie acquièrent une familiarité aux sites de nidification et d'élevage utilisés, conférant ainsi des avantages par la connaissance de ces derniers (Anderson et al. 1992).

Un fait intéressant à noter chez l'espèce que nous avons étudiée est qu'il y a une augmentation du nombre d'individus qui tentent de nicher près du site d'élevage principal durant les années où les oiseaux de proie nichent dans ce secteur. Cette situation survient uniquement lors des pics de lemmings qui suivent un cycle de 3-4 ans (Bêty et al. 2001). Nos résultats démontrent que durant ces années les oies obtiennent un succès de nidification beaucoup plus élevé que la normale, comparable à celui connu par les individus nichant à haute densité dans la colonie principale. Cette situation représente donc la stratégie de reproduction idéale du fait qu'elle maximise la production de jeunes et favorise une meilleure croissance par un accès rapide au site d'alimentation, tout en éliminant les coûts associés aux déplacements. Cependant, pour les années où il y a absence de nidification par les oiseaux de proie, les oies tentant de nicher à faible densité au site d'élevage principal connaissent un succès de nidification assez faible allant parfois jusqu'à l'échec total dans les années de forte prédation.

Le fait que nous retrouvions des oies nichant aux deux sites (colonie principale et site d'élevage) à chaque année nous porte à croire que les avantages retirés permettent à ces différentes stratégies de se maintenir. Un aspect intéressant concernant le maintien de ces différentes stratégies et pouvant faire l'objet d'études plus détaillées serait d'examiner la stratégie de reproduction au niveau individuel. En effet, la population de Grande Oie des neiges nichant à l'Île Bylot est suivie depuis plus d'une décennie et comporte une proportion élevée d'individus marqués pour lesquels nous possédons une banque de données permettant de tester la possibilité qu'un même individu puisse alterner d'une stratégie à l'autre. On pourrait se demander, par exemple: Est-ce qu'il existe une certaine plasticité au niveau comportemental qui ferait en sorte que des individus utilisent certaines années le site d'élevage, et d'autres années la colonie principale comme site de nidification? Au contraire, existe-t-il un déterminisme génétique conférant une fidélité à un site particulier pour la nidification ou l'élevage des jeunes? L'utilisation de l'information spatiale (emplacement du nid) et de celle portant sur la reproduction des individus marqués qui a été récoltée tout au long de cette étude à long terme pourrait donc nous aider à examiner cette possibilité. L'utilisation d'outils moléculaires en génétique des populations pourrait également donner des informations supplémentaires en comparant le génotype des individus utilisant une ou l'autre des stratégies.

Une question importante concernant la nidification des oies à notre site d'étude demeure cependant en suspend: Pourquoi la colonie principale n'est pas établie au site d'élevage principal? Cette situation offrirait pourtant aux individus le meilleur des deux situations en permettant, d'abord, un succès de nidification élevé (nicher à haute densité) et, ensuite, un accès rapide aux sites d'alimentation, épargnant ainsi les coûts associés aux déplacements dans les habitats sub-optimaux. Cette question demeure entière et pourra également faire l'objet d'études plus poussées. Jusqu'à présent, seulement certains éléments de réponse peuvent nous permettre d'essayer de comprendre cette situation. Premièrement, il existe des différences dans la topographie et l'arrangement des habitats entre le site d'élevage principal (camp-1) et le site de nidification principal (camp-2). Tremblay et al. (1997) ont d'ailleurs suggéré que ces différences puissent expliquer en partie des différences dans le succès de nidification, certains types d'habitats retrouvés à la colonie principale favorisant une diminution du taux de prédation. Une autre piste à envisager est le fait que la Grande Oie des neiges soit une espèce coloniale et que ce type de comportement peut avoir des implications au niveau du choix des sites dans lesquels elles se reproduisent (Rolland et al. 1998). Est-ce que, par exemple, la majorité des oies nichent en colonie au site de nidification principal étant donné sa position centrale sur l'île par rapport aux autres sites d'élevage potentiels, position qui minimiserait la distance parcourue pour le plus grand nombre d'individus? Est-ce que la densité de prédateurs retrouvés dans cette région est plus faible qu'ailleurs sur l'île? Des études descriptives récentes sur les habitats retrouvés à notre site d'étude (Massé et al. 2001, Duclos 2002) ainsi que la mise en évidence d'interactions trophiques indirectes entre les différentes espèces associées à la reproduction de l'Oie des neiges (Bêty et al. 2002) seront sûrement des éléments clefs pour répondre à ces questions.

Sur la base de nos résultats, nous proposons que les parents choisissent les sites de nidification et d'élevage en essayant d'optimiser tous les aspects reliés à la reproduction, soit de la ponte des œufs à l'envol des jeunes. La superposition des sites de nidification et d'élevage devrait en théorie représenter la situation idéale. Cependant, chez les espèces pour lesquelles ce n'est pas le cas, le déplacement des familles afin d'accéder aux meilleurs sites après l'éclosion, même si cela implique de grandes distances, doit contrebalancer les coûts encourus lors de ces déplacements pour qu’il y ait maintien de ce type de comportement.

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