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INTERACTIONS TROPHIQUES INDIRECTES, PRÉDATION ET STRATÉGIES DE REPRODUCTION CHEZ L'OIE DES NEIGES NICHANT DANS LE HAUT-ARCTIQUE

Thèse
présentée
à la Faculté des études supérieures
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ATTESTATION

Ce 21e jour du mois septembre de 2001, les personnes soussignées, en leur qualité de membres du jury de la thèse de Joël Bêty, ont assisté à la soutenance de cette thèse.

NOMS	UNIVERSITÉ	SIGNATURE
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RÉSUMÉ SUCCINCT

Notre objectif était d'examiner l'effet des interactions trophiques indirectes et stratégies de reproduction sur la productivité et la performance reproductive des individus chez la Grande Oie des neiges (*Chen caerulescens atlantica*) nichant dans le Haut-Arctique. Nous montrons que le succès de nidification des oies est positivement associé à l'abondance de lemmings et que la prédation a un effet considérable sur la productivité des nids d'oies. Nous présentons des évidences empiriques et expérimentales démontrant que i) l'association des oies avec des rapaces lors de fortes abondances de lemmings peut réduire les risques de prédation des nids et ii) les réponses numériques et comportementales de prédateurs communs représentent le principal mécanisme responsable de l'interaction indirecte entre les oies et les populations cycliques de rongeurs. Finalement, un suivi télémétrique indique que les oies ajustent leur stratégie de reproduction (date et taille de ponte) en fonction de leur migration et condition corporelle de façon à optimiser le succès reproducteur attendu.

Joël Bêty – Candidat :

Gilles Gauthier – Directeur de recherche :

RÉSUMÉ LONG

L'objectif de cette thèse était d'examiner l'effet des interactions trophiques indirectes et des stratégies de reproduction sur la productivité et la performance reproductive des individus chez la Grande Oie des neiges (*Chen caerulescens atlantica*) nichant dans le Haut-Arctique. Les données ont été récoltées de 1993 à 2000 à l'île Bylot (Nunavut). Nous avons d'abord évalué l'effet des visites de nids sur l'activité des prédateurs et le taux de prédation des œufs d'oies. Nos résultats indiquent que nos paramètres de nidification n'étaient pas biaisés par nos activités de recherche. Ensuite, nous avons testé des prédictions de deux hypothèses pouvant expliquer l'interaction indirecte potentielle entre les populations cycliques de lemmings et les oiseaux de l'Arctique, soit l'hypothèse d'association avec des rapaces et l'hypothèse des proies alternatives (réponses des prédateurs communs). Nous présentons des évidences empiriques et expérimentales démontrant que l'association avec des rapaces lors des pics de lemmings réduit localement les risques de prédation des nids. Nous montrons aussi que le succès de nidification des oies est positivement associé à l'abondance de rongeurs même en l'absence d'association et que les réponses numériques et comportementales de prédateurs communs représentent le principal mécanisme qui génère une interaction entre les oies et les lemmings. Des observations comportementales ainsi qu'un suivi de l'activité de reproduction ont permis d'identifier les Renards arctiques (*Alopex lagopus*) et les Labbes parasites (*Stercorarius parasiticus*) comme prédateurs clés générant des variations marquées dans l'intensité de prédation des œufs. Nous présentons également des évidences montrant que i) la prédation a un effet considérable sur la productivité des nids d'oies et ii) les populations de lemmings peuvent avoir, à court-terme, des effets positifs et, à long-terme, des effets négatifs sur les oies via les prédateurs. Finalement, nous avons testé des prédictions d'un modèle de taille de ponte dépendante de la condition qui est basé sur l'hypothèse du coût-du-délai. Un suivi télémétrique d'individus effectué à la principale halte migratoire (sud du Québec) et sur l'aire de reproduction indique que les oies ajustent leur stratégie de reproduction (date et taille de ponte) en fonction de leur migration et condition corporelle de façon à optimiser le succès reproducteur attendu.

Joël Bêty – Candidat :

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ABSTRACT

The objective of this thesis was to examine the effects of indirect trophic interactions and reproductive strategies on the nesting production and individual breeding success of greater snow geese (*Chen caerulescens atlantica*). The data were collected from 1993 to 2000 in the High-Arctic at the migratory bird sanctuary of Bylot Island (Nunavut). We first verified the effect of investigator disturbance on the activity of predators and predation rate of goose eggs. Although some predators can take advantage of the presence of investigators, our results indicated that goose nesting parameters estimated in this study were not biased by nest visits. Second, we tested some predictions of two hypotheses proposed to explain the potential indirect interaction between cyclic lemming populations and arctic-nesting birds: the nesting association hypothesis (protective association with birds of prey) and the alternative prey hypothesis (responses of shared predators). We provide empirical and experimental evidence that nesting association with birds of prey during peak lemming years reduces nest predation risk at the local level. We also show that goose nesting success is positively associated with rodent abundance even in absence of nesting association and that the numerical and behavioural responses of shared predators is the main mechanism generating an indirect interaction between lemmings and geese. Monitoring of the breeding activity and detailed behavioural observations illustrate that arctic foxes (*Alopex lagopus*) and parasitic jaegers (*Stercorarius parasiticus*) are the key predators generating marked annual variation in egg predation intensity. We present evidence that predation has considerable effects on goose nesting production and that lemming populations can have both short-term positive effects and long-term negative effects on nesting geese through shared predators. Finally, we tested some predictions of a condition-dependent individual optimal clutch size model based on the cost-of-delay hypothesis. Radio-tracking of marked individuals on their main staging area (southern Quebec) and breeding ground indicates that geese adjust their breeding strategy (laying date and clutch size) relatively to their body condition and migration chronology in order to optimize the expected reproductive success.

Joël Bêty – Candidat :

Gilles Gauthier – Directeur de recherche :

AVANT-PROPOS

Cet ouvrage comprend 4 chapitres principaux rédigés sous la forme d'articles scientifiques. La thèse inclut aussi une introduction générale et se termine par une conclusion générale. Chacun des chapitres est complet et ne nécessite pas la lecture des autres chapitres pour être compris. Dans tous les cas, je suis l'auteur principal de ces articles. En plus de mon directeur de thèse, Gilles Gauthier, les coauteurs Jean-François Giroux (co-directeur) et Erkki Korpimäki ont contribué à l'élaboration des objectifs ou au moment de la rédaction de manuscrits (Chapitres 2, 3 et 4 et Chapitres 2 et 3, respectivement). Les Chapitres 1, 2 et 3 sont publiés ou acceptés comme publication dans les revues *Journal of Field Ornithology*, *Oikos* et *Journal of Animal Ecology*, respectivement. Le Chapitre 4 sera soumis à la revue *American Naturalist*.

En écologie terrestre, les travaux de recherche à long-terme nécessitent généralement la contribution de nombreux individus. Cette étude ne fait pas exception, bien au contraire. C'est avec énormément de plaisir et de passion que j'ai concentré la majorité de mon énergie sur ce projet initié il y a maintenant quelques années. Néanmoins, ma contribution personnelle ne représente qu'une partie des efforts déployés pour la récolte des données que j'ai utilisées dans ma thèse. C'est pourquoi j'aimerais premièrement remercier les différents intervenants qui ont permis la réalisation de ce projet.

Mes premiers mots d'éloge sont offerts à mon directeur, Gilles Gauthier, et Austin Reed, co-responsable du projet de l'île Bylot. À l'image des pionniers, ils ont réussi à mettre sur pied un projet de recherche de grande envergure et puis, au fil des ans, à convaincre de multiples collaborateurs d'unir leurs efforts pour mieux comprendre l'écologie de l'Île Bylot. Il est vrai que le mariage entre les oies et un environnement aussi splendide que l'écosystème arctique génère à lui seul énormément de motivation et d'enthousiasme chez les gens qui tentent de mieux les comprendre. Toutefois, la mise en place de travaux à long terme chez une espèce qui côtoie un environnement extrême nécessite une détermination et une volonté que peu de gens expriment. L'organisation que nécessite l'accumulation de données à long-terme à un site d'étude localisé à plus de 3000 km au nord de votre bureau de travail représente en soit un exploit digne de mention. Puisque j'ai eu la chance d'utiliser certaines de ces informations, je suis extrêmement reconnaissant envers les initiateurs du projet. De plus, un autre collaborateur unique, mon co-directeur Jean-François Giroux, représente le principal maître d'œuvre et superviseur du projet de suivi télémétrique d'envergure mis en place le long du fleuve St-Laurent. J'aimerais spécialement le remercier pour la collaboration très bénéfique et étroite qu'il a su mettre en place entre les nombreux membres des équipes de recherche poursuivant différents objectifs.

Évidemment, ces travaux à long-terme ont nécessité la contribution de nombreuses personnes qu'il sera difficile de tous nommer et envers qui j'ai beaucoup de reconnaissance. J'ai eu l'opportunité de côtoyer certaines de celles-ci et j'aimerais les remercier personnellement, soit Denis Lepage, Louis Lesage, Pascale Otis, Chantal Pineau, Monique Poulin, Mohamed Righi, et Jean-Pierre Tremblay. En plus des travaux à long-terme, plusieurs personnes ont participé au marquage des oies et à la récolte des données dans le cadre spécifique de mon projet, soit notamment (en ordre alphabétique) Arnaud Béchet, Jonatan Blais, Grégoire Côté, Diane Dauphin, Frédéric Demers, Réjean Deschênes, Karine Dubreuil, Isabelle Duclos, Mathieu Dumas, Dominique Fiset, Julie Lambert, Josée Lefèbvre, Julien Mainguy, Hélène Massé, Stéphane Menu, Amos Ootovak, Joasie Ootovak, Sam Ootovak, Luc Pelletier, Thomas Pewataluk, Gérald Picard, Catherine Poussart, Eric Reed, Mathilde Renaud, Stéphanie Rioux, Francis St-Pierre, Yanie Porlier, Nadia Nadeau et René Théreault. J'aimerais particulièrement souligner la contribution de Nathalie Piedboeuf et Isabelle Chouinard pour la qualité de leur travail et la confiance qu'elles m'ont démontrée en investissant beaucoup de leur énergie dans la collecte d'information le long du fleuve St-Laurent. Finalement, il y a une personne, Diane Leclerc, qui a contribué à accumuler de précieuses données pour chacun des thèmes abordés dans ma thèse. Je suis le seul témoin de l'ensemble des efforts, parfois surhumains, déployés par cette personne sur le terrain. Je suis persuadé qu'il m'aurait été impossible d'atteindre l'ensemble de mes objectifs sans son énergie et sa persévérance. Merci.

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En terminant, je souhaite souligner l'appui inconditionnel des membres de ma famille qui, en plus d'avoir participé activement à la préparation du matériel de recherche (et oui…), ont démontré un intérêt constant envers mon projet. Ma compagne de vie, Diane, mérite les derniers mots d'éloges pour sa participation, sa compréhension, son énergie et son respect de ma passion!

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Introduction

Une des plus importantes questions abordées par la science de l'écologie concerne les facteurs qui déterminent la répartition et l'abondance des organismes vivants. Depuis plusieurs décennies, les écologistes s'interrogent notamment sur le rôle des interactions trophiques pour expliquer la structure et la dynamique des communautés (ex.: Paine 1966, Cody et Diamond 1975, Holt 1977, Batzli et al. 1980, Price 1992, Strong 1992, Bazely et Jefferies 1996, Oksanen et Oksanen 2000). Est-ce que l'abondance et la distribution des organismes sont principalement déterminées par les niveaux trophiques inférieurs (*bottom-up forces*) ou supérieurs (*top-down forces*) dans les systèmes multitrophiques? Récemment, cette question a été largement débattue et étudiée dans une variété d'écosystèmes naturels (ex.: Karr et al. 1992, Menge 1992, Power 1992, Price 1992, Strong 1992, Moran et al. 1996, Polis 1999). Le principal consensus émergent de ces discussions est que l'importance relative des niveaux trophiques inférieurs ou supérieurs dans la structure des communautés varie grandement entre les systèmes ainsi qu'à l'intérieur d'un même système (Olff et al. 1999). Bien que ces deux points de vue étaient considérés comme opposés à l'origine, les discussions actuelles tendent plutôt à les intégrer dans une même théorie. Ainsi, le nouveau défi est maintenant d'identifier les conditions (biotiques et abiotiques) où l'une ou l'autre de ces deux forces est dominante et de déterminer comment elles interagissent et s'influencent mutuellement.

Les écosystèmes se composent de multiples interactions trophiques qui varient dans le temps et l'espace. Traditionnellement, les modèles de communautés ont mis l'accent sur les interactions trophiques « directes », tels la prédation ou la compétition, où des changements dans l'abondance et la distribution d'une espèce résulte de son interaction directe avec une autre espèce. Cependant, les interactions trophiques « indirectes », soit une espèce qui influence la distribution et l'abondance d'une autre espèce à travers une interaction directe avec d'autres espèces, peuvent aussi jouer un rôle important dans les communautés (Strauss 1991). Bien qu'il existe une multitude d'effets indirects possibles et que leur impact potentiel soit bien démontré en milieu aquatique (ex.: Menge 1995), leur rôle demeure particulièrement obscur dans les écosystèmes terrestres (Chase 2000, Sinclair et al. 2000).

Quatre catégories générales d'effets indirects ont été identifiées jusqu'à maintenant, soit les liaisons écologiques, comportementales, environnementales et chimiques (Miller et Kerfoot 1987, Strauss 1991). Les effets écologiques indirects se font par l'intermédiaire de changements dans l'abondance; les effets comportementaux par l'intermédiaire de changements du comportement indépendamment de l'abondance; les effets environnementaux à travers des altérations des conditions abiotiques et les effets de type chimique par l'intermédiaire de diverses substances chimiques. Théoriquement, la variété des types d'effets indirects possibles est presque illimitée (Abrams 1987, 1992).

Lorsque des victimes (proies ou hôtes) sont attaquées par un ou des ennemis naturels communs (prédateur ou pathogène), l'existence d'interactions indirectes entre les populations de victimes est alors possible (Holt et Lawton 1994). Des proies qui ont en commun un ou plusieurs prédateurs peuvent interagir indirectement par l'intermédiaire de la réponse fonctionnelle (variation dans le nombre de proies consommées) et la réponse numérique (variation dans la reproduction, la survie et l'agrégation) des prédateurs (Holt et Kotler 1987, Abrams et Matsuda 1996). Bien que possiblement très répandu (Holt 1977, Holt et Lawton 1994), ce type d'interaction indirecte n'a pas été étudié convenablement en milieu naturel, particulièrement dans les écosystèmes terrestres où l'on retrouve des populations cycliques (Abrams et al. 1998).

Dans ma thèse, j'aborderai entre autres le concept d'interaction trophique indirecte chez des herbivores qui ont des prédateurs en commun. Les herbivores jouent un rôle central dans la plupart des communautés écologiques. Dans le but de comprendre la composition et la dynamique des communautés, il est essentiel de se questionner sur les facteurs qui influencent l'abondance et la distribution des herbivores (Olff et al. 1999). Cinq principaux facteurs naturels peuvent déterminer l'abondance et la productivité annuelle d'une population d'herbivores, soit la prédation, la disponibilité et la qualité de la nourriture, les maladies, les parasites et les conditions climatiques.

Interactions indirectes et populations cycliques dans les écosystèmes nordiques

Le rôle crucial que jouent les petits mammifères dans les écosystèmes nordiques est reconnu depuis longtemps, particulièrement comme consommateurs primaires et comme source de nourriture majeure pour une multitude de prédateurs vertébrés spécialistes et généralistes (Fitzgerald 1981, Korpimäki et Krebs 1996). Dans la toundra arctique et au nord de l'Europe, les fluctuations de populations de campagnols (*Clethrionomys* et *Microtus*) et de lemmings (*Lemmus* et *Dicrostonyx* spp.) suivent généralement un patron cyclique ayant une période de 3 à 5 années et une amplitude variant de 25:1 à 200:1 (Krebs 1993, Hanski et Korpimäki 1995). Ces cycles sont généralement synchronisés sur d'assez grandes étendues géographiques et aussi entre les espèces qui vivent en sympatrie (Erlinge et al. 1999, Stenseth 1999).

Les causes des fluctuations cycliques d'abondance ont fait l'objet de nombreuses recherches (Korpimäki et Krebs 1996, Stenseth 1999, Krebs et al. 2001). Les études récentes portant sur les cycles de petits mammifères suggèrent que les facteurs extrinsèques susceptibles de créer de telles variations sont i) une forte mortalité causée par des prédateurs spécialistes (ex.: Hansson 1987, Hanski et al. 1991, Hanski et Korpimäki 1995), ii) un faible taux de reproduction ou de survie dû à une réduction d'abondance de nourriture de haute qualité (ex.: Seldal et al. 1994, Turchin et al. 2000), ou encore iii) un effet interactif de la prédation et d'un manque de nourriture (ex.: Krebs et al. 1995, Hansson 1999, Krebs et al. 2001). À l'opposé, une explication intrinsèque présume que la croissance de la population est autorégulée (ex.: Krebs et al. 1973, Charnov et Finerty 1980). Pour l'instant, l'hypothèse de sénescence maternelle demeure la plus plausible parmi les explications intrinsèques (Boonstra et al. 1998). Cette hypothèse suggère que des changements dans la qualité maternelle (ex.: modification dans la structure d'âge des femelles reproductrices) surviennent lors des pics de densité. Ces modifications pourraient mener à un déclin de la population et une phase de faible abondance dans le cycle (Boonstra et al. 1998).

En dépit de recherche intensive, les hypothèses les plus plausibles ont rarement été testées à l'aide d'expériences menées en milieu naturel (Korpimäki et Krebs 1996). Toutefois, les travaux les plus récents impliquant des manipulations expérimentales suggèrent fortement que les cycles et la synchronie géographique seraient causés principalement par une interaction prédateur-proie (Korpimäki et Norrdahl 1998, Klemola et al. 2000, Ims et Andreassen 2000). Les hypothèses entourant les causes des fluctuations cycliques de petits mammifères ne sont pas traitées dans ma thèse. J'aborde plutôt certaines hypothèses qui se rattachent à leurs effets directs et indirects sur la communauté de vertébrés terrestres.

Des fluctuations considérables dans l'abondance et la productivité ont été observées chez certaines populations d'oiseaux nichant dans les milieux nordiques parallèlement aux variations d'abondance de petits mammifères (Charadriidés et Scolopacidés: Summers et Underhill 1987, Martin et Baird 1988, Summers et al. 1998; Anatidés: Summers 1986, Pehrsson 1986, van Impe 1996; Phasianidés: Angelstam et al. 1984, Leclercq et al. 1997). La prédation a été suggérée comme étant un des facteurs pouvant potentiellement synchroniser ces fluctuations (Lack 1954, Angelstam et al. 1984). Dès 1979, Roselaar avait suggéré que les variations de productivité des oies de l'Arctique puissent être liées indirectement aux fluctuations des populations de lemmings par l'intermédiaire de la réponse fonctionnelle et numérique des prédateurs (cité dans Greenwood 1987). Cette suggestion de l'existence d'une interaction trophique indirecte avait été largement ignorée jusqu'à ce que Summers (1986) reprenne cette hypothèse en mettant en relation les cycles de lemmings et la production annuelle de jeunes observée en hiver chez la Bernache cravant (*Branta bernicla bernicla*). Cette publication avait alors suscité beaucoup de controverses et de débats (ex.: Owen 1987, Dhondt 1987, Boyd 1987, Greenwood 1987, Summers et Underhill 1987, Sutherland 1988, Ebbinge 1989). La principale conclusion tirée de ces multiples publications était que seules des observations réalisées sur l'aire de reproduction des oiseaux permettraient de mettre en évidence une relation causale entre l'abondance de lemmings et la productivité des oiseaux de l'Arctique. Depuis, les quelques observations rapportées ont permis de constater la complexité des interactions trophiques même dans cet écosystème relativement simple (ex.: Spaans et al. 1998).

Une nouvelle hypothèse a plus récemment été proposée pour expliquer le lien potentiel entre les cycles de petits mammifères et la productivité des populations d'oiseaux. L'hypothèse d'association suggère qu'à forte abondance de petits rongeurs certaines espèces d'oiseaux profitent d'une association bénéfique avec des rapaces au moment de la nidification (Underhill et al. 1993, Lepage et al. 1996). Puisque la prédation des nids est une des variables les plus importantes qui affectent le succès reproducteur des oiseaux (Ricklefs 1969), ceux-ci ont développé une multitude de stratégies pour limiter les risques de prédation. Une de ces stratégies est de nicher en association avec une espèce agressive (ex.: Groom 1992, Norrdahl et al. 1995), un comportement qui est souvent rapporté dans les habitats arctiques et sub-arctiques (Blomqvist et Elander 1988, Götmark 1989, Larsen et Grundetjern 1997). Les oiseaux qui placent leur nid près d'une espèce qui défend vigoureusement le voisinage de son nid contre les prédateurs peuvent ainsi bénéficier d'une exclusion partielle ou totale des prédateurs (Dyrez et al. 1981, Wiklund 1982).

Ce type d'association est bien connu chez les oies et canards qui nichent à l'intérieur du territoire d'oiseaux de proie tels le faucon pèlerin (*Falco peregrinus*), la buse pattue (*Buteo lagopus*) et le harfang des neiges (*Nyctea scandiaca*) (Syroechkovskiy et al. 1991, Underhill et al. 1993, Summers et al. 1994, Kostin et Mooij 1995, Tremblay et al. 1997). Ces prédateurs démontrent généralement une réponse numérique rapide suite aux changements de densité de proies (Korpimäki et Norrdahl 1989, Potapov 1997, Wiklund et al. 1998). Les harfangs des neiges et les buses pattues sont des prédateurs nomades et spécialistes de petits rongeurs. Ainsi, ces rapaces nichent principalement lorsque les rongeurs sont abondants (Parker 1974, Miller et al. 1975, Fitzgerald 1981, Parmelee 1992). En conséquence, la nature opportuniste de l'association bénéfique avec des rapaces peut être un mécanisme additionnel permettant de lier les variations du succès des oiseaux et les cycles d'abondance de petits mammifères.

Étonnamment, les hypothèses permettant d'expliquer l'interaction indirecte potentielle entre les cycles de rongeurs et la productivité des oiseaux demeurent encore basées largement sur des observations effectuées sur les aires d'hivernage. Les quelques observations effectuées dans l'Arctique impliquent souvent plusieurs effets confondants qui compliquent l'interprétation et compromettent la validité des conclusions (ex.: Syroechkovskiy et al. 1991, Underhill et al. 1993, Kostin et Mooij 1995, Spaans et al. 1998). En somme, les réponses numérique et fonctionnelle des prédateurs aux cycles de petits mammifères et leurs impacts sur la communauté aviaire demeurent encore très peu connus (Norrdahl et Korpimäki 2000, Wilson et Bromley 2001). Ces systèmes offrent un cadre général très intéressant pour l'étude des interactions trophiques indirectes chez les vertébrés terrestres.

De l'individu à la population

Contrairement aux physiologistes qui mettent l'accent sur les mécanismes par lesquels les organismes vivants acquièrent et allouent l'énergie aux différentes fonctions vitales, les écologistes ont une perspective centrée davantage sur les populations et les communautés. Toutefois, la perspective écologique repose en grande partie sur les conséquences des stratégies comportementales et d'allocation des ressources utilisées par les individus d'une population. En conséquence, le comportement et l'énergétique des individus sont de plus en plus intégrés à l'écologie des populations et des communautés (ex.: DeAngelis et Gross 1992, Sutherland 1996, Wiens et Farmer 1996). On voit donc naître des modèles de population qui reposent sur les stratégies comportementales et énergétiques des individus (ex.: Mooij et DeAngelis 1999, Pettifor et al. 2000).

Basé sur la prémisse que l'énergie disponible aux organismes vivants dans un milieu donné est limitée, de nombreuses théories reliant l'énergétique à des phénomènes tels le comportement de quête alimentaire (ex.: Ludwig et Rowe 1990, Schmidt 1999), les stratégies de reproduction (ex.: Ryder 1970, Drent et Daan 1980, Thomas 1990), la diversité des communautés écologiques et la dynamique trophique des écosystèmes (ex.: Oksanen et al. 1981, Oksanen et Oksanen 2000) ont été développés. Plusieurs de ces théories ont été bâties sur des prémisses d'optimisation ou d'équilibre. Par exemple, on s'attend à ce que les stratégies d'histoire de vie des animaux soient adaptées au niveau individuel en fonction des conditions environnementales (ex.: disponibilité de nourriture, risque de prédation ou conditions climatiques) et des caractéristiques de l'individu (ex.: taille corporelle, expérience ou statut social) (Stearns 1992). Si les individus sont capables de percevoir ces différences, leurs stratégies d'histoire de vie devraient suivre des normes de réaction optimales en fonction des circonstances qui prévalent (Kisdi et al. 1998).

La quantité totale de ressources qu'un animal peut acquérir étant limitée, les individus doivent obligatoirement faire des compromis dans l'allocation relative des ressources à leur maintenance, croissance et reproduction. Chez les espèces à reproduction sexuée, un intérêt considérable s'est développé autour des processus évolutifs qui déterminent la relation entre le moment de la reproduction et l'investissement des ressources dans la production de jeunes (ex.: Einum et Fleming 2000, Nager et al. 2000, Thomas et al. 2001). Pour comprendre cette relation, certains mécanismes semblent déterminants, soit les compromis que font les parents entre i) reproduction et survie, ii) reproduction présente et future et iii) nombre et qualité des jeunes produits (Williams 1966, Stearns 1992). Plusieurs observations récentes suggèrent que le compromis entre le nombre et la qualité des jeunes pourrait être l'élément clé qui génère des différences interindividuelles dans l'allocation des ressources et la phénologie de la reproduction (ex.: Humphries et Boutin 2000, Lepage et al. 2000, Murphy 2000). Une bonne connaissance des stratégies d'allocation des ressources et des facteurs environnementaux qui influencent la performance des individus permet à la fois de mieux comprendre les adaptations évolutives et la dynamique des populations (Stonehouse et Perrins 1977).

Allocation des ressources et phénologie de la reproduction

Les facteurs qui influencent l'allocation des ressources dans la reproduction et la performance des individus sont évidemment d'une extrême importance dans la dynamique d'une population. La plupart des animaux vivent dans des milieux saisonniers où les coûts et les bénéfices associés à la survie et la reproduction varient dans le temps. Chez la majorité des espèces d'oiseaux, les individus qui nichent tôt au cours d'une saison obtiennent un meilleur succès de reproduction que les individus tardifs (Perrins 1970, Daan et al. 1988, Rohwer 1992). Le déclin saisonnier se reflète généralement dans plusieurs composantes du succès reproducteur tels la taille de ponte, la survie et le taux de recrutement des jeunes produits. Les facteurs déterminant la taille de ponte ont été le sujet de nombreuses études depuis les premières hypothèses formulées par David Lack (1947, 1954, 1967) qui tenta d'expliquer l'évolution des dates de ponte et tailles de ponte moyenne dans les populations. Puisque le déclin saisonnier de la taille de ponte est un phénomène presque universel (Klomp 1970), de nombreux efforts ont été déployés pour tenter d'apporter une seule et même explication à ce phénomène.

Le déclin saisonnier de la taille de ponte est typiquement associé à un déclin saisonnier de la valeur des jeunes produits au cours d'une saison (ex.: Perrins 1966, Cooke et al. 1984, Daan et al. 1990). Puisque les parents qui retardent le moment de la reproduction souffrent d'un coût associé au déclin dans la valeur reproductive des oeufs, cela suggère qu'ils soient contraints à nicher plus tard par des facteurs physiologiques ou environnementaux (Rowe et al. 1994). Plusieurs évidences (empiriques et expérimentales) indiquent que la taille de ponte et le moment de la reproduction sont vraisemblablement contraints par la condition corporelle des individus (Daan et al. 1988, Meijer et al. 1990). Sur la base de telles observations, Drent et Daan (1980) ont proposé que le moment et le nombre d'œufs pondus pouvaient résulter du conflit entre les avantages de pondre tôt (qualité des jeunes plus élevée et augmentation de leur valeur reproductive) et les avantages d'un délai du moment de la reproduction (acquisition de nutriments, augmentation de la condition corporelle et augmentation de la taille de ponte). Cette hypothèse du coût-du-délai a la qualité d'incorporer à la fois les causes fondamentales (*ultimate causes*) et les causes immédiates (*proximate mechanisms*) pour expliquer la taille de ponte chez les oiseaux en général. L'hypothèse de Drent et Daan (1980) a ensuite été formalisée et généralisée de façon mathématique par Rowe et al. (1994) dans un modèle dynamique. Ce modèle prédit des combinaisons de dates de ponte et tailles de ponte qui sont optimisées par les individus en fonction de leur capacité à acquérir des ressources de l'environnement. De plus, ce modèle dynamique permet de tester plusieurs prédictions dérivées du concept général du coût-du-délai.

Pour plusieurs, les oies de l'Arctique ont été considérées comme une exception au modèle du coût-du-délai puisque aucun avantage associé au délai du moment de reproduction n'avait été identifié chez ces reproducteurs sur épargne (*extreme capital breeders*) (Drent et Daan 1980). En effet, les réserves endogènes accumulées avant l'arrivée des oies sur l'aire de reproduction étaient considérées comme la source de nutriments unique pour la formation des œufs (Ankney et MacInnes 1978). Un autre modèle, l'hypothèse de ré-allocation des nutriments, avait alors été proposé pour expliquer le déclin saisonnier de la taille de ponte (Ryder 1970, Newton 1977). Cette hypothèse suppose qu'après leur arrivée, les individus ne peuvent pas acquérir de nouveaux nutriments et que tout délai réduit la quantité de ressources disponibles pour la vitellogénèse. Cependant, des études récentes ont démontré que les oies s'alimentent après leur arrivée et les nutriments exogènes acquis sur l'aire de reproduction peuvent contribuer à la formation des œufs (Budeau 1991, Bromley et Jarvis 1993, Choinière et Gauthier 1995, Ganter et Cooke 1996, Carrière et al. 1999). En conséquence, l'hypothèse du coût-du-délai est maintenant considérée comme un modèle permettant possiblement d'expliquer le patron d'allocation des ressources dans la production des œufs chez les oies de l'Arctique (Ganter et Cooke 1996, Lepage et al. 2000).

Objectifs de la thèse

Les principaux objectifs de cette thèse sont d'examiner l'effet des interactions trophiques indirectes et des stratégies de reproduction sur la productivité annuelle et la performance des individus d'une population d'oiseaux herbivores nichant dans l'écosystème arctique. D'une part, j'aborde ces thèmes en relation avec la prédation, une force sélective importante dont l'impact est souvent sous-estimé chez les oiseaux (Newton 1998). D'autre part, je traite des variations interindividuelles de la stratégie de reproduction, plus particulièrement des aspects associés à la phénologie de la reproduction et l'allocation optimale des ressources dans la formation des oeufs. Ainsi, en plus du contexte évolutif, ma thèse intègre des aspects complémentaires (niveau trophique, population et individu) qui sont essentiels à la compréhension de la dynamique des populations et la dynamique trophique des écosystèmes.

Système à l'étude

L'espèce étudiée en détail dans le cadre du présent ouvrage, la Grande Oie des neiges (*Chen caerulescens atlantica*), représente un sujet de choix pour l'étude des interactions trophiques et des stratégies de reproduction. D'abord, la Grande Oie des neiges est un herbivore strict qui élève une seule couvée par année et pour qui la prédation des nids est la cause proximale la plus fréquente des échecs de nidification (Lepage et al. 1996, Tremblay et al. 1997). Ensuite, elle niche dans le Haut-Arctique, un écosystème qui confère plusieurs avantages. C'est un environnement avec un assemblage d'espèces relativement simple où la relation prédateur-proie est visible et quantifiable. De plus, les fluctuations d'abondance de proies observées dans la toundra arctique (cycles de lemmings) offrent une excellente opportunité d'étudier la dynamique des systèmes prédateurs-proies dans des conditions contrastées (i.e.

abondance et rareté de proies). Cette situation particulière permet d'évaluer la réponse des prédateurs aux fluctuations d'abondance de proies (Boutin 1995) et de tester des hypothèses reliées aux interactions trophiques directes et indirectes. Puisque les oies adultes sont peu vulnérables à la prédation, l'effet des prédateurs est surtout concentré sur les œufs et les jeunes oies. Je m'attarderai plus spécifiquement à la prédation des oeufs. D'autre part, l'Oie des neiges représente un excellent modèle pour tester les prédictions de modèles théoriques de décisions reproductives optimales. En effet, les oiseaux qui se reproduisent dans le milieu arctique sont soumis à des contraintes saisonnières ayant de fortes incidences sur leur succès reproducteur (Barry 1962, Newton 1977, Lepage et al. 2000). Une telle situation facilite l'étude des variations interindividuelles de la stratégie d'allocation des ressources dans la reproduction et leurs conséquences sur la performance des individus.

Finalement, l'intérêt de cet ouvrage n'est pas uniquement académique. Comme plusieurs autres espèces d'oies à travers le monde, la population de la Grande Oie des neiges fait présentement l'objet de préoccupations majeures auprès des gestionnaires de la faune. En effet, cette population a augmenté dramatiquement au cours des dernières décennies, passant de 50 000 individus au milieu des années 1960 à près de 800 000 au tournant du siècle (Reed et al. 1998). L'intensification de l'agriculture sur les aires d'hivernage et les haltes migratoires est identifiée comme un facteur important responsable de la récente croissance démographique (Batt 1998). Plusieurs chercheurs pensent que la disponibilité de la nourriture à l'hiver était le principal facteur limitant des populations d'oies en Amérique du Nord avant que les oies n'envahissent le milieu agricole pour se nourrir (Batt 1997). Cette explosion démographique est aussi associée à un accroissement significatif et inquiétant de la pression de broutement sur les milieux naturels, surtout sur l'aire de reproduction et les haltes migratoires. Puisque la Grande Oie des neiges a un impact majeur sur la dynamique des communautés végétales de ces habitats fragiles (Giroux et Bédard 1987, Gauthier et al. 1996, Giroux et al. 1998b), les décisions de gestion associées à cette population sont d'une grande importance. Or, une bonne gestion dépend du niveau de compréhension des facteurs qui affectent la dynamique d'une population.

Division de la thèse

Dans un premier chapitre, j'aborde un aspect méthodologique crucial pour ma thèse. En effet, les dérangements causés par les activités de recherche, principalement les visites de nids répétées, peuvent potentiellement biaiser l'estimation des paramètres de nidification chez les oiseaux. Ces effets sont très difficiles à prévoir et peuvent varier selon la vulnérabilité de l'espèce, les habitats ou les communautés de prédateurs (revu par Götmark 1992). En utilisant une approche expérimentale multiple, j'évalue l'effet des visites de nids sur l'activité des prédateurs et les taux de prédation des œufs chez l'Oie des neiges. Ceci me permet de quantifier l'impact de nos activités de recherche sur l'estimation de paramètres utilisés dans des tests d'hypothèses retrouvés dans les autres chapitres de la thèse.

À l'intérieur du deuxième chapitre, je mets en parallèle les deux principaux mécanismes non-exclusifs pouvant potentiellement générer une interaction trophique indirecte entre les populations cycliques de lemmings et les oies de l'Arctique. Je teste certaines prédictions dérivées de l'hypothèse d'association avec des rapaces et l'hypothèse des proies alternatives (réponses fonctionnelle et numérique des prédateurs). En associant les fluctuations d'abondance de lemmings et le succès de nidification des oies, j'évalue l'importance relative de ces deux mécanismes dans l'interaction trophique indirecte hypothétique. De plus, j'incorpore la densité de la proie alternative (nids d'oie) pour ajouter une nouvelle dimension à l'étude de la relation entre la productivité des populations d'oiseaux et les cycles de petits mammifères.

Le troisième chapitre focalise sur les prédictions dérivées de l'hypothèse d'une interaction indirecte lemmings-oies causée par les réponses fonctionnelle et numérique des prédateurs. Les effets indirects sont généralement prédits en terme de changements d'abondance à l'équilibre, ce qui est difficile à définir et à mesurer chez des populations qui ne démontrent pas de point d'équilibre (cycles). De plus, l'étude de la réponse comportementale des prédateurs plutôt que la réponse fonctionnelle est plus appropriée pour définir la nature de l'effet indirect entre des proies, particulièrement lorsque les proies démontrent des comportements anti-prédateurs (Abrams et Matsuda 1993). En conséquence, j'utilise des indicateurs associés aux mécanismes générant des effets indirects, tels l'effort des prédateurs envers les types de proie, la pression de prédation sur les œufs et la réponse numérique des prédateurs aux fluctuations d'abondance de lemmings (voir Holt et Lawton 1994).

Finalement, le quatrième et dernier chapitre aborde le concept de phénologie et d'allocation optimale des ressources dans la reproduction chez les oiseaux. Mon approche théorique est basée sur le modèle dynamique de combinaisons optimales « date de ponte et taille de ponte » dépendantes de la condition corporelle des individus (Rowe et al. 1994). Ce modèle repose sur l'hypothèse du coût-du-délai (Drent et Daan 1980) et permet d'expliquer le déclin saisonnier de la taille de ponte chez les oiseaux. Plusieurs prédictions issues de ce modèle théorique n'ont jamais été examinées en milieu naturel. Dans cette section, je teste certaines de ces prédictions en incorporant les variations interindividuelles de condition corporelle pré-migratoire et de chronologie de migration chez des Oies des neiges marquées à l'aide de radio-émetteurs.

Chapitre 1

EFFECTS OF NEST VISITS ON PREDATOR ACTIVITY AND PREDATION RATE IN A GREATER SNOW GOOSE COLONY

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Résumé

Nous avons évalué l'effet de nos visites de nids sur l'activité des prédateurs et le taux de prédation des œufs dans une colonie de Grande Oie des neiges (*Chen caerulescens atlantica*) localisée dans le Haut Arctique. L'étude a été menée au cours de deux années où le taux de prédation des nids était modéré (1996) ou faible (1997). D'abord, nous avons comparé le taux d'activité (nombre de présences par h) et le comportement des prédateurs dans la colonie en présence et en l'absence de perturbations causées par les visites de nids. Au cours d'une des deux années, le taux d'activité et le temps passé à la colonie par les Goélands bourgmestres (*Larus hyperboreus*) et les Labbes parasites (*Stercorarius parasiticus*) étaient plus élevés lors des visites de nids qu'en l'absence de perturbations. De plus, la probabilité d'attaque par les prédateurs de nids était plus élevée (4.8 fois) lors de notre présence dans la colonie au cours d'une année. Néanmoins, la technique de revisite immédiate a démontré que le pourcentage des œufs subtilisés par les prédateurs était faible (<0.7% des oeufs) suite à une visite des nids marqués. De plus, nous n'avons détecté aucune différence significative de la taille de ponte moyenne à la fin de l'incubation ou du succès de nidification entre des nids visités à plusieurs reprises (8 visites) et des nids moins perturbés (<3 visites). Quoique certains prédateurs puissent être attirés par et prendre avantage de notre présence, nos résultats indiquent que nos estimations des paramètres de nidification dans cette colonie d'Oie des neiges ne sont pas biaisées par les visites de nids. Cependant, l'effet des perturbations causées par les activités de recherche pourrait être plus important chez des espèces d'oiseaux Arctiques qui sont incapables de défendre avec succès leurs nids contre les prédateurs ou lorsque la pression de prédation est très élevée.

Abstract

We assessed the effect of nest visits by researchers on the activity of nest predators and predation rate of eggs in a High Arctic greater snow goose (*Chen caerulescens atlantica*) colony. The study was conducted in years of moderate (1996) and low (1997) overall nest predation rate. We first compared activity rate (number of presences per h) and behavior of nest predators in the colony with and without investigator disturbance. In one year out of two, activity rate and time spent in the colony were higher during nest visits than under undisturbed conditions for glaucous gulls (*Larus hyperboreus*) and parasitic jaegers (*Stercorarius parasiticus*). Moreover, presence of investigators significantly increased (4.8 times) the probability of nest attack by predators in one year. Nevertheless, the immediate revisit technique showed that the percentage of goose eggs robbed by predators in monitored nests was low during a nest visit (<0.7% of eggs). In addition, we found no significant difference in mean clutch size at the end of incubation or nesting success between nests that were visited repeatedly (8 visits) and those less disturbed (<3 visits). Although some predators can be attracted by and take advantage of the presence of investigators, our results indicate that nesting parameters estimated for this snow goose colony are not biased by nest visits. However, the effect of investigator disturbance could be more important in other arctic nesting bird species that are unable to successfully defend their nest against predators or when predation pressure is very high.

Introduction

Disturbance by researchers can potentially bias measures of nesting parameters in birds. For instance, repeated visits to nests may increase nest abandonment or predation rates (Livezey 1980, Westmoreland and Best 1985). Although the "biological uncertainty principle" recognizes the possibility that observers may inadvertently influence nesting success, it is almost impossible to determine failure rates of nests without visiting them (Lenington 1979). In a review of the effect of nest visits on breeding birds, Götmark (1992) concluded that researchers seeking unbiased estimates of nesting parameters should evaluate their own impact. Nevertheless, there are still few studies that use adequate methods to determine the effect of nest visits (Mayer-Gross et al. 1997). In addition, many questions about the proximate mechanisms affecting nesting failure remain unanswered, particularly the impact of human activity on the behavior of nest predators (Strang 1980, Götmark et al. 1990, Götmark 1992, Mayer-Gross et al. 1997).

Many factors, including tolerance of the study species to disturbance, degree of disturbance, community of predators, and habitat structure, can influence the impact of nest visits (Major 1990, Götmark 1992, Hannon et al. 1993, Armstrong 1996, Olson and Rohwer 1998). The effect of the activity of researchers can also vary annually in relation to changes in biotic or abiotic factors (Ellison and Cleary 1978, White and Thurow 1985, Rodway et al. 1996, Ortega et al. 1997). Finally, species nesting in open habitats can be especially susceptible to disturbance by investigators because avian predators can more easily detect exposed eggs or people searching for nests (Götmark and Åhlund 1984).

We assessed the effect of nest visits by researchers on the activity of predators and predation rate in a High Arctic greater snow goose (*Chen caerulescens atlantica*) colony. First, we compared the activity rate and behavior of predators in the presence and absence of investigators in the colony. Second, we tested for potential loss of eggs as a result of displacement of territorial goose pairs during visits using the immediate revisit technique. Third, we evaluated the impact of nest visits on partial clutch predation by comparing mean clutch size of control nests (undisturbed) with that of nests visited several times. Finally, we compared nesting success of highly and lightly disturbed nests.

Study area and methods

We conducted the study in 1996 and 1997 at the migratory bird sanctuary of Bylot Island (72°53'N, 78°55'W), Nunavut Territory, Canada. We made observations and monitored nests in a large but patchy goose colony (typically > 4000 nests) located around a narrow valley (ca 0.5 km wide) surrounded by low hills with gentle slopes and extensive upland habitat. The nesting habitat had a low and sparse plant cover dominated by arctic willow (*Salix arctica*), bell-heather (*Cassiope tetragona*) and various graminoids (see Lepage et al. 1996 and Tremblay et al. 1997 for details of the areas).

The greater snow goose is a ground-nesting precocial species. It is single-brooded and does not renest after loss of a clutch (Lepage et al. 2000). Nest initiation is typically very synchronized, and about 90% of the nests are initiated within eight d (Lepage et al. 1996). Duration of incubation period is approximately 24 d (Poussart et al. 2000). Nest desertion is rare (estimated at < 2%, Tremblay et al. 1997), and predation is the main cause of nest failure for geese on Bylot Island (Lepage et al. 1996, Chapter 2). Goose nest predators are, in decreasing order of importance, arctic foxes (*Alopex lagopus*), parasitic jaegers (*Stercorarius parasiticus*), glaucous gulls (*Larus hyperboreus*), and common ravens (*Corvus corax*) (Chapter 2).

General field methods

Goose nests were found by systematic searches during the laying or early incubation period and marked with orange wooden sticks at a distance of 10 m from the nest. Eggs were individually marked with waterproof black ink. Nests were located with a Global Positioning System receiver (GARMIN GPS-75; ± 25 m). Local nest density was defined for each goose nest as the total number of nests found at any time within a 1-ha circle centered on the focal nest (minimum nest density according to this method was thus 1 nest ha^{-1}, see Lepage et al. 1996). This provided an index of spatial and temporal variations in nest aggregation and genuine nest density. Nest visits were conducted by two or three people walking close together (generally <30 m between each person) and eggs were covered with nest material at each visit. Typically, a researcher stayed a few minutes (<5 min) at a nest to collect data (count, mark, or weigh eggs or young). When a fox approached to 100 m of researchers during nest visits, they left the disturbed area until the fox moved far away (>1 km).

Response of predators

In 1996 and 1997, we compared the activity rate (number of presences per h) and behavior of predators in the goose colony during nest visits by investigators (treatment) and when investigators were absent (undisturbed conditions: control). All observations were conducted at one experimental plot (ca 50 ha) where conditions (habitat and nest dispersion) were typical of those encountered in the overall goose colony. Each year, four observation sessions of 240 min were conducted without investigator presence in the goose colony (1996: 24, 30 June, 4 and 6 July; 1997: 24, 28 June, 3 and 5 July) and were used as control. A total of five sessions were done during nest visits by investigators, i.e. the treatment (three sessions in 1996: 25, 26 June and 9 July; two sessions in 1997: 21 June and 6 July). Duration of observations for the treatment ranged from 90 to 180 min per session and was a function of the time that investigators were in the colony. Overall, 16 h of observations were conducted under undisturbed conditions in each year, and 6.25 and 5 h during nest visitations in 1996 and 1997, respectively. All sessions occurred during the incubation period between 0700 and 1100 because normal nest visits occurred between 0700 and 1800 and were concentrated in the morning.

Observations were conducted from a blind located at the highest elevation point in one corner of the experimental plot. Observations generally started 10 min after entering the blind because predators were unaffected by our presence as soon as we disappeared inside the blind. We recorded the number of predators staying within the plot for at least 1 min (including predators flying over the experimental plot). The 1-min criterion was used to eliminate the few observations of avian predators that were traveling at high speed across the plot and clearly not foraging. We noted the time spent in the plot (± 1 min). The behavior of predators was classified as "attack" (predator attempting to rob one or more goose nests during its presence) or "passage" (presence without nest attack). Although predators were not marked, individuals that were seen moving out and then back inside the plot were counted only once. No predators were breeding on the plot. We used binoculars to detect and identify predators and a spotting scope to determine the outcome of their attacks. Nest attacks were considered successful if at least one egg was preyed upon.

Immediate revisit technique

Goose nests used for the immediate revisit experiments (Sedinger 1990) will be referred to as the highly disturbed nests. All nests used in this experiment were located at >1 km from the 50 ha experimental plot used to study predator activity (see above). Following an initial visit to all nests, investigators moved far enough (>300 m) to allow nesting pairs to return to their territories. When virtually all pairs had returned (<30 min after the end of the initial visit), nests were immediately revisited. The number of eggs depredated between the two visits was recorded. In 1996 and 1997, we did immediate revisits three times during the incubation period (early, mid and late incubation stages). The behavior of geese in response to researchers visiting nests was recorded at nests randomly selected among the highly disturbed group (1997 only). We recorded the distance of the observer from the nest when the female flushed (estimated to nearest 5 m) and the presence or absence of nest material over the eggs when researchers arrived at the nest. Covered nests were defined as nests with >75% of the clutch covered by nest material.

Disturbance and partial clutch predation

In 1997, to evaluate the effect of nest visits on partial clutch predation, we compared mean clutch size of highly disturbed versus undisturbed nests. All undisturbed nests were located at >150 m from any disturbed area (150 m is the maximum distance at which females flushed when approached during incubation; see results). Highly disturbed nests were those monitored for the immediate revisit experiment and were visited a total of eight times, once at the end of laying and seven times during the incubation period (including three revisits). Undisturbed nests were visited only once at the end of the incubation to sample clutch size, and no nest markers were used. We compared the date at which incubation started (incubation date) for a random sample of undisturbed and disturbed nests. Incubation date was determined using a linear relationship between an egg density index [mass/(length x breadth)^2] and stage of incubation (Lepage et al. 1996, Gauthier, unpubl. data). In Greater Snow Geese, there is a steep seasonal decline in clutch size (–0.20 egg day^{-1}, Lepage et al. 2000). Because median incubation date did not differ either between undisturbed and highly disturbed nests (Wilcoxon's rank sum test: 14.5 June, range 10-20, n = 19 and 14 June, range 10-21, n = 38, respectively; $Z = -0.33$, $P = 0.74$), we assumed that these two groups had the same initial mean clutch sizes.

Disturbance and total nest failure

To evaluate the effect of nest visits on total nest failure, we compared nesting success of lightly and highly disturbed nests in 1997. Lightly disturbed nests were visited only once or twice during incubation. Highly disturbed nests were those used for the immediate revisit experiment and were visited seven times during incubation (see above). All nests were found during the laying or early incubation period and were visited during the hatching period to determine their fate. A nest was considered successful if at least one egg hatched. For nests found after the laying period, laying date (start of egg laying) was determined by estimating incubation stage (see above) or by backdating from hatching date (Lepage et al. 1999). Total clutch size was defined as the total number of eggs marked in a nest. Nests completely depredated during egg laying were excluded from analysis of clutch size.

Data analysis

Generalized Linear Models (procedure GENMOD of SAS Institute Inc. 1996) were used to examine the response of predators to investigator presence in the colony. Poisson regressions were used to model the activity rate of predators. Poisson regressions are well suited for counts where the variance increases with the mean, as was the case here (Agresti 1996). The loglinear model used was

$$\log(\mu) = \log(\mathrm{dr}) + \beta_0 + \beta_1\,(\mathrm{Year}) + \beta_2\,(\mathrm{Treatment}) + \beta_3\,(\mathrm{Year{*}Treatment})$$

where μ is the expected number of predators observed, dr is the duration of observation (min), and β_i are the regression coefficients. The model included the variables Year (1996 = 1, 1997 = 0), Treatment (nest visit = 1, control = 0) and the interaction term. The deviance was used to evaluate model fit (Agresti 1996). Overdispersion (defined as greater variability than predicted by the random component of the model) is common in the modeling of Poisson counts (Agresti 1996). If data were overdispersed (deviance/df >2), we used an overdispersion parameter to adjust standard errors and likelihood ratio statistics (DSCALE option of the GENMOD procedure). Standard errors of parameter estimates are inflated in models using an overdispersion parameter (SAS Institute inc. 1993: 32), which increases risks of type II error. In these cases, we also analyzed each year separately and suppressed the overdispersion parameter if the data fitted the model well (deviance/df <2). Likelihood ratios were used to test the significance of a variable in the model with other variables already included. If the interaction term was not significant, it was deleted from the model. Exponentiating the slope (β)

associated with the treatment variable gave the ratio of predator activity rate observed in the treatment relative to control (a ratio of 1 means no effect of treatment, Agresti 1996). The 95% confidence intervals for parameters were based on the profile likelihood function (LRCI option of the GENMOD procedure). The length of time predators stayed in the plot was compared using Wilcoxon's rank sum tests (Siegle and Castellan 1988:128). In this analysis, we pooled data for all sessions of observation for control and treatment to increase sample size.

We used logistic regression (LOGISTIC procedure, SAS Institute Inc. 1996) to evaluate the impact of investigator presence in the colony on the probability of nest attack by a predator (attack = 1, passage = 0). This model incorporated the variables Year (1996 = 1, 1997 = 0), Treatment (nest visit = 1, control = 0) and the interaction term. If the interaction term was not significant, it was deleted from the model. Because the total number of attacks was low (zero cell count: Hosmer and Lemeshow 1989:126), we pooled data for all predator species and sessions of observation for control and treatment. Exponentiating the slope (β) associated with the treatment gave the ratio of the treatment effect relative to control (a ratio > 1 means that probability of nest attack by predators is higher for treatment relative to control). The RISKLIMITS option of the LOGISTIC procedure was used to obtain the 95% Wald confidence intervals for these ratios.

Laying dates were compared using Wilcoxon's rank sum tests. We compared mean nest density and mean clutch size using *t*-tests. When variances were heteroscedastic, an approximate *t*-test based on unequal variances was used to test for differences in group means. Logistic regression was also used to evaluate the effect of repeated nest visits on nesting success (success = 1, failure = 0). This model incorporated the variables Type (highly disturbed nests = 1, lightly disturbed nests = 0), Density (nest density calculated for each goose nest) and the interaction term. Because we showed in an earlier analysis that the fate of a goose nest is independent of the fate of its nearest neighbors (Chapter 2), we considered each goose nest as an independent observation in all analyses. Statistical tests were two-tailed and significance levels were set at 0.05. Values provided are mean ± SE unless stated otherwise.

Results

Percentage of successful nests in the monitored colony was near average in 1996 (61%) and high in 1997 (86%; 1994 to 1999: mean ± SD = 60 ± 24%, range = 22 to 86%, Chapter 2). Goose nest density was higher in 1997 than in 1996, with 5.7 ± 0.2 and 4.2 ± 0.2 nests ha^{-1}, respectively ($t = 5.59$, df = 539, $P < 0.0001$; 1994 to 1999: mean ± SD = 5.5 ± 1.1, range = 4.1 to 6.7, Chapter 2).

Response of predators

The impact of investigator presence on the activity rate of avian predators was variable across predator species and years (Figure 1, Table 1). In 1997, the activity estimate for glaucous gulls was 11.9 times (95% CI: 5.5 to 29.7) higher during nest visits than under undisturbed conditions. However, activity of gulls was not affected by nest visits in 1996 (ratio = 0.7, 95% CI: 0.3 to 1.6). In contrast, we detected a slight increase in parasitic jaeger activity rate during nest visits only in 1996 (ratio = 2.6, 95% CI = 1.18 to 5.57). No significant effect of investigator presence on the activity of ravens was detected. In 1997, gulls and jaegers spent more time in the plot during nest visits than under undisturbed conditions (gulls, 3.7 ± 0.7 min [n = 26] vs 1.1 ± 0.2 min [n = 7], $Z = 2.77$, $P = 0.006$; jaegers, 2.3 ± 0.9 min [n = 3] vs 1.2 ± 0.1 [n = 18], $Z = 1.96$, $P = 0.05$, respectively for disturbed and undisturbed conditions). The time spent in the plot was not significantly affected by investigator disturbance for ravens in 1997 and all avian predator species in 1996 (all $P > 0.10$). The total number of arctic foxes observed on the experimental plot was too low (n = 12) to allow statistical analysis.

About 10% of predator observations in the colony resulted in attacks on goose nests (Table 2). The impact of nest visits on the behavior of predators was different in 1996 and 1997 (as shown by the significant interaction term, Table 3). In 1997, the probability that a predator attacked a nest was 4.8 times (95% CI: 1.4 to 17.0) higher during nest visits than during undisturbed conditions. In contrast, the probability of attack tended to be lower during nest visits in 1996 but the difference was not significant (ratio = 0.4, 95% CI: 0.1 to 1.6). Nevertheless, the total number of successful attacks was low in both years. In 1996, only two out of four nest attacks observed during nest visits were successful compared to five out of 17 under undisturbed conditions. Comparable figures in 1997 were three successes out of 11 nest attacks during nest visits and zero out of five under undisturbed conditions.

Immediate revisit technique

Female geese flushed from their nest when an investigator approached (flushing distance: 75 ± 5 m, range: 15-150 m, n = 32). When disturbed, some females covered their nest with material before leaving (32%, 41% and 47% of the females during the early [n = 95], mid [n = 95] and late [n = 94] incubation periods, respectively). Typically, males and females stayed within 150 m when an investigator was around their nest and they came back near their nest (<10 m) less than 10 min after the investigator's departure. Virtually all nesting pairs were at their nest, or close to it, after 30 min. In both 1996 and 1997, nest predation was rare during nest visits by investigators. Predation events that occurred during a nest visit were always partial clutch losses of 1 egg/nest. Percentage of eggs lost during nest visits ranged from 0.0 to 0.7% and did not vary within incubation stage or between years (Table 4).

Disturbance and partial clutch predation

Average clutch size of highly disturbed nests declined slightly during the incubation period (early incubation: 3.9 eggs ± 0.1, end of incubation 3.8 eggs ± 0.1, paired *t*-test: $t = 2.5$, $P = 0.01$, n = 94). Nest density did not differ between undisturbed (5.7 ± 0.4 nests ha^{-1}, n = 63) and highly disturbed nests (4.9 ± 0.2, n = 94) at the end of incubation ($t = 1.54$, df = 100.4, $P = 0.13$). Despite repeated nest visits, we did not detect difference in average clutch size recorded at the end of the incubation period between undisturbed (3.8 eggs ± 0.1, n = 63) and highly disturbed nests ($t = 0.04$, df = 155, $P = 0.97$; difference between means: 0.006, 95% CI: –0.345 to 0.357). We considered a difference in clutch size of 0.38 egg (10%) as a minimum for a biologically significant effect in our system (see Steidl et al. 1997). This value is lower than the inter-annual variations observed in clutch size (1994 to 1999; mean ± SD = 3.8 ± 0.4 eggs, range = 3.1 to 4.2 eggs, Chapter 2). Because the 95% confidence interval of the observed difference between means excludes this value, we therefore consider the null hypothesis of no biologically significant effect of nest visits on partial nest predation to be true.

Disturbance and total nest failure

At the beginning of incubation, mean nest density was slightly higher in lightly disturbed nests (5.7 ± 0.2 nests ha^{-1}, n = 291) than in highly disturbed nests (5.0 ± 0.2, n = 98; $t = 2.33$, df = 225.6, $P = 0.02$). Median laying date was similar between the two groups (10 June, range 8-13, n = 291, for lightly disturbed and 11 June, range 7-19, n = 39, for highly disturbed; $Z = 1.10$, $P = 0.27$). Mean initial clutch size was slightly higher for lightly disturbed nests (4.2 ± 0.1, n = 258) than for highly disturbed nests (4.0 ± 0.1, n = 95) ($t = 1.96$, df = 351, $P = 0.05$). Nesting success was not related to nest density ($\chi^2 = 0.16$, df = 1, $P = 0.69$) and did not differ between highly (87.8%, n = 98) and lightly disturbed nests

(85.6%, n = 285; $\chi^2 = 0.46$, df = 1, $P = 0.50$; interaction term, $P = 0.88$, was dropped from the model). If we again consider a difference of 10% as a minimum for a biologically significant effect, then the 95% confidence interval of the observed difference between nesting success in highly disturbed and lightly disturbed areas (2.2%, 95% CI: –5.5 to 9.9%) excludes this value. This threshold of 10% is much lower than the inter-annual variations observed in snow goose nesting success (see above). We therefore consider the null hypothesis of no biologically significant effect of repeated nest visits on nesting success to be true.

Discussion

We found that presence of researchers in a greater snow goose colony affected the activity of nest predators (glaucous gulls and, to a lesser extent, parasitic jaegers) but these effects were variable among years. Moreover, investigator presence increased the probability of nest attack by predators in only one year out of two. Few papers have reported data on the behavior of nest predators in response to visits by researchers (Götmark 1992, Mayer-Gross et al. 1997). Previous studies also suggested that jaegers and gulls could be attracted to disturbed areas in open habitats and sometimes take eggs in unattended nests of other waterfowl species (Strang 1980, Götmark and Åhlund 1984). Unlike Götmark and Åhlund (1984), we did not find evidence that corvids were repelled by human presence at our study site.

Despite the effect of human presence in the colony on the behavior of predators, our observations showed that nest visits had little effect on greater snow goose nest predation. First, few successful nest attacks by predators were observed during nest visits. Second, the percentage of eggs depredated during nest visits was extremely low (<0.7 %) in both years of the study. Third, mean clutch size at the end of incubation did not differ between highly disturbed and undisturbed nests. Finally, repeated nest visits did not reduce nesting success. Therefore, even if predators can sometimes rob a few eggs during nest visits, the overall impact on nesting parameters seems to be low. However, because we lack spatial replications of our experiments and we conducted our study in years of moderate to low nest predation rate, we must be careful with generalization to other areas and years.

Under undisturbed conditions, greater snow goose breeding pairs are highly attentive to their nests (Reed et al. 1995) and females cover their eggs with nest material before departing for a recess. They can successfully defend their clutch against foxes and avian predators when they are at their nest or close to it (<10 m; Chapter 2). However, when researchers visit nests, nesting pairs vacate their territory and leave their clutch without protection. Consequently, human presence in the colony creates a temporary disturbed area with many exposed nests. Avian nest predators, because of their high mobility, can rapidly find this potential source of food in open habitats. Because the number of unattended nests located in the disturbed area mainly depends on local nest density and nest aggregation, human presence can create more opportunities for predators at high nest density. As goose nest density was higher in 1997, this might explain why activity of avian nest predators was more influenced by investigator disturbance in that year than in 1996.

Overall abundance of predators and availability of alternative prey might also have an effect on the response of predators to disturbance created by investigators. The activity rate of gulls and jaegers observed in the goose colony under undisturbed conditions (control) was very similar in 1996 and 1997 (Figure 1), a pattern that was confirmed by additional observations conducted over the whole 24-h period (Bêty and Gauthier, Chapter 3). This suggests that changes in predator abundance did not contribute to between-year variation in the response of avian predators to human disturbance. In the arctic tundra, the abundance of lemmings, the primary prey of many predator species, follows fairly regular cycles of three to five years (Krebs 1964, Sittler 1995). These fluctuations can affect the predation pressure on nesting birds and predation intensity is generally higher when lemmings are scarce (Martin and Baird 1988, Underhill et al. 1993, Chapter 2). At our study site, lemming abundance reached a peak in 1996 but declined considerably in 1997 (2.34 versus 0.91 lemmings 100 trap-nights^{-1}, Chapter 2). Therefore, differences in response of predators to investigator disturbance in the colony might also be explained by variations in the availability of alternative prey for nest predators. However, despite the large difference in lemming abundance, egg loss during nest visits was low in both years of the study.

Many researchers have pointed out that mammal like foxes may discover nests by following human tracks in the vegetation or human scent (Götmark 1992). However, there is little evidence that researcher disturbance increases mammalian predation rates (Götmark 1992, Skagen et al. 1999, Lloyd et al. 2000). We believe that human trails or scent did not increase the predation rate by foxes at our study colony for several reasons. First, we frequently walked criss-crossing paths inside and outside the colony (up to 3 km from any goose nest) to accomplish activities other than nest visits. Under such circumstances, it could be unprofitable for scent predators to follow human trails, as suggested by Hannon et al. (1993). Second, predators must associate human tracks or scent with food (Götmark

1992). Even if foxes could find a nest by following human scent, the probability of robbing eggs remains low if parents are at the nest, which reduces the likelihood that foxes could associate human scent with food. However, if arctic foxes are already present in the colony during nest visits, they can rapidly take advantage of the displacement of territorial pairs to rob eggs, as some foxes were not afraid by investigators (JB, pers. obs.). Thus, the temporary interruption of nest visiting that we made when a fox was close to investigators (<100 m) most likely reduced the impact of disturbance on nest predation.

Conclusions

Our observations confirm that nest predators can be attracted by and take advantage of investigator presence in a greater snow goose colony. Nevertheless, our results show that few eggs were robbed during nest visits at our study site in years with moderate to low nest predation. Several factors could contribute to this low impact. First, parents came back close to their nest rapidly after visits. Second, they can successfully protect their nest against predators. Third, precautions were taken during nest visits to reduce opportunities for predators. In our annual nest monitoring program, goose nests are generally found during the laying period, visited once during incubation, and revisited during hatching to determine their fate (Lepage et al. 2000). Our results suggest that activities of researchers do not bias nesting parameters obtained in this way. However, the effect of investigator disturbance could be more important in other arctic nesting bird species that are less tenacious to their nest, unable to successfully defend their nest against predators, or that rely more on cryptic nests for defense against predators.

TABLE 1. Regression models[a] estimating the impact of nest visits (treatment) on the activity rate of avian predators observed in a greater snow goose colony during the incubation period, Bylot Island, Nunavut Territory, 1996-1997.

Predator species	Year	Variables	df	ß	SE	χ^2	*P*
Glaucous gull	1996-97	Intercept	1	-4.92	0.38		
		Year	1	1.15	0.43	0.75	0.385
		Treatment	1	2.48	0.43	10.12	0.002
		Year*Treatment	1	-2.84	0.63	25.28	<0.001
Common raven	1996-97	Intercept	1	2.98	0.14		
		Year	1	-0.46	0.20	5.42	0.020
		Treatment	1	-0.09	0.23	0.16	0.685
		Year*Treatment	1	0.21	0.46	0.20	0.653
Parasitic jaeger	1996	Intercept	1	4.30	0.28		
		Treatment	1	0.94	0.40	5.54	0.02
	1997	Intercept	1	-3.92	0.44		
		Treatment	1	-0.68	1.20	0.38	0.54

[a] Models assume that predator number follows a Poisson distribution. The fit of the full model was satisfactory for the gull and raven data (deviance = 15.4 and 12.5, respectively, df = 9). A correction for overdispersion was used for the parasitic jaeger data in 1997 (deviance = 15.0, df = 4) but not in 1996 (deviance = 5.2, df = 5).

TABLE 2. Behavior of nest predators at a greater snow goose colony during nest visits by investigators (treatment) and in the absence of investigator disturbance (control), Bylot Island, Nunavut Territory, 1996-1997.

	1996		1997	
Behavior	Control	Treatment	Control	Treatment
Attack[a]	14 (14%)	3 (7%)	4 (4%)	8 (17%)
Passage[b]	83 (86%)	41 (93%)	92 (96%)	38 (83%)
Total	97	44	96	46

[a] Predator attempting to rob ≥1 goose nest during its presence in the colony.
[b] Presence of a predator in the colony without a nest attack.

TABLE 3. Logistic model estimating the impact of nest visits (treatment) on the probability of nest attacks by predators in a greater snow goose colony during the incubation period, Bylot Island, Nunavut Territory, 1996-1997.

Variables	df	ß	SE	χ^2	*P*
Intercept	1	-3.14	0.51	37.69	< 0.001
Year	1	1.36	0.59	5.34	0.02
Treatment	1	1.58	0.64	6.04	0.01
Year*Treatment	1	-2.41	0.92	6.82	0.009

TABLE 4. Number of eggs lost during visits to greater snow geese nests. Numbers estimated by the immediate revisit technique conducted during early, mid and late incubation stages, Bylot Island, Nunavut Territory, 1996-1997.

			No. of eggs		
Incubation Stage	Year	n[a]	Before	After	Lost
Early	1996	88	301	300	1
	1997	95	374	374	0
Mid	1996	85	285	283	2
	1997	95	368	367	1
Late	1996	82	275	275	0
	1997	94	360	359	1

[a] n = number of nests

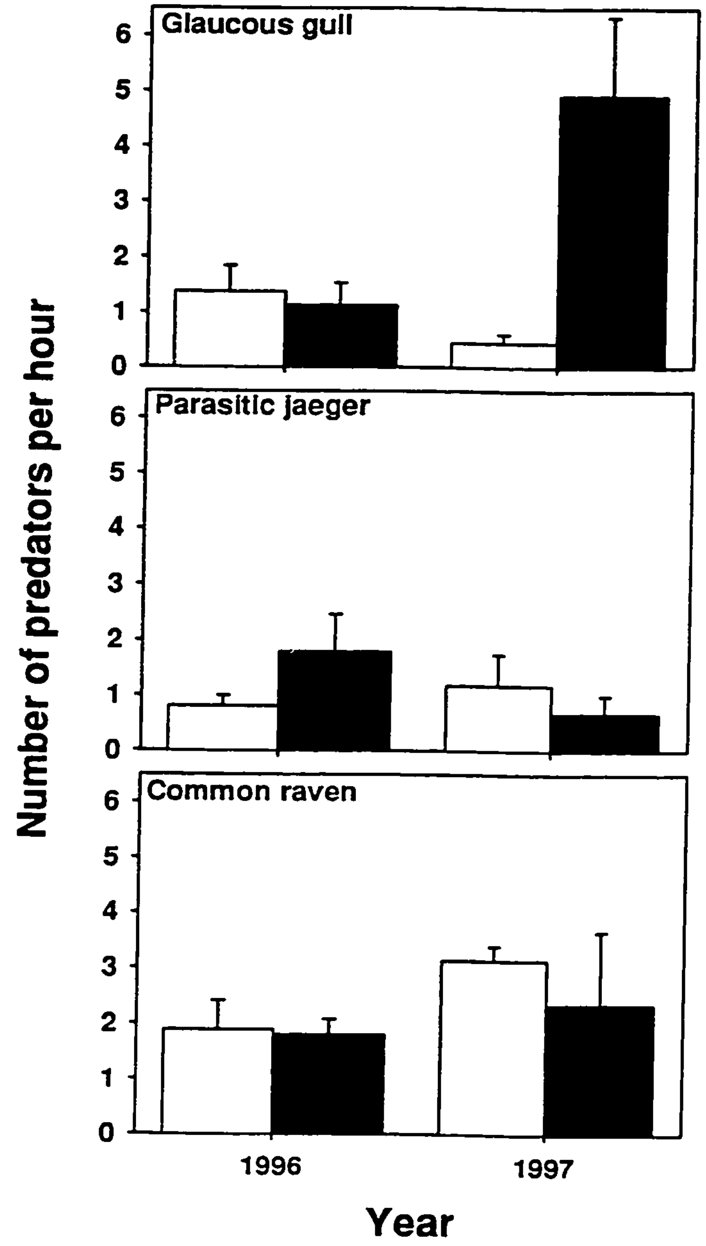

FIGURE 1. Activity rate of avian predators (mean ± SE number of predators observed per hour) at a greater snow goose colony during nest visits by investigators (treatment: black bars) and in absence of investigator disturbance (control: white bars) during the incubation period, Bylot Island, Nunavut Territory, 1996-1997 (control, n = 4 in both years, treatment, n = 3 in 1996 and n = 2 in 1997).

Chapitre 2

ARE GOOSE NESTING SUCCESS AND LEMMING CYCLES LINKED? INTERPLAY BETWEEN NEST DENSITY AND PREDATORS

Bêty, J., Gauthier, G., Giroux, J.-F. and Korpimäki, E. 2001. Oikos. 93: 388-400.

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Résumé

Le lien entre les cycles de lemmings et les variations du succès reproducteur des oiseaux de l'Arctique serait possiblement causé par des variations de la pression de prédation (l'Hypothèse des Proies Alternatives, HPA) et une association bénéfique avec des oiseaux de proies (l'Hypothèse d'Association, HA). Nous avons utilisé des données récoltées au cours de deux cycles de lemmings pour évaluer si les fluctuations de densité de lemmings étaient associées au succès de nidification des Grandes Oies des neiges (*Chen caerulescens atlantica*) nichant dans le Haut-Arctique canadien. Nous avons testé certaines prédictions des deux hypothèses, HAP et HA, chez des oies nichant à basse et à haute densité. Le succès de nidification des oies a varié de 22% à 91% entre les années et le principal prédateur des œufs était le Renard arctique (*Alopex lagopus*). La nidification en association avec des Harfangs des neiges (*Nyctea scandiaca*) a été observée seulement lors des années de pic d'abondance de lemmings chez les oies nichant à basse densité. Le succès de nidification des oies diminuait progressivement avec l'augmentation de la distance par rapport aux harfangs et atteignait un plateau à 550 m. Des expériences avec des nids artificiels indiquent que les harfangs peuvent exclure les prédateurs autour de leurs nids et ainsi réduire le taux de prédation sur les œufs d'oie. Le taux annuel de succès des nids d'oies était positivement associé avec l'abondance de rongeurs et généralement plus bas lors des années de faible abondance de lemmings. Cette relation était présente même après l'exclusion des nids d'oies sous l'effet de la protection des harfangs. Cependant, à haute densité de nids, le taux d'échec était inversement dépendant de la densité. En conséquence, les variations annuelles de la densité des nids d'oies ont influencé la synchronie entre les cycles de lemmings et les oscillations du succès de nidification. Nos résultats indiquent que i) HPA est le principal mécanisme qui lie les cycles de lemmings et le succès de nidification des oies et que ii) l'effet bénéfique d'association avec des rapaces lors des pics d'abondance de lemming (HA) agit localement. Cette étude suggère aussi que les stratégies de reproduction utilisées par les oiseaux (la proie alternative) peuvent influencer la synchronie entre les oscillations de leur succès reproducteur et les cycles de rongeurs.

Abstract

The suggested link between lemming cycles and reproductive success of arctic birds is caused by potential effects of varying predation pressure (the Alternative Prey Hypothesis, APH) and protective association with birds of prey (the Nesting Association Hypothesis, NAH). We used data collected over two complete lemming cycles to investigate how fluctuations in lemming density were associated with nesting success of greater snow geese (*Chen caerulescens atlantica*) in the Canadian High Arctic. We tested predictions of the APH and NAH for geese breeding at low and high densities. Goose nesting success varied from 22% to 91% between years and the main egg predator was the arctic fox (*Alopex lagopus*). Nesting associations with snowy owls (*Nyctea scandiaca*) were observed but only during peak lemming years for geese nesting at low density. Goose nesting success declined as distance from owls increased and reached a plateau at 550 m. Artificial nest experiments indicated that owls can exclude predators from the vicinity of their nests and thus reduce goose egg predation rate. Annual nest failure rate was negatively associated with rodent abundance and was generally highest in low lemming years. This relationship was present even after excluding goose nests under the protective influence of owls. However, nest failure was inversely density-dependent at high breeding density. Thus, annual variations in nest density influenced the synchrony between lemming cycles and oscillations in nesting success. Our results suggest that APH is the main mechanism linking lemming cycles and goose nesting success and that nesting associations during peak lemming years (NAH) can enhance this positive link at the local level. The study also shows that breeding strategies used by birds (the alternative prey) could affect the synchrony between oscillations in avian reproductive success and rodent cycles.

Introduction

In arctic tundra and northern Europe, vole (*Clethrionomys* and *Microtus* spp.) and lemming (*Lemmus* and *Dicrostonyx* spp.) populations vary enormously in size over time and these fluctuations follow fairly regular cycles of three to five years (Krebs 1964, Hanski and Korpimäki 1995). Marked between-year variations in the reproductive success of several species of arctic ground-nesting birds have also been observed and related to cyclical changes in the abundance of small mammals (e.g. Summers 1986, Martin and Baird 1988, van Impe 1996). Two non-exclusive hypotheses have been proposed to explain this potential link.

The Alternative Prey Hypothesis (APH) states that the link is caused by a varying annual predation pressure on alternative prey resulting from the functional and numerical responses of predators to rodent densities (Lack 1954, Angelstam et al. 1984). When rodent (main prey) densities are high, predators primarily feed on them, reach high breeding densities and produce large litters. When the main prey populations decrease, predators turn to eggs and young of birds (alternative prey) and produce few or no young. Consequently, alternative prey should suffer most from predation during the decline and low phase of the rodent cycle.

The Nesting Association Hypothesis (NAH) states that some arctic bird species improve their reproductive success by nesting in association with birds of prey (Underhill et al. 1993, Lepage et al. 1996). Enhanced protection of eggs against predators gained by arctic geese and ducks nesting within the territories of aggressive birds of prey such as rough-legged hawks (*Buteo lagopus*) and snowy owls (*Nyctea scandiaca*) is well documented (e.g. Syroechkovskiy et al. 1991, Summers et al. 1994, Kostin and Mooij 1995). These nomadic, specialist predators are common in an area when lemmings are abundant but rare or absent when lemmings are scarce (Potapov 1997, Wiklund et al. 1998). Consequently, this opportunistic, protective association could be a mechanism driving the relationship between fluctuations in reproductive success of arctic birds and lemming cycles.

Density of breeding birds may also influence the link between rodent cycles and nest predation rate. Nest density affects predation rate (i.e., depredated nests/total) in numerous bird species (Newton 1998) and fluctuations in the availability of alternative prey for predators can lead to selection for different nesting densities (e.g. solitary vs colonial nesters: Hogstad 1995). Moreover, foraging theory predicts that changes in the predator-prey community could potentially determine the range of nest densities that results in profitable foraging by nest predators and thus influence the spatial and temporal patterns in nest predation rate (Schmidt 1999).

The suggestion of a link between lemming cycles and reproductive success of arctic birds is mostly based on winter observations of bird populations. Direct observations on the impact of fluctuations in lemming populations on bird nest predation pressure are scarce (Spaans et al. 1998), and the potential effects of varying predation pressure (APH) and association with birds of prey (NAH) are confounded in many studies (e.g. Syroechkovskiy et al. 1991, Underhill et al. 1993, Kostin and Mooij 1995). We studied the highly dynamic interaction between lemmings, predators and birds in a high-arctic-nesting species, the greater snow goose (*Chen caerulescens atlantica*). We used data collected over two complete lemming cycles to investigate whether oscillations in lemming population and goose nesting success were linked at both low (small colonies) and high (large colony) breeding densities. We tested predictions of the APH and NAH to evaluate which of these two mechanisms could best explain the relationship between lemming cycles and nest predation rate. Based on the APH, we predicted that predation rate on goose nests would be related to lemming abundance even in absence of birds of prey. More specifically, we expected that predation on nests would be lower during peak lemming years than during years of low lemming abundance. Based on the NAH, we predicted that predation rate would be lower for geese nesting in association with birds of prey than for those nesting without association in high lemming years.

Material and methods

Study area and species

We conducted the study at the Bylot Island migratory bird sanctuary, Nunavut Territory, Canada (73° 08' N, 80° 00' W), the most important breeding site of greater snow geese (>25 000 pairs in 1993: Reed et al. 1998). Data were collected at two nesting areas separated by 30 km, Site-1 (ca 50 km^2) and Site-2 (ca 16 km^2). Geese nested at low density at Site-1 (typically in groups of 10 to 20 nests, occasionally up to 300; also isolated nests) in comparison to high density at Site-2 (large patchy colony, typically >4000 nests). The Site-1 area is a large glacial valley (2-5 km wide) bordered by steep hills to the north and southeast, and rolling hills to the southwest. The Site-2 area is located around a narrow valley (ca 0.5 km wide) surrounded by low hills with gentle slopes and extensive upland habitats (see Lepage et al.

1996 and Tremblay et al. 1997 for details of the areas). Density of other land birds at these two sites is low compared to geese (see Lepage et al. 1998, Gauthier et al. 1996).

The greater snow goose is a ground-nesting precocial species. It is single-brooded and does not renest after a failure of a clutch (Lepage et al. 2000). Nest desertion is rare (estimated at <2%, Tremblay et al. 1997) and predation is the main cause of nest failure on Bylot Island (Lepage et al. 1996). As laying progresses, nest attentiveness by the female increases and time spent on the nest by incubating females averages 92% (Poussart et al. 2000). During the brief incubation recesses, females are accompanied by their mate, remain close to their nest (usually <20 m) and feed most of the time (Reed et al. 1995).

Goose egg predators in the two study areas include glaucous gulls (*Larus hyperboreus*), common ravens (*Corvus corax*), parasitic and long-tailed jaegers (*Stercorarius parasiticus* and *S. longicaudus*), and arctic foxes (*Alopex lagopus*). All avian predators are generalist except breeding long-tailed jaegers which depend primarily on lemmings (Maher 1970, Hussell and Holroyd 1974, Fitzgerald 1981, Wilson 1999). Arctic foxes are also generalists although their diet is heavily dependent on lemmings (Macpherson 1969, Angerbjörn et al. 1999).

Nesting associations with snowy owls and rough-legged hawks occur on our study area (Lepage et al. 1996, Tremblay et al. 1997). The presence of snowy owls has a strong effect on the location of goose colonies at Site-1. Owl nests are initiated ≥2 weeks earlier than goose nests (Lepage et al. 1996). Two species of lemmings co-exist on our study area. The brown lemming (*Lemmus sibiricus*) occurs in wet lowlands (polygon fen) whereas the collared lemming (*Dicrostonyx groenlandicus*) prefers dry upland habitat (Gauthier et al. 1996). Adults brown and collared lemmings weigh 40-100 g (Krebs 1964, Wilson 1999) and a fresh goose egg 90-130 g.

Goose nesting parameters

Goose nests were monitored from 1993 to 1999 at Site-1 and from 1994 to 1999 at Site-2. Nests were found by systematic searches during laying or early incubation period and mapped with a Global Positioning System receiver (± 25 m). Nests were marked with orange wood sticks at a distance of 10 m and eggs were individually marked with waterproof black ink. Nests were revisited in the first half of incubation, during the hatching period and after goslings had left in order to determine their fate. A nest was considered successful if at least one egg hatched. Total clutch size was defined as the maximum number of eggs found in a nest, after the start of incubation. For nests found after the laying period, laying date (date for laying the first egg) was determined by estimating incubation stage, or by backdating from hatching date (see Lepage et al. 1999 for details). Nest density was defined for each goose nest as the number of nests within a 1-ha circle centred on the focal nest (minimum nest density according to this method was thus 1 nest ha^{-1}). Mean nest density was calculated separately for each nesting area and year. This provided an index of spatial and temporal variations in nest aggregation and genuine nest density. Some nests found during late incubation period were not used for the calculation of nesting parameters (e.g. success, clutch size) but were used to characterize nest distribution and evaluate nest density. Including all nests found at any time during the nesting season provides a better estimate of the maximum nest density.

Nest predators

From 1996 to 1999, we conducted behavioural observations at Site-2 during the incubation period in a plot (ca 50 ha) where conditions (habitat and nest dispersion) were typical of those encountered in the goose colony monitored. This allowed us to observe a large number of goose nests (>125). Each year, we did 24 4-h observation sessions systematically rotated throughout the 24-hour cycle. We recorded all attacks by predators attempting to rob goose nests. We used binoculars (7×35) to detect and identify predators and a spotting scope (20-60×) to determine the outcome of their attacks. Nest attacks were considered successful if at least one egg was preyed upon. The low nest density precluded direct observations at Site-1. However, previous observations suggest that the relative importance of predators is similar at both sites (Lepage et al. 1996, Tremblay et al. 1997).

Lemming abundance

Lemming abundance was estimated in July from 1994 to 1999 with snap-trap censuses at Site-1. Trapping was done in two study plots representing the two main habitat types (wet lowland and dry upland), except in 1994 (only one plot in wet lowland). In each plot, 50 Museum Special traps baited with peanut butter and rolled oat were set every 10 m on two line transects (100 m apart) for 10-11 d and were checked once a day (Shank 1993). We standardised the total number of lemmings trapped over the whole period to the number of animals caught per 100 trap-nights (= lemming index). We subtracted 0.5 night for each sprung trap to improve estimates of sampling effort and control for sitespecific rates of trap-springing (Beauvais and Buskirk 1999). Similar trapping conducted from 1997 to 1999 at Site-2 showed a high spatial synchrony in the phase of the lemming cycle between the two goose nesting areas (see Results). Synchrony at the regional scale is typical in lemmings (Erlinge et al. 1999). We therefore considered our estimate of lemming abundance obtained at Site-1 as a general index of lemming abundance on the two study areas.

In 1993, lemming abundance was based on density of lemming winter nests, which is well correlated with early summer lemming density (Wilson 1999; see also Sittler 1995). Lemming nest surveys were conducted on Bylot Island in 1993 and 1996 at two sites of 100 ha and 50 ha, respectively (3.72 and 2.52 nests ha^{-1}, respectively: Olivier Gilg unpubl. data; see Sittler 1995 for details of the method). The ratio of lemming abundance to nest survey obtained in 1996 was applied to the 1993 nest survey to estimate lemming abundance that year. As the number of snowy owls is positively correlated with lemming abundance in the Arctic tundra (Wiklund et al. 1998), we also validated our estimate with the number of owl nests found during these 2 years.

Artificial nest experiments

Goose eggs were simulated with domestic chicken eggs, which are smaller but similar in shape and colour. Three eggs were placed in simulated nest bowls and covered with goose down collected in nests during previous years. Nest locations were marked with short bamboo canes. Rubber gloves were worn during nest deployment and visit. Artificial nests were not used to estimate predation rate on natural nests but were used in conjunction with real nest data to provide an index of spatial variation in predation risk (see Berg 1996, Valkama et al. 1999).

We conducted an experiment to test the hypothesis that owls reduce predation risk on goose eggs around their nest. The experiment was replicated around two snowy owl nests in different years. In each replicate, five artificial nests were distributed at 5, 30, 50, 100 and 150 m along four perpendicular transects starting at the owl nest and twenty other nests were similarly placed in a control area 2 km away from the owl nest. To avoid straight patterns of distribution, we placed nests at varying distance on either side of line transects. Nests were located in upland habitats and checked after 1, 2, 3, 4, 6, 8, 11 and 17 d of exposure. A nest was considered depredated when at least one egg had been destroyed or removed.

We tested at Site-2 the hypothesis that geese can protect conspecific nests at high breeding density by defending their own nest surroundings. Four artificial nests were placed at 5, 10, 20 and 30 m along 30-m-long transects, each transect starting at a different goose nest and running away from it. The minimum distance of 5 m was used because over 98% of goose nests were separated by >5 m at both nesting areas. Transects were oriented so that minimum distance with other goose nests was >30 m. We placed ten transects at mid-incubation and repeated the experiment 6 d later with 20 additional transects for a total of 120 artificial nests at 30 different goose nests. Transects were set from 19.00 to 21.00. All nests were revisited after 2 and 5 h of exposition to predators.

Statistical analyses

Laying dates (expressed in Julian date, 1 = 1 January) were compared using Kruskal-Wallis test (Siegel and Castellan 1988). We used *t*-test to compare mean clutch size and nest density. When variances were heteroscedastic, an approximate *t*-test based on unequal variances was used. Correlation analyses were made using Spearman rank correlation (r_s). To increase sample size in the correlation analysis of mean nest density and median laying date, we combined our data to those of Lepage et al. (1996) collected at the same study sites.

We used multiple linear regression (procedure GLM of SAS Institute Inc. 1996) to examine the relationship between relative laying date (deviation from the median laying date in each year), relative clutch size (deviation from mean clutch size) and distance from the nearest snowy owl nest. Models also included year as independent variable. Generalised Linear Models (procedure GENMOD of SAS) with logit link function were used to perform logistic regression analyses. We first evaluated the relationship between goose nesting success (success = 1, failure = 0) and distance from owls using logistic regression model including variables distance, year and nest density. Type 3 contrasts using the likelihood ratio statistics were used to test the significance of a variable in models with other variables already included. If an interaction term was not significant, it was deleted and the model was rerun. Interactions were deleted one at a time from higher to lower levels, until only significant interactions remained (Christensen 1990).

We used a logistic regression with an inflection point to test for the presence of a threshold distance (distance from owl) beyond which the protective influence of breeding owl was absent. The approach is analogous to method used to estimate transition point in linear regression (Bacon and Watts 1971).

The logistic model (run with procedure GENMOD of SAS with logit link function) included variables distance-f, year and nest density. The variable distance-f took the value of the distance from the nearest owl for goose nests located at distance ≤ inflection point and took the value of the inflection point if distance > inflection point. Models were run with inflection point varying from 100 to 2000 m, incrementing this value by 25 to 200 m each time. The position of the inflection point associated with the best fitting model, which was the model with the lowest deviance (Agresti 1996), was selected as the threshold distance. Models were also run separately for each year to examine differences between years.

The previous analyses use each goose nest as an independent observation. We tested the hypothesis that spatial patterns of predation were random, i.e. that the probability that a nest is depredated is independent of the fate of its nearest neighbours. We compared proportion of nests for which the nearest neighbour was successful versus depredated using 2 × 2 contingency tables and Fisher's exact tests (see Larivière and Messier 1998 for details).

To evaluate the effect of lemming abundance on annual variations in goose nesting success, we used a multiple logistic regression including the variables lemming index, nesting area and mean nest density. The CONTRAST statement of the GENMOD procedure was used to compare nesting success in a logistic model using three levels of lemming abundance (low, intermediate and high). Statistical tests were two-tailed and significance levels were set at 0.05. Values are reported as mean ± 1 standard error.

Results

Goose nesting parameters

From 1993 to 1999, nesting success was determined for 1912 goose nests found early in the nesting period. Overall annual goose nesting success varied considerably among years (22% to 91%) and success was always lower at Site-1 than at Site 2 except in 1996 (Figure 1). From 1994 to 1999, timing of breeding was similar at both nesting areas (median laying date 11 June: $\chi^2 = 0.007$, df = 1, $P = 0.93$) and clutch size was slightly higher at Site-1 (4.3 ± 0.1) than at Site-2 (3.8 ± 0.1: $t = 6.5$, df = 1580, $P < 0.001$; Table 1). Nest density was highly variable among years but was always higher at Site-2 than at Site-1 (2.3 to 6.2 times higher, all $P < 0.001$; Table 1). Annual mean nest density and median laying date were not related at Site-1 ($r_s = -0.04$, $n = 10$, $P = 0.92$). However, mean nest density was lower in late nesting season at Site-2 colony ($r_s = -0.78$, $n = 7$, $P = 0.05$).

Importance of nest predators

A total of 318 attacks by predators on goose nests were observed during 384 h of observation and 66 (21%) of them were successful. Each year, arctic fox was the main predator and was responsible for 44% of all attacks on nests and for 45% of successful ones. Other important egg predators were parasitic jaegers, glaucous gulls and common ravens that accounted for 30, 16 and 10% of the attacks and 18, 21 and 14% of successful ones, respectively. Contrary to avian predators, successful attacks by foxes generally resulted in predation of more than one egg and often in total nest predation. Out of 27 successful attacks by foxes with a known number of eggs preyed upon, 15 (56%) resulted in loss of ≥2 eggs (2.5 ± 0.2 eggs) comparatively to only two out of 18 for avian predators. Nesting geese were capable of defending their nests against predators. When parents were close to their nests (≤10 m), successful attacks by predators were rare [8% ($n = 121$) for arctic foxes and 2% ($n = 83$) for avian predators].

Lemming cycle and nesting association

Peak in lemming abundance occurred in 1993 and 1996 and owl nests ($n = 21$) were found only in these two years (Figure 2). At Site-1, nesting association with owls was observed in both years that owls nested (see also Lepage et al. 1996). We found goose nests around (<600 m) all owl nests but two in 1993. The median number of goose nests per owl nest was ten ($n = 18$, range 1 to 270). Goose nests at Site-1 were clustered around owl nests with 75% and 87% of nests at ≤600 m in 1993 and 1996, respectively (Figure 3). At Site-2, only one of the two owls was located in the goose colony (38% of monitored goose nests were at ≤600 m). However, this owl abandoned its nest during incubation at a time when geese were finishing laying. The other owl nest was at >2 km from the colony and hatched successfully.

There was a weak relationship between laying date and distance from owl at Site-1 in both 1993 and 1996 ($\beta = 7.2 \times 10\text{-}4 \pm 2.6 \times 10\text{-}4$, $r^2 = 0.02$, $P = 0.006$, $n = 383$; year and interaction term, $P > 0.3$). Similarly, clutch size slightly declined as distance from owl increased ($\beta = 3.1 \times 10^{-4} \pm 1.0 \times 10^{-4}$, $r^2 =$

0.02, $P = 0.003$, n = 369; year and interaction term, $P > 0.4$). Nest failure was lower close to owl nests than further away (distance, $\chi^2 = 4.50$, $P = 0.03$; year, $\chi^2 = 11.13$, $P = 0.008$; nest density, $\chi^2 = 0.07$, $P = 0.79$; all interaction terms, $P > 0.40$; df = 1, n = 337). Because distance to owls and nest density were correlated (1993, $r_s = -0.43$, $P < 0.001$, n = 283; 1996, $r_s = -0.36$, $P < 0.001$, n = 108), we repeated analyses excluding the variable distance from the model (Agresti 1996). Risk of nest failure was not significantly related to nest density ($\chi^2 = 0.38$, df = 1, $P = 0.54$). At Site-2, the single owl nest that was abandoned in early incubation in 1996 had no effect on goose nesting success (distance, $\chi^2 = 0.23$, df = 1, $P = 0.63$, n = 247). In 1994, some geese nested close to a rough-legged hawk nest at Site-1 (see Lepage et al. 1996). The proportion of successful nests tended to be higher for nests located at <550 m from the hawk (60%, n = 10) compared to nests located further away (31%, n = 32; Fisher's exact test, $P = 0.14$).

We examined if the protective effect of owls on goose nests disappeared beyond a certain distance at Site-1. The use of an inflection point in the logistic regression model improved the fit compared to a model without it (reduction in deviance up to 1.7, Δ df = 0). The best fitting model had an inflection point located at 550 m (deviance = 213.7, df = 334, Figure 4). The inflection point was remarkably similar in both years, indicating that goose nesting success progressively declined as distance from owls increased but reached a plateau beyond 550 m (Table 2, Figure 5). Overall failure rate of nests located in the estimated protective area of owls was 7% lower compared to nests located outside (9%, n = 269 vs 16%, n = 68, respectively).

Artificial nest experiments

Results from the two artificial nest experiments conducted around snowy owls at Site-1 further supported the hypothesis that owls reduced predation risk on goose nests located around their nest. For nests (n = 40) located in control areas, 88% were preyed upon after 3 d and 100% after 6 d. In comparison, for nests (n = 40) located around owls, only 13% were depredated after 3 d and 38% over the full length of the experiment (17-d exposition period). Eighteen goose nests were located at <550 m from owl nests used for the experiment. Mean distance between goose and artificial nests was 61 ± 6 m (range 10 to 164 m).

Predation rate on artificial nests placed around goose nests at Site-2 colony in 1998 was also very high. After only 2 h, overall predation rate was 73%, 66%, 70% and 53% on artificial nests placed at 5, 10, 20 and 30 m, respectively (distance, $\chi^2 = 2.18$, df = 1, $P = 0.14$; date, $P = 0.33$, and interaction term, $P = 0.43$, were dropped; n = 120). All nests were destroyed after 5 h of exposure to predators. No egg was depredated in the 30 real goose nests during these experiments. Direct observations showed that artificial nest predation was mostly (>90%) confined to arctic foxes.

Randomness of predation patterns

We found no evidence for spatial dependence in goose nest survival at both nesting areas from 1993 to 1999 except in 1996 (Site-1 only) and 1994 (Table 3). The significant spatial dependence observed twice at Site-1 occurred in two years where geese nested in association with birds of prey (owls in 1996 and hawk in 1994). By creating protective areas around their nests, birds of prey could cause a non-random pattern of predation among goose nests leading to a significant spatial dependence. However, we did not detect significant spatial dependence at Site-1 in 1993 despite the presence of owls (Fisher's exact test, $P = 0.37$), possibly due to the very low predation rate (9%) observed that year. We have no explanation for the weak but significant spatial dependence observed at Site-2 in 1994. Nevertheless, an overall test including all years showed no significant spatial dependence in failure rate at Site-2 ($\chi^2 = 10.79$, df = 6, $P = 0.10$).

Lemming abundance, nest density and failure rate

At both nesting areas, goose nesting success was positively related to lemming abundance (Figure 6A). However, differences emerged between nesting areas where geese used different nesting strategies (as shown by the significant interaction terms; Table 4). First, the relationship between lemming abundance and nesting success was steeper at Site-1 than at Site-2. Second, nest failure rate was inversely density-dependent at Site-2 (large colony) whereas no effect of nest density was detected at Site-1 (small colonies; Figure 6B). At Site-1, inter-annual variations in nest success closely tracked the cyclic fluctuations in lemming population. The proportion of successful nests was 87.7% (n =349), 42.4% (n = 93) and 16.2% (n =80) during years of high (1993, 1996), intermediate (1994, 1997, 1998) and low (1995, 1999) lemming abundance, respectively (Contrasts: df = 1, $P < 0.001$ in all cases). At Site-2, the combined effects of fluctuations in nest density and lemming abundance created a different pattern. Despite high lemming abundance, nesting success was lower in 1996 (61.4%, n = 249), a year of relatively low nest density, than during years with intermediate lemming abundance but high nest density (1994, 1997 and 1998; 76.8%, n = 896; $P < 0.001$). As in Site-1, nesting success was lowest during low lemming years (1995 and 1999; 29.4%, n = 245; $P < 0.001$).

Mean nest density was not linearly related to lemming index (Site-1: $r_s = 0.60$, $P > 0.15$, n = 7; Site-2: $r_s = 0.14$, $P > 0.50$, n = 6, see Table 1). Nonetheless, density was higher during the two peak lemming years at Site-1 (2.93 ± 0.14 nests ha^{-1}) compared to other years (1.22 ± 0.04 nests ha^{-1}; $t = -12.2$, df = 444.3, $P < 0.001$). The clustering of goose nests around owls mainly explains why density was higher during peak lemming years as mean density of goose nests located at >550 m from owls (1.26 ± 0.05 nests ha^{-1}) was similar to density observed in other years ($t = -0.72$, df = 284, $P = 0.47$).

To eliminate the confounding effect of nesting association with owls in the relationship between lemming abundance and nest success at Site-1, we analysed data excluding nests (n = 269) in the estimated protective area of owls (<550 m) during peak lemming years. In contrast to the model with all nests, the influence of lemming abundance on nesting success no longer differed between nesting areas (interaction nesting area × lemming index: $\beta = -0.31$, 95% CI: -0.81 to 0.16, $\chi^2 = 1.66$, df = 1, $P = 0.20$; dropped from the final model in Table 5; Figure 6). Analyses using the overall density of nests at Site-1 or the density calculated only for nests located outside the protective area gave similar results. Therefore, the link between lemming and nest success was present in both nesting areas even after excluding the confounding positive effect of nesting association with owls in peak lemming years.

Discussion

The main finding of this study was that abundance of lemmings is closely associated with nest predation rate in arctic-nesting greater snow geese but that nesting strategies used by geese can affect this relationship. Other studies have also reported reduced failure rate on bird nests during peak lemming years but were unable to discriminate the confounding effects of varying predation pressure (APH) and association with birds of prey (NAH) (e.g. Syroechkovskiy et al. 1991, Underhill et al. 1993, Summers et al. 1994, Kostin and Mooij 1995, Spaans et al. 1998). In this study, we were able to assess these hypotheses independently.

Alternative Prey Hypothesis (APH)

Our results are in accordance with the prediction of APH that predation pressure on goose nests is low at peak lemming abundance and high during the low phase of the rodent cycle. This general pattern was observed at both high and low goose breeding densities. Correlation between bird nesting success and rodent densities have also been described for other species in northern ecosystems and taken as evidence in favour of the APH (Newton 1998).

Annual variations in predation pressure can result from both the numerical and functional responses of predators to lemming cycles. Arctic fox, the main goose nest predator, is probably the key predator leading to cyclic fluctuations in predation pressure. Foxes are considered generalist predators but their breeding success and population dynamics are strongly affected by lemming populations where the species co-exist (Macpherson 1969, Angerbjörn et al. 1999). Foxes reproduce only once a year and their reproductive output is generally high when lemming are abundant and negligible when lemming populations crash (Tannerfeldt and Angerbjörn 1998). Thus, the numerical response of foxes to varying densities of lemmings will often have a 1-yr time lag (Angerbjörn et al. 1999). On the other hand, a diet shift (type III functional response, Holling 1959) is typical for generalist predators when their prey populations change. The potential of vertebrate predators to shift on alternative preys has been well demonstrated in northern ecosystems (e.g. Angelstam et al. 1984, Korpimäki et al. 1990, O'Donoghue et al. 1998). However, when bird breeding density is high, eggs could still be the primary prey of arctic foxes during the nesting period even if the rodent abundance is relatively high (Stickney 1991). Therefore, the relative impacts of the numerical and functional responses of predators to lemming cycles on bird egg predation still remain to be investigated.

Nesting Association Hypothesis (NAH)

Although our results support the Alternative Prey Hypothesis, they also show that nesting associations with birds of prey during peak lemming years (NAH) can enhance the positive link between lemming cycles and nest success. Nesting associations have often been reported, but are especially common among tundra birds. This might be due to the varying and sometimes intense predation pressure suffered by arctic-nesting birds (Larsen and Grundetjern 1997). As predicted by the NAH, failure rate of nests located close to owl nests was lower than for nests located further away, even though nesting associations occurred in peak lemming years. The main explanation for this relationship is likely the protective influence of owls that chase predators away from the vicinity of their nests (Litvin et al. 1985, Underhill et al. 1993, Tremblay et al. 1997). Our results obtained with artificial nests are the first experimental evidence supporting this hypothesis.

Because owl nests were at the centre of goose colonies (Lepage et al. 1996), the spatial distribution of goose nests could have affected their vulnerability (i.e. nests close to owls were in a central position at high density whereas those located further from owls were at the periphery at low density). However, we found no significant effect of nest density on the risk of predation around owls. Experiments with artificial nests also showed that 1) geese did not protect conspecific nests by defending their own nest surroundings and 2) foxes could easily reach and prey upon nests located in a dense colony. Thus, it seems that edge or density effects had little influence on nest predation rate around owl nests.

Litvin et al. (1985) reported that snowy owls could exclude foxes within a 200-300 m radius of their nests, and up to 500 m during years of high lemming abundance. Our estimation of the threshold protective distance around owl nests (550 m) using an objective criterion (inflection point logistic regression) is in accordance with these previous suggestions. Nesting near owls during peak lemming years probably entails little cost because owls do not prey on eggs and rarely on young birds (Lepage et al. 1996). However, when lemming availability decreases, nesting associations with lemming predators can be unreliable (Larsen and Grundetjern 1997) as young and adult ducks and geese could then become more susceptible to attacks by owls (Dorogoi 1990).

The impact of the positive nesting association with owls at the goose population level remains unknown, but it may be small. First, owls nested in our study area only in peak lemming years. Second, even in those years density of nesting owls was generally <0.2 pairs per km^2 at our study area (Lepage et al. 1998), a density comparable to other arctic regions (Fitzgerald 1981). Thus, the size of the protective area and the low availability of breeding owls considerably limit the number of birds that can use this strategy. Moreover, the timing and pattern of snowmelt are additional constraints that may limit the ability of arctic birds to take full advantage of nesting association with owls (Lepage et al. 1996).

Predation rate and nest density

We found that predation rate was inversely density-dependent at high breeding density. Annual variations in nest density were more likely a consequence of variations in the number of birds attempting to breed in the area than of variations in nest dispersion (see also Lepage et al. 1996). Climatic conditions on the breeding grounds are considered as a dominant factor affecting the breeding effort of arctic and sub-arctic nesting geese. When late snowmelt and low spring temperature prevail, the breeding effort is low (Barry 1962, Gauthier et al. 1996, Skinner et al. 1998). When predation rate is inversely density-dependent, a reduced breeding effort (hence, low nest density) due to poor spring weather conditions will thus lead to increased nest predation rate in colonial birds.

In colonies, the dilution effect (predators swamping) is probably the main mechanism causing inversely density-dependent nest predation rate (Wittenberger and Hunt 1985). Even if predators show a strong functional response to the availability of eggs, the number of eggs depredated will be restricted by the density of predators and thus explain why the proportion of eggs depredated is lower at high nest density (Newton 1998). Group defence and mutual vigilance are additional factors that may account for a reduced predation risk at high nest density (Wittenberger and Hunt 1985). However, our artificial nest experiments showed that geese could not efficiently protect a conspecific nest against foxes, although mutual protection could be more effective against avian predators. Because nest density is lower in late nesting years, other factors correlated with the timing of breeding, such as nest attentiveness by females, could contribute to high predation rate at low nest density. However, Poussart et al. (2001) found no relationship between nest initiation date and nest attentiveness in greater snow geese.

Bird productivity, nest density and lemming cycles

Some authors have suggested that climatic conditions (Angelstam et al. 1985) and the breeding range of a species (van Impe 1996) could influence the relationship between small mammal population cycles and annual bird productivity. We showed that nesting strategies of birds is another important factor that can contribute to the different patterns of annual fluctuations observed in the breeding productivity of arctic nesting species.

For instance, the breeding productivity (percentage of first-year birds in the winter population) of several arctic-nesting waders and the brent geese (*Branta b. bernicla*) follows fairly regular three-year cycles and was associated to the lemming cycles (Summers and Underhill 1987, Summers et al. 1998). These species breed at low nest density and their eggs are highly vulnerable to arctic foxes (Sutton 1932 cited in Summers and Underhill 1987, Underhill et al. 1993, Spaans et al. 1998). A cyclic pattern in reproductive success was also reported in the white-fronted geese (*Anser a. albifrons*, van Impe 1996), a large body-size goose which can efficiently defend its nest against foxes but which also nests at low density (Syroechkovskiy et al. 1991, Rogacheva 1992). At low density, nest predation rate either increases with density of nests, particularly when birds are unable to defend their nests against predators (e.g. Hoi and Winkler 1994; see also Larivière and Messier 1998), or is density-independent (e.g. Niemuth and Boyce 1995). In these cases, annual variations in predation pressure could be the dominant factor generating oscillations in breeding productivity.

In greater snow geese, annual breeding productivity varies considerably (25-fold amplitude) but with no evidence of cyclic patterns (Gauthier et al. 1996, Reed et al. 1998). We showed that oscillations in snow goose nesting success were synchronized with lemming cycles only at low breeding density. For geese nesting at high density (large colony), nest failure rate was inversely density-dependent and annual variations in mean nest density were independent of lemming abundance. In such cases, factors affecting nest density dampened the effect of lemming cycles on nest predation rate and thus explain why the overall breeding productivity is not cyclic even though the predation pressure is still dependent on lemming abundance.

The synchrony in fluctuations of rodent populations over the whole breeding range of a species could also influence the breeding productivity at the population level (Angelstam et al. 1985). For instance, spatial synchrony in lemming population growth can disappear between sites separated by >400 km, and cyclic patterns across the whole Palaearctic tundra are considered asynchronous (Erlinge et al. 1999). In greater snow geese, the latitudinal and longitudinal breeding range exceeds 1000 km over the Canadian arctic archipelago, and is broken up by many physical barriers such as mountain ranges, ice caps and sea channels (Reed et al. 1998). Consequently, lemming cycles and predation pressure may vary asynchronously throughout the breeding range. Therefore, we may not detect cyclic fluctuations in breeding productivity at the population level even if predation pressure and goose nesting success are locally driven by rodent cycles.

Conclusion

We suggest that varying predation pressure (APH) is the main mechanism linking lemming cycles and nest predation rate although nesting association with birds of prey (NAH) can further enhance the link at the local level. However, independent variations in breeding effort (hence nest density) could mask an otherwise cyclic pattern in bird productivity. Our results indicate that breeding strategies used by birds (the alternative prey) could modify the link and the synchrony between oscillations in avian reproductive success and rodent cycles.

TABLE 1. Annual nesting parameters of greater snow goose nests monitored at two areas, Site-1 (S1, small colonies) and Site-2 (S2, large colony) on Bylot Island from 1993 to 1999. Mean ± SE.

	1993	1994		1995		1996		1997		1998		1999	
	S1	S1	S2	S1	S2	S1	S2	S1	S2	S1	S2	S1	S2
N	283	46	285	72[a]	69	113	246	35	291	19[a]	331[a]	5[a]	180[a]
Laying date[b]	6	7	11	11	10	12	14	11	10	10	7	12	18
Clutch size	4.5 ± 0.1	4.5 ± 0.2	3.6 ± 0.1	5.1 ± 0.5	3.7 ± 0.1	4.0 ± 0.1	4.0 ± 0.1	4.9 ± 0.3	4.2 ± 0.1	4.7 ± 0.5	4.0 ± 0.1	3	3.1 ± 0.1
Nest density[c]	3.4 ± 0.2	1.1 ± 0.1	6.7 ± 0.2	1.4 ± 0.1	5.5 ± 0.3	1.8 ± 0.1	4.2 ± 0.2	1.2 ± 0.1	5.7 ± 0.2	1.1 ± 0.1	6.6 ± 0.2	1.0 ± 0.0	4.1 ± 0.2

[a] N for clutch sizes was smaller in those years (1995 S1, N = 16; 1998 S1, N = 7; 1998 S2, N = 301; 1999 S1, N = 1; 1999 S2, N = 107).

[b] Median laying date in June.

[c] Nest ha^{-1}.

TABLE 2. Logistic model with inflection point testing the effect of distance from the nearest breeding owl on goose nesting success at Site-1 in 1993 and 1996 (n = 337). We used the inflection point (distance-550) associated with the best fitting model. The variable distance-550 was equal to the actual distance from the nearest owl for a nest located at ≤550 m and was set at a constant value of 550 m for nests located at >550 m. Nest density and interaction terms were not significant and were dropped from the model.

Variables	df	ß	SE	χ^2	*P*
Intercept	1	2.27	0.46		
Year	1	1.31	0.37	12.02	<0.001
Distance-550	1	-0.0027	0.0011	6.19	0.01

TABLE 3. Ratio of observed/expected frequency of successful-successful (S-S) and failed-failed (F-F) pairs of nests used to test the hypothesis that the probability of a nest being depredated is independent from the fate of its neighbour. Values >1 indicate higher than expected frequencies (i.e. the fate of a nest is linked to the fate of its nearest neighbour). *P*-values for Fisher's exact tests are indicated with asterisk (** $P < 0.01$, *** $P < 0.001$, otherwise $P > 0.05$). The number of nests used for these analyses are shown in parentheses for Site-1 and Site-2, respectively.

	Site-1			Site-2		
Year (n)	S-S		F-F	S-S		F-F
1993 (231, -)	1.0		0.0[a]	–[b]		–[b]
1994 (31, 287)	2.6	***	1.5	1.1	**	1.3
1995 (68, 171)	1.7		1.0	1.0		0.8
1996 (91, 239)	1.1	***	3.0	1.0		1.0
1997 (24, 269)	1.0		1.0	1.0		0.9
1998 (17, 314)	4.2		1.1	1.0		1.1
1999 (5, 175)	–[c]		–[c]	1.2		1.0

[a] Number of F-F observed in 1993 at Site-1 = 0 (expected = 1.3).

[b] No data available at Site-2 in 1993.

[c] Sample size too small to perform statistical analysis.

TABLE 4. Multiple logistic regression model testing the effect of nesting area, lemming abundance and mean nest density on goose nesting success from 1993 to 1999 (n = 1912 nests). Correlation between predicted and observed annual nesting success at a given nesting area was significant ($r_s = 0.89$, $P < 0.001$, n = 13). Interaction terms that were not significant were dropped from the model.

Variables	df	ß	SE	χ^2	*P*
Intercept	1	-1.34	0.30		
Nesting area	1	-1.99	0.46	18.68	<0.0001
Lemming index	1	1.13	0.20	84.48	<0.0001
Mean nest density	1	-0.07	0.28	3.14	0.08
Area × Lemming index	1	-0.46	0.21	4.86	0.03
Area × Mean nest density	1	0.66	0.28	5.48	0.02

TABLE 5. Multiple logistic regression model testing the effect of nesting area, lemming abundance and mean nest density on goose nesting success from 1993 to 1999 (n = 1643). Model excludes nests under the protective influence of breeding owls at Site-1 during the two peak lemming years. Correlation between predicted and observed annual proportion of successful nests at a given nesting area was significant ($r_s = 0.87$, $P = 0.001$, n = 13). Interaction terms that were not significant were dropped from the model.

Variables	df	ß	SE	χ^2	*P*
Intercept	1	-1.16	0.32		
Nesting area	1	-2.24	0.50	20.33	<0.0001
Lemming index	1	0.70	0.08	90.33	<0.0001
Mean nest density	1	0.0009	0.20	9.26	0.002
Area × Mean nest density	1	0.59	0.21	7.35	0.007

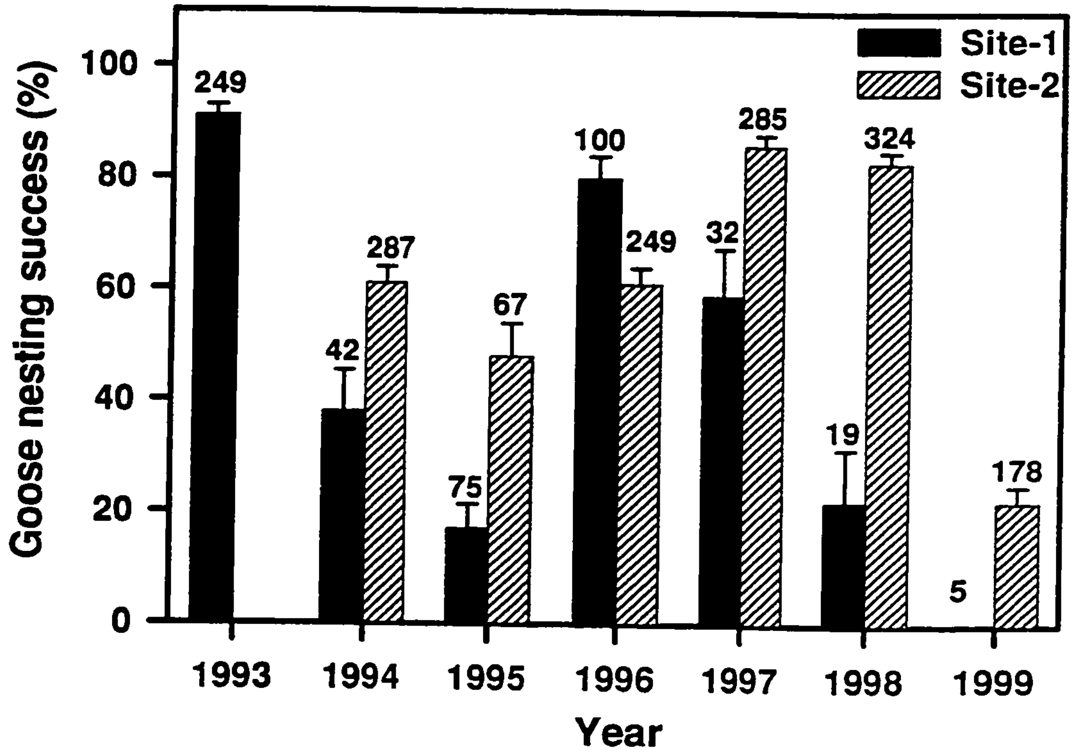

FIGURE 1. Annual fluctuations in greater snow goose nesting success (proportion of nests where at least one egg hatched successfully) at two nesting areas, Site-1 (low breeding density, small colonies: 1993 to 1999) and Site-2 (high breeding density, large colony: 1994 to 1999), on Bylot Island. Numbers represent sample sizes and error bars are SE.

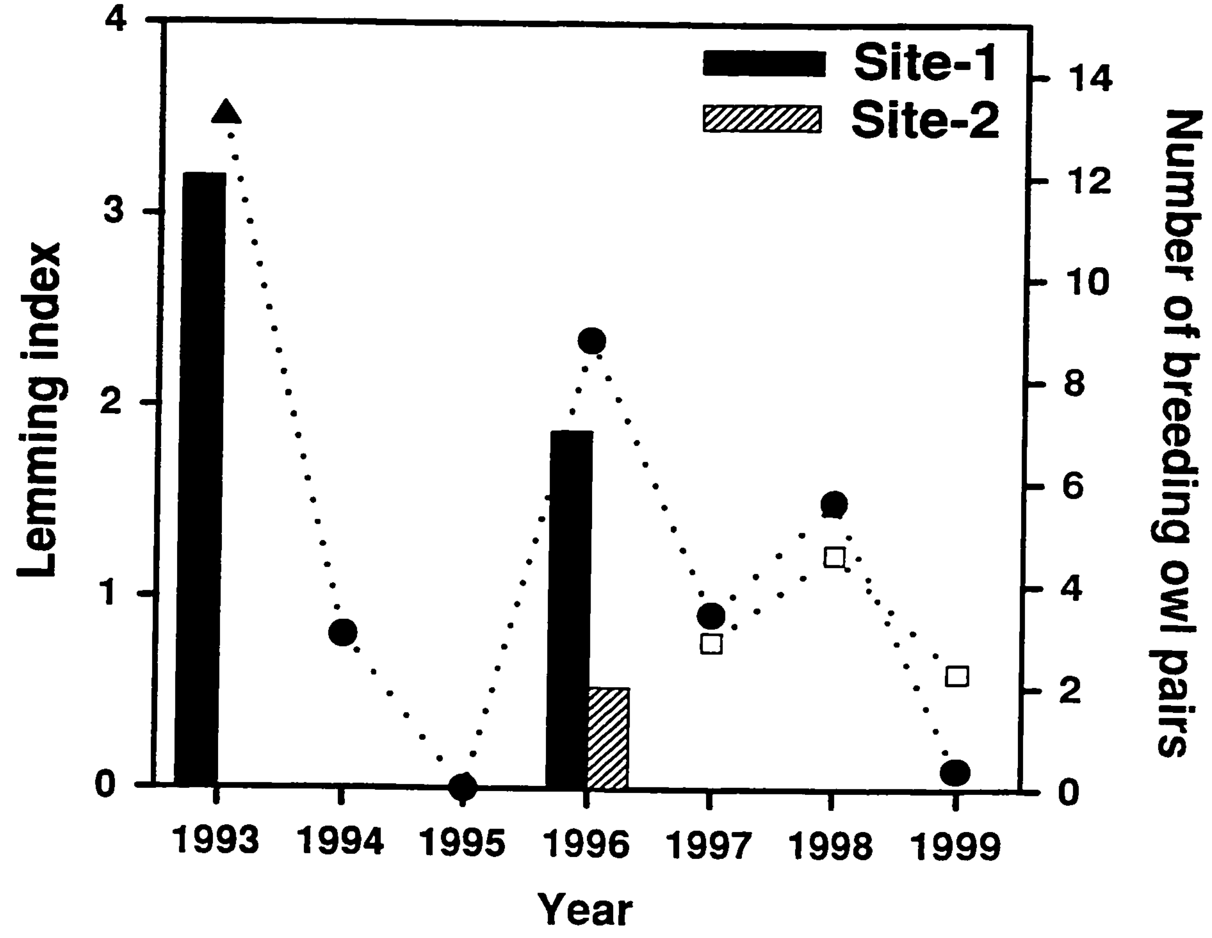

FIGURE 2. Index of lemming abundance (pooled number of Lemmus sibiricus and Dicrostonyx groenlandicus caught per 100 trap-nights) at Site-1 from 1994 to 1999 (●) and at Site-2 from 1997 to 1999 (□), Bylot Island. Lemming index at Site-1 in 1993 (▲) was estimated from lemming nest survey data, based on the ratio lemming nest survey/lemming abundance obtained in 1996 (see Methods). The number of breeding snowy owl pairs recorded at Site-1 (ca 50 km^2: 1993 to 1999) and at Site-2 (ca 16 km^2: 1994 to 1999) is also shown (bars).

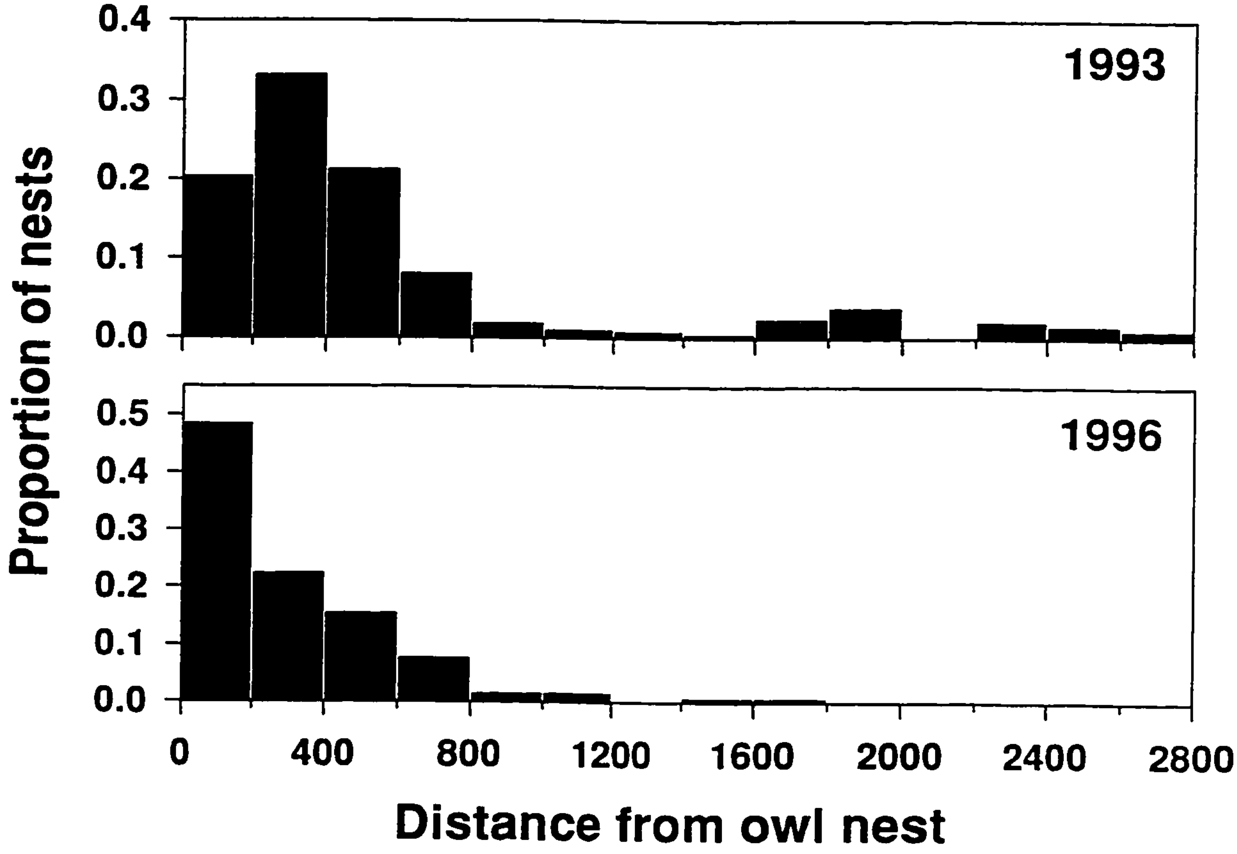

FIGURE 3. Distribution of snow goose nests found at Site-1 area in relation to distance (m) from the nearest snowy owl nest in 1993 (n = 351) and 1996 (n = 115).

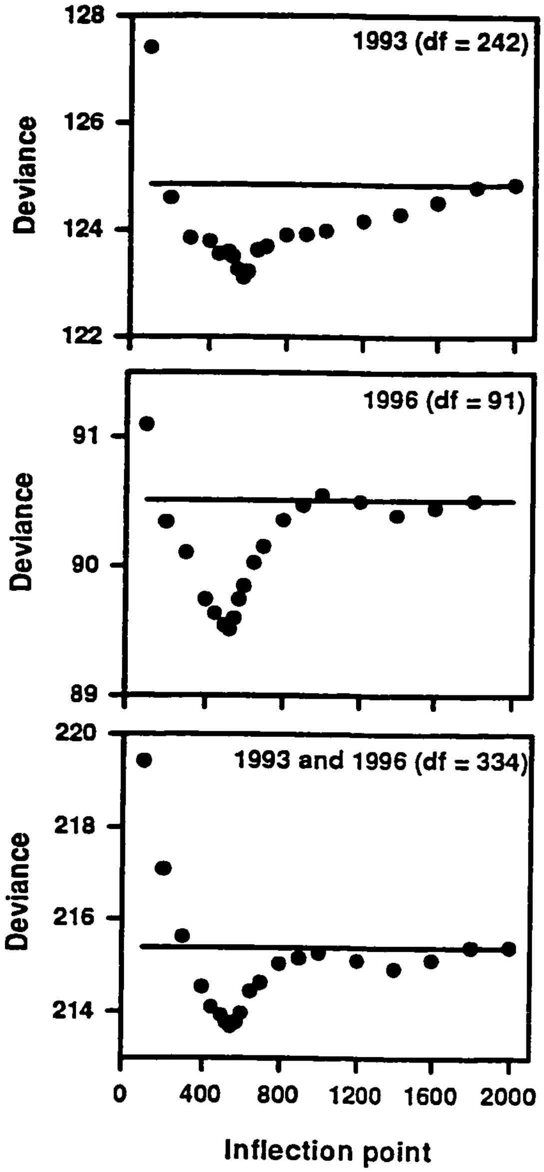

FIGURE 4. Change in model fit in relation to the inflection point (distance from nearest owl nest in m) used in logistic regression analyses to test for a threshold distance beyond which the protective influence of owls on goose nesting success was absent (see Methods). Solid lines represent deviance for logistic models without inflection point. The degrees of freedom were the same for all models presented in a panel.

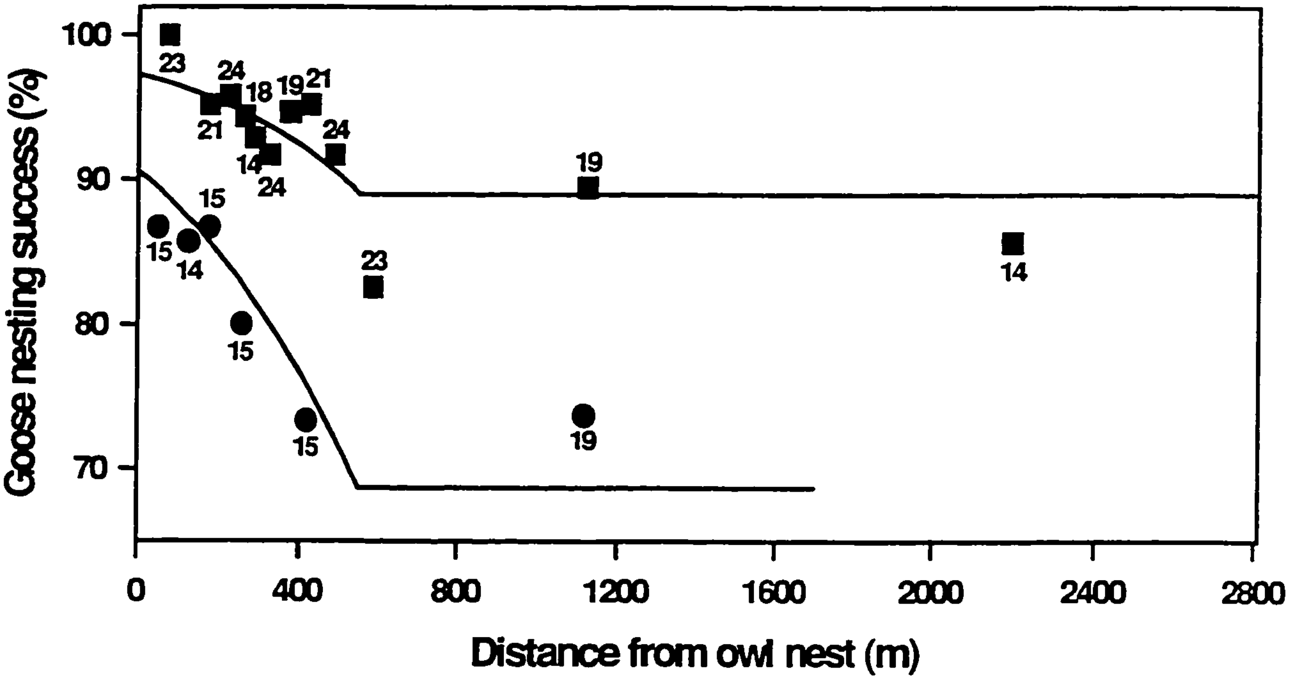

FIGURE 5. Relationship between goose nesting success and distance from nearest owl nests at Site-1 during the two peak lemming years (1993, ■: 1996, ●). The regression curves (solid lines) were obtained with the best fit logistic model with an inflection point (inflection point = 550 m). To illustrate the adequacy of the model, each point represents proportion of successful nests grouped by distance interval (sample size is shown near each point).

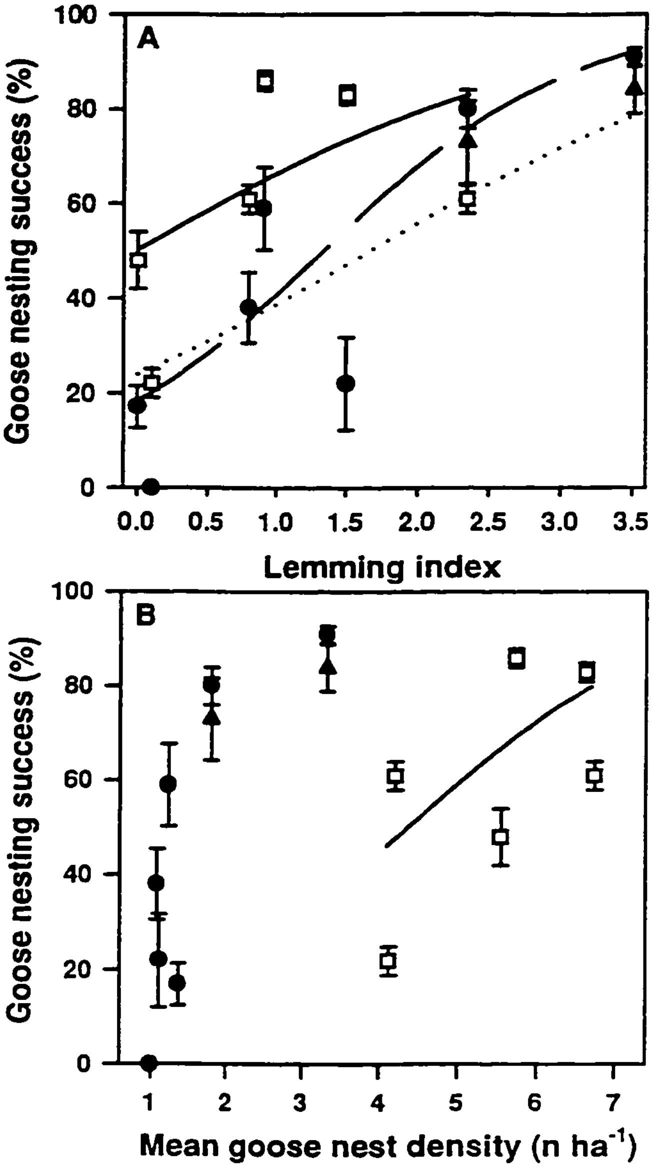

FIGURE 6. Relationship between goose nesting success and (A) lemming density index (pooled number of Lemmus sibiricus and Dicrostonyx groenlandicus caught per 100 trap-nights) or (B) mean goose nest density at two nesting areas. To illustrate the adequacy of the model, annual nesting success (mean ± SE) are given for each area (Site-1, ●, from 1993 to 1999; Site-2, □, from 1994 to 1999; Site-1 excluding nests under the protective influence of owls in 1993 and 1996, ▲). Regression curves obtained with multiple logistic regression analyses are shown. Models either include all nests, solid line (Site-2) and long dash line (Site-1, n = 1912 in total), or exclude nests within the estimated protective influence of owls at Site-1 during the two peak lemming years, dotted line (in this model, regression lines at Site-2 remained almost the same; n = 1643 in total).

Chapitre 3

SHARED PREDATORS AND INDIRECT TROPHIC INTERACTIONS: LEMMING CYCLES AND ARCTIC-NESTING GEESE

Bêty, J., Gauthier, G., Korpimäki, E. and Giroux, J.-F. 2002. Journal of Animal Ecology. In press.

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Résumé

Nous avons testé l'hypothèse que les cycles de populations de lemmings puissent indirectement affecter les Grandes Oies des neiges (*Chen caerulescens atlantica*) nichant dans l'Arctique par l'intermédiaire de la réponse comportementale et numérique de prédateurs communs. L'étude s'est déroulée à L'île Bylot dans le Haut-Arctique canadien au cours de deux cycles de lemmings. Nous avons étudié les changements du comportement de quête alimentaire et du taux d'activité des Renards arctiques, Labbes parasites, Goélands bourgmestres et Grands Corbeaux dans une colonie d'oies durant un cycle de lemmings. De plus, l'activité de reproduction des renards a été observée à des tanières au cours de sept années. Nous avons aussi évalué la réponse totale des prédateurs, soit le nombre d'œufs prélevés, à l'aide du suivi de nids d'oies (cinq années) et d'expériences avec des nids artificiels. Les Renards arctiques étaient plus efficaces lors des attaques dirigées vers les lemmings que vers les oeufs parce que les prédateurs étaient contraints par la défense des nids par les oies. Les prédateurs ont augmenté leur effort de quête alimentaire en direction des œufs suite au déclin d'abondance de lemmings. Les taux d'activité dans la colonie d'oies ont varié 3.5-fois chez les Renards arctiques et 4.8-fois chez les Labbes parasites, et ont été maximaux respectivement deux et trois ans après le pic de lemmings. La productivité annuelle des Renards arctiques semblait principalement dépendante de la densité de lemmings. La réponse totale des prédateurs a varié 2.7-fois, représentant 19% à 88% de la productivité annuelle d'œufs par les oies, et a été la plus basse lors des années de pics d'abondance de lemmings. Les Renards arctiques et les Labbes parasites ont été identifiés comme étant les deux prédateurs clés produisant des variations annuelles marquées de l'intensité de prédation des œufs. Cette étude suggère fortement que les populations de lemmings aient, à court terme, des effets positifs indirects et, à long terme, des effets négatifs indirects sur les oies nichant dans l'arctique. Le résultat de ces effets indirects opposés est probablement une compétition apparente entre les rongeurs et plusieurs espèces d'oiseaux de l'Arctique.

Abstract

We investigated the hypothesis that cyclic lemming populations indirectly affect arctic-nesting greater snow geese (*Chen caerulescens atlantica*) through the behavioural and numerical responses of shared predators. The study took place on Bylot Island in the Canadian High Arctic during two lemming cycles. We recorded changes in foraging behaviour and activity rate of arctic foxes, parasitic jaegers, glaucous gulls and common ravens in a goose colony during one lemming cycle and we monitored denning activity of foxes for seven years. We evaluated the total response of predators (i.e. number of eggs depredated) using surveys of goose nests (five years) and artificial nest experiments. Arctic foxes were more successful in attacking lemmings than goose nests because predators were constrained by goose nest defence. Predators increased their foraging effort on goose eggs following a lemming decline. Activity rates in goose colony varied 3.5-fold in arctic foxes and 4.8-fold in parasitic jaegers, and were highest two and three years after the lemming peak, respectively. The breeding output of arctic foxes appeared to be primarily driven by lemming numbers. Predators consumed 19-88% of the annual goose nesting production and egg predation intensity varied 2.7 fold, being lowest during peak lemming years. Arctic foxes and parasitic jaegers were the key predators generating marked annual variation in egg predation intensity. Our study provides strong support for short-term, positive indirect effects and long-term, negative indirect effects of lemming populations on arctic-nesting geese. The outcome between these opposing indirect effects is likely an apparent competition between rodents and many terrestrial arctic-nesting birds.

Introduction

The role of trophic interactions in determining the distribution and abundance of organisms is a long standing debate among ecologists. Traditionally, community models have emphasized the role of direct interactions. Indirect interactions, in which a species can indirectly alter the abundance of another species through its direct interactions with a third species, may also be important (Strauss 1991). Despite an increase in interest, the actual role of indirect effects in natural communities is still far from clear (Menge 1995, Chase 2000).

Prey that share the same predators can indirectly interact via the functional (changes in kill rates) as well as the numerical response (changes in reproduction, survival, or aggregation) of predators (Holt 1977). Prey availability can influence the behaviour of predators and modulate the predation rate experienced by a prey species through the functional response of predators. For example, within a given habitat patch, an increase in the density of a focal prey may reduce predation rate on an alternative prey because of predator saturation or selectivity (Abrams and Matsuda 1996). This type of short-term, indirect interaction is called apparent mutualism (Holt 1977, Abrams and Matsuda 1993). In patchy environments where predators are mobile and prey items are not uniformly distributed, co-occurring prey may also indirectly interact via the aggregative response of predators (Holt 1984). If predators select patches with the preferred prey type (i.e. local numerical response), predation rate of alternative prey located in other patches may be reduced, again leading to short-term apparent mutualism among prey (Holt and Lawton 1994). Alternatively, an increase in the density of one prey may eventually lead to an increase in predator numbers and thus enhance predation on alternative prey. This long-term indirect interaction mediated by the numerical response (reproduction or survival) of shared natural enemies could lead to a reduction in the number of the alternative prey, an effect called apparent competition (Holt 1977).

Indirect interactions mediated by predators have not been well studied in natural systems that exhibit periodic fluctuations (Abrams et al. 1998). Recent theoretical and empirical evidence indicates that periodic multiannual density fluctuations in northern populations of voles and lemmings (3- to 5-year cycles) may result from interactions between food supply, rodents and their predators (Hanski and Korpimäki 1995, Stenseth 1999). Parallel cyclic fluctuations in abundance or breeding success of some bird species have been taken as evidence of indirect trophic interactions mediated by shared predators (Lack 1954, Angelstam et al. 1984, Summers 1986). However, the relative importance of the numerical and functional responses of different predator species on the avian community is still largely unknown (e.g. Norrdahl and Korpimäki 2000, Wilson and Bromley 2001). This is especially true in arctic ecosystems where long-term studies of the interactions between predators and co-existing prey are scarce. A better understanding of the role of indirect interactions in these communities requires a detailed knowledge of long- and short-term responses of predators to changes in prey availability (Holt and Lawton 1994).

We studied direct and indirect interactions among herbivore prey and predators in the Canadian High Arctic where the assemblage of terrestrial vertebrate species is relatively simple and the predator-prey interaction is quantifiable by means of direct observations. In our study area, the annual nesting success of greater snow geese (*Chen caerulescens atlantica*) is positively associated with the overall abundance of brown lemmings (*Lemmus sibiricus*) and collared lemmings (*Dicrostonyx groenlandicus*) (Chapter 2). Primary goose egg predators are, in decreasing order of importance, arctic foxes (*Alopex lagopus*), parasitic jaegers (*Stercorarius parasiticus*), glaucous gulls (*Larus hyperboreus*) and common raven (*Corvus corax*) (Tremblay et al. 1997, Chapter 2). All four predator species are highly opportunistic omnivores that also eat lemmings (Fitzgerald 1981).

Our main objective was to test the hypothesis that lemmings, the focal prey, indirectly affect snow geese, an alternative prey, through the responses of shared predators. We tested several predictions of this hypothesis with respect to the response of predators to lemming population cycles. First, if predators show a preference for lemmings, they should hunt them primarily until their density declines. Second, abundance of predators in goose nesting areas should be lower at high lemming densities and increase following lemming declines. Third, the breeding production of predators should be higher at high than at low lemming density. Finally, the total response of predators (i.e. the product of the number of predators and the number of eggs taken per predator) should be cyclic and lowest in peak lemming years.

To test these predictions, we first looked at inter-annual changes in foraging behaviour and activity rate of nest predators in a goose colony during a complete lemming cycle. Second, we examined denning activity and litter sizes of the main nest predator, the arctic fox, under fluctuating lemming densities. Finally, we evaluated the total response of nest predators using surveys of goose nests and artificial nest experiments.

Material and methods

Study area and species

We conducted the study at the Bylot Island migratory bird sanctuary, Nunavut, Canada (72°53'N, 78°55'W), the most important breeding site of greater snow geese (>25 000 pairs in 1993: Reed, Giroux and Gauthier 1998). Density of most terrestrial bird species is low relatively to snow geese (estimated to be <2 pairs per 100 ha in most species; Lepage et al. 1998). Nesting geese are mostly concentrated in two areas (<100 km^2) on the South plain of Bylot Island (ca. 1600 km^2; see Lepage *et al.* 1998 and Bêty et al. 2001). We made observations and nest monitoring in a large goose colony (typically >4000 nests over ca 16 km^2) located around a narrow valley (ca 0.5 km wide) surrounded by gently slopping hills (see Lepage et al. 1996 and Tremblay et al. 1997 for details of the areas). Two species of lemmings co-exist in our study area and, in contrast to nesting geese, they occur over all the South plain. The brown lemming prefers wetlands (polygon fen) and feeds primarily on graminoids (grasses and sedges) (Gauthier et al. 1996, Negus and Berger 1998). By contrast, the collared lemming prefers dry upland habitat and feeds mainly on dicotyledonous plants (Negus and Berger 1998). Adult brown and collared lemmings weigh 40-100 g (Krebs 1964, Wilson 1999) and a fresh goose egg 90-130 g.

The greater snow goose is a strict herbivore. Like brown lemmings, geese depend mostly on wetland graminoids for their food (Gauthier et al. 1996). However, even in years of peak abundance, lemmings consume a small proportion of above-ground biomass compared to geese as shown by the long-term monitoring of vegetation in goose and lemming exclosures (G. Gauthier, unpublished data). Geese are single-brooded and do not renest after failure of a clutch (Lepage et al. 2000). Nest initiation occurs in June and is typically very synchronized (about 90% of nests initiated within eight days; Lepage et al. 1996). Low nest density occurred in late nesting seasons and is likely a consequence of reduction in overall geese breeding effort under unfavourable climatic conditions (Gauthier et al. 1996, Lepage et al. 1996, see also Chapter 2). As laying progresses, nest attentiveness by the female increases and time spent on the nest by incubating females averages 92% and does not vary seasonally (Poussart et al. 2000). Duration of incubation period is approximately 24 days (Poussart et al. 2000). During the brief incubation recesses, females are accompanied by their mate and feed most of the time (Reed et al. 1995). Nest desertion is rare (estimated at < 2%, Tremblay et al. 1997) and predation is the main proximate cause of nest failure (Lepage et al. 1996). Egg predators can raise no more than one litter/brood per year (Fitzgerald 1981).

Lemming abundance

Index of lemming abundance was obtained in July from 1994 to 2000 with snap-trap censuses. Trapping was done in two study plots (wet lowland and dry upland), except in 1994 (only one plot in wet lowland). In each plot, we set 50 baited traps for 10-11 days (see Chapter 2 for details of the methods). Study plots were located in a goose brood-rearing area 30 km from the monitored goose colony. Similar trapping conducted from 1997 to 2000 at the goose colony showed a spatial synchrony in the fluctuation of lemming abundance at the regional scale (Chapter 2, Bêty and Gauthier unpubl. data).

Behaviour and activity of predators

From 1996 to 1999, we conducted detailed behavioural observations during the incubation period in a plot (ca 50 ha) where conditions (habitat and nest dispersion) were typical of those encountered in the whole monitored goose colony. The number of goose nests located in the observation zone was estimated at the beginning of the incubation by visual counts of breeding pairs. This was used as an index of nest density in foraging behaviour analyses (see below). Each year, we did 24 4-h observation sessions systematically rotated throughout the 24-h cycle and spread throughout the incubation period. The photoperiod is 24-h daylight during the goose nesting period. We conducted observations from a blind and predators appeared unaffected by our presence once we were inside the blind. We recorded the number of predators staying at least 1 min within the plot (including predators flying over). The 1-min criterion was used to eliminate the few observations of avian predators that were travelling at high speed across the plot and clearly not foraging. To calculate the annual activity rate of predators (number of presences per 24 h), we randomly assigned each 4-h observation session to form a total of four days of observation (i.e. four replicates of a complete 24-h cycle). We used binoculars (7×35) to detect and identify predators and a spotting scope (20-60×) to determine the outcome of their attacks.

Nest attacks were defined as any attempt by a predator to rob goose eggs. Avian predators most often tried to reach goose nest from the air (rapid and direct flight toward a nest) but sometimes on foot (mostly ravens). Foxes usually initiated attacks from a distance of >10 m and ran at high speed straight towards a goose nest. At the time of the attack, we noted the presence or absence of protecting adults around the nest and scored the distance to the nest of the nearest goose if present [0 m (female incubating), 1-10 m and >10 m]. Nest attacks were considered successful if at least one egg was preyed upon. From 1997 to 1999, we systematically recorded attacks of arctic foxes on lemmings during their presence in the goose colony. Generally, when foxes spotted a lemming, it stopped moving, swayed the head and jumped or dug rapidly to capture the prey. Attack rates on lemming are not available for avian predators because it was too difficult to confirm their attacks by direct observation.

Breeding activity of predators

From 1994 to 2000, we searched for and monitored arctic fox dens in the vicinity (up to 40 km) of the goose colony. Dens were visited at least once in June or early July to check for signs of fox presence (i.e. fresh scats, tracks, prey remains or recent digging). Dens with signs of activity were revisited later during the summer (July and August) to determine the presence and number of pups. Litter size was defined as the highest number of pups observed at any visit. These estimates must be regarded as a minimum number (Garrott et al. 1984). New dens were found every year, because the size of the surveyed area increased during the study (ca 240 km^2 at the end of the study). We are confident that we found the majority of dens present in the surveyed area. We assumed that the annual proportion of breeding dens among those surveyed was representative of the total number of dens present over the entire area. The proportion of breeding dens multiplied by the mean litter size and the density of dens was used as an index of the yearly breeding production of foxes. The low breeding density of glaucous gulls and parasitic jaegers in the study area (estimated at <0.3 pairs per 100 ha) precluded adequate monitoring of their breeding activity and little evidence for breeding was reported for common ravens (Lepage et al. 1998).

Predation on goose eggs

We monitored goose nests from 1996 to 2000. Nests were found by systematic searches mostly during the laying or early incubation periods and mapped with a Global Positioning System receiver (± 25 m). Eggs were marked individually and signs of nest predation were noted on each visit (see Chapter 2). Although jaegers and gulls may be temporally attracted by the presence of investigators in the goose colony, nesting parameters are not biased by our visits (see Chapter 1). AA nest was considered successful if at least one egg hatched. We estimated nest density (nests per 50 ha) by dividing the number of nests found by the area of the search zone measured with RANGES V using concave polygons (Kenward and Hodder 1996). The extent of the search zone ranged from 91 to 268 ha and was higher in years of low nest density to permit the location of an adequate number of nests (>175). We considered both total and partial nest predation in our estimation of the total number of eggs depredated (ED) as follows:

$$\mathrm{ED} = [(\mathrm{NMR} \times \mathrm{TCL}) + (1 - \mathrm{NMR}) \times (\mathrm{TCL} - \mathrm{CSH})] \times \mathrm{ND}$$

where NMR is the nest mortality rate for the entire nesting period, TCL is the total clutch laid (total number of eggs marked in a nest), CSH is the clutch size at hatch (number of eggs in successful nests) and ND is the nest density. This statistic is an index of the total response of predators, i.e. the product of the number of predators and the number of eggs taken per predator. However, total or partial nest predation during laying, (i.e. before nests were found by investigators) could lead to an underestimation of ND or TCL. Thus, our evaluation of ED is a minimum estimate of egg predation and may be negatively biased at high predation rate.

We estimated the relative contribution of each predator species to the total response (i.e. the number of eggs depredated by each species *i*, ED*i*) using the nest attack rates observed in the colony. We assumed that the proportion of successful attacks by avian predators was similar to arctic foxes in a given year, as found for all years combined (see Results). Finally, we weighted attacks by allowing twice as many eggs for each successful attack by foxes compared to avian predators (based on data from Chapter 2 and Bêty & Gauthier, unpublished). The estimated relative contribution of predator species *i* was thus defined as:

$$\mathrm{ED}i = \left[\frac{(AR_i \times W_i)}{\sum (AR_i \times W_i)}\right] \times \mathrm{ED}$$

where AR is the attack rate (number of nest attacks per 96h) and W is the weighted factor (1 for avian predators and 2 for arctic foxes).

Artificial nest experiment

We used artificial nests to experimentally assess the inter-annual variation in predation pressure on goose nests and as an additional index of the total response of egg predators. Goose eggs were simulated with domestic hen eggs. Three eggs were placed in simulated nest bowls and covered with goose down collected in old nests. Nest locations were marked with small, inconspicuous bamboo canes. Rubber gloves were worn during nest deployment and visits. A nest was considered depredated when at least one egg had been destroyed or removed. In 1997 and 1998, artificial nests were distributed in three plots (ca 300 m × 300 m) separated by >1 km and located in the patchy goose colony. The experiment was done in the same three plots in both years. Within each plot, nests were placed in three habitat types (mesic flat tundra, mesic hilly tundra, and wet polygon fen). Two 80-m long transects separated by 50 m were positioned in each habitat type. Five nests separated by 20 m were placed on each transect (total 30 nests/plot). Nests were set from 19.00 to 21.00 h and checked after 2, 5, 8 and 12 h of exposure to predators. We used nest remains to identify predators (birds or arctic fox). Nests depredated by foxes were characterized by a small hole in the goose down covering eggs, the absence of eggshell around the nest and sometimes fresh fox faeces in the nest. In contrast, scattered goose down and, generally, broken eggs or eggshells were found around nests depredated by avian predators. We calibrated our method by coupling direct observations from a blind and analyses of artificial nests remains. These observations confirmed 1) that predators of artificial nests were the same as those of real goose nests and 2) the validity of our nest remains criteria to identify predator type (100% concordance for 101 nests where predators were observed; 81 by arctic foxes, 20 by parasitic jaegers and glaucous gulls).

Statistical analyses

The foraging behaviour of predators was analysed using Generalized Linear Models with logit link function. Type 3 contrasts with the likelihood ratio statistics were used to test the significance of a variable in models with other variables already included. Non-significant interactions were removed, one at a time from higher to lower levels, until only significant interactions remained (Christensen 1990). There are potential sources of lack of independence in some analyses of foraging behaviour of predators. First, we were unable to properly distinguish all individuals, and therefore we could not calculate the true (i.e. inter-individual) variances of our measures of foraging behaviour. However, we were most concerned by the pattern of year-to-year changes in predator foraging as the availability of prey changed (e.g. O'Donoghue et al. 1998). Second, attacks on different nests performed by the same predator during a single visit at the colony are repeated measures. In these cases, we used Generalized Estimating Equations (GEE) with the logit link function (procedure GENMOD of SAS using the statement REPEATED, SAS Institute Inc. 1999). This analysis considers each predator visit as statistically independent but assumes that multiple attacks by the same predator are correlated (Fitzmaurice et al. 1993, Horton and Lipsitz 1999). The number of attacks per visit was low and unbalanced. Consequently, we used an exchangeable structure to model the working correlation matrix (i.e. matrix with one correlation coefficient for all individuals and repeated attacks, see Horton and Lipsitz 1999). Annual variations in activity rate of predators were analysed with one-way ANOVA (year).

The Mayfield method was used to calculate daily nest mortality rate and the Product Method was used to evaluate nest mortality rate for the whole nesting period because mortality rate varied considerably throughout the lifetime of nests (Johnson 1979). We calculated nest losses and exposure following Klett and Johnson (1982). We used 2 periods delimited by nest visits sequence: "early" nesting stage (laying and first seven days of incubation) and "mid/late" nesting stage (8th day of incubation until hatching). Pairwise comparisons of nest mortality rates were made with *Z*-tests (Johnson 1979). We considered each goose nest as independent because the fate of a goose nest is independent of the fate of its nearest neighbours (Chapter 2). We calculated hourly survival rate in artificial nests (Mayfield estimate) using the plot (not the nest) as the sampling unit. Annual variations in artificial nest mortality rate and relative importance of predators were analysed with Kruskal-Wallis tests. All statistical tests were performed with SAS statistical software version 8. All probabilities are two-tailed and significance levels were set at 0.05. Values are reported as mean ± 1 SE.

Results

Lemming cycles and foraging behaviour of predators

Our study spanned two lemming cycles (periods of three and four years) with three peaks and two declines in abundance (Figure 1). The number of collared lemmings trapped remained low over this period and only brown lemmings exhibit marked annual variation in abundance. The number of goose nests located in the observation plot at the beginning of incubation varied considerably during the lemming cycle, with 150, 413, 448 and 124 nests from 1996 to 1999, respectively. Over this period, a total of 2431 observations of nest predators were made during 384 h of observations. Based on short-term recognizable patterns of pelt colour, we estimated the minimum number of arctic foxes foraging in the goose colony at four to six each year from 1996 to 1999.

Foxes were much more successful in capturing lemmings than goose eggs. Success rate of attacks was 21% (n = 141) on eggs and 92% (n = 26) on lemmings (GEE: $\chi^2 = 17.3$, df = 1, $P < 0.0001$, median number of attacks per visit to the colony = 2, range 1 to 9). Success rate of attacks by avian predators on eggs was also low (20%, n = 176, median number of attacks per visit = 1, range 1 to 3). Because geese can defend their nests against predators, the fate of nest attacks was strongly influenced by the distance of the birds from their nest. Fox attacks were much less successful when geese were incubating (8% success, n = 118) than during incubation recesses (91% success when parents were at >1 m from the nest, n = 23; GEE: $\chi^2 = 19.6$, df = 1, $P < 0.0001$). Avian predators never attacked when females were sitting on the nest and they were 10 times as likely to rob eggs when geese were at >10 m from their nests (21% success, n = 63) than when they were at a distance of 1-10 m (2% success, n = 83; GEE: $\chi^2 = 10.3$, df = 1, $P = 0.001$, data pooled for all avian predator species).

The proportion of attacks by foxes while goose females were on the nest incubating was negatively related to lemming abundance, ranging from 91% (n = 47) at low lemming abundance to 76% (n = 42) at high lemming abundance (GEE: lemming index, $\chi^2 = 5.72$, $P = 0.02$; nest density, $\chi^2 = 0.17$, $P = 0.68$, and interaction term, $\chi^2 = 0.01$, $P = 0.94$, were removed. Df = 1 in all cases). Similarly, the proportion of attacks by avian predators in presence of parents near the nest decreased from 97% (n = 107) at low lemming abundance to 80% (n = 44) at high lemming abundance (GEE: lemming index, $\chi^2 = 5.15$, $P = 0.02$; nest density, $\chi^2 = 15.04$, $P = 0.0001$; interaction term removed, $\chi^2 = 1.66$, $P = 0.20$. Df = 1 in all cases). Increases in frequency of attacks with low probability of success indicate that predators put more effort into robbing eggs at low lemming abundance. Lemming abundance did not influence the success rate of attacks by foxes when geese were close to their nests (GEE: $\chi^2 = 0.42$, df = 1, $P = 0.52$; sample size was too small for a similar analysis with avian predators). Consequently, the overall success of attacks on goose nests decreased at low lemming abundance (Figure 2). Thus, despite an apparent increase in foraging effort on goose nests at low lemming abundance, predators were less successful due to effective nest defence by geese.

From 1997 to 1999, 44% (n = 152) of visits by foxes in the goose colony resulted in the attack of a least one prey (lemming or goose nest). Foxes always attacked only one type of prey in a given visit. Overall, 80% (n = 124) of fox attacks in the goose colony were directed toward goose nests and 20% toward lemmings. We analysed separately the effects of nest density and lemming abundance on the probability of nest attacks during a visit because both variables varied in parallel way during the three years. The proportion of visits with attacks by foxes did not vary with lemming abundance (logistic model: $\chi^2 = 0.43$, df = 1, $P = 0.51$) or nest density ($\chi^2 = 0.05$, df = 1, $P = 0.82$) and was similar among years (yearly mean = 0.46 ± 0.03, $\chi^2 = 2.64$, df = 2, $P = 0.27$). Moreover, when foxes attacked prey, the mean number of attacks performed during a visit did not vary among years (yearly mean: 1.8 ± 0.1 attacks per visit, Kruskal-Wallis test, $\chi^2 = 0.54$, df = 2, $P = 0.76$). The probability that attacks were directed toward nests instead of lemmings was negatively related to lemming abundance, ranging from 100% (n = 47) at low lemming abundance to 50% (n = 48) at moderate lemming abundance (GEE: $\chi^2 = 17.30$, df = 1, $P < 0.0001$). As the overall probability of attack remained stable among years, this indicates that at high lemming abundance foxes reduced their foraging effort on goose eggs when visiting the colony. The proportion of attacks directed toward goose nests also decreased with increasing nest density (GEE: $\chi^2 = 15.6$, df = 1, $P < 0.0001$). However, this negative association likely resulted from the parallel variation of nest density and lemming abundance. We suggest that lemming abundance primarily influenced foraging decisions of arctic foxes because at low lemming abundance foxes concentrated their foraging effort on nests despite their low availability, and at high lemming abundance foxes partially ignored nests despite their relatively high availability.

Activity rate and reproduction of predators

During one lemming cycle (1996 to 1999), changes in activity rate of predators in the goose colony varied among species (Figure 3). Annual activity rate varied 3.5-fold in arctic foxes ($F_{[3,12]} = 23.6$, $P < 0.001$, data log-transformed) and 4.8-fold in parasitic jaegers ($F_{[3,12]} = 124.9$, $P < 0.001$). Highest activity of foxes occurred two years after the lemming peak density, whereas highest activity of parasitic jaegers occurred in the low phase, three years after the lemming peak. In contrast, activity rates of common ravens and glaucous gulls showed little variation throughout the lemming cycle (variations of <1.6-fold: gulls, $F_{[3,12]} = 2.9$, $P = 0.08$; ravens, $F_{[3,12]} = 0.89$, $P = 0.47$).

From 1994 to 2000, a total of 37 arctic fox dens were found (overall estimated density of 15.4 dens per 100 km^2). Presence of breeding foxes was confirmed in five out of seven years but not in 1994 and 1995 when the number of monitored dens was small (Table 1). A total of 77 cubs were observed in 21 dens (mean = 3.67 ± 0.39). Arctic foxes showed a numerical response to rodent densities as their lowest breeding output occurred at low lemming abundance (Table 1).

Total response of predators

From 1996 to 2000, we determined the fate of 1224 goose nests. There were large annual variations in both nest density (3.6-fold) and daily nest mortality rate (12 and 24-fold difference during the early and mid/late nesting periods, respectively; Table 2). The total response of predators varied by 2.7-fold and the lowest predation pressure on nests occurred in peak lemming years (Figure 4). On average, the total number of eggs depredated represented 39 ± 13% of the estimated annual potential nesting production, reaching 88% in 1999, a year of low lemming abundance and low nest density (Table 2, Figure 1). The estimated relative contribution of each predator species to the total response indicates that arctic foxes and parasitic jaegers together caused between 75% (1996) and 94% (1998) of all egg predation (Figure 5). The relative contribution of foxes and jaegers to the total number of eggs depredated varied markedly among years (2.8 and 17.7-fold variation, respectively). In contrast, estimated egg predation by glaucous gulls and common ravens was low and relatively constant despite large fluctuations in prey availability. Their combined impact reduced by <13% the yearly potential goose nesting production.

Results from artificial nest experiments are consistent with those obtained from real goose nests. The mortality rate of artificial nests during the first 5 h of exposure was 2.6 times higher in 1998, two years after the lemming peak, than in 1997 (0.31 ± 0.07 vs. 0.12 ± 0.03, n = 3 plots per year, $\chi^2 = 3.85$, df = 1, $P = 0.05$, Figure 6). Mortality after 12 h of exposure was very high in both years (>90%), which reflects the high vulnerability of nests in the absence of protecting adults. As in real goose nests, arctic fox was the main predator and its relative importance was lower in 1997 than in 1998 (mean proportion of nests depredated by foxes was 77 ± 11% and 100 ± 0%, respectively, n = 3 plots per year, $\chi^2 = 4.35$, df = 1, $P = 0.04$). These experiments showed that annual variations in nest predation rate and in the relative importance of different predators were not due to behavioural changes of geese such as nest attentiveness or nest defence intensity.

Discussion

The predictions of the hypothesis that cyclic lemming populations indirectly affect the breeding production of snow geese through direct interactions with shared predators were supported by our results. First, predators appeared to hunt primarily lemmings (the focal prey) although attack rates on geese increased in low lemming years. Second, activity rates of predators in the goose colony were generally reduced in peak lemming years. Third, arctic foxes showed a numerical response to rodent densities. Finally, the predation pressure on goose eggs was cyclic and lowest in peak lemming years. It appears that the indirect interaction is mediated by both the behavioural and numerical responses of shared predators to oscillations in rodent abundance. This is one of the first field evidence of such interactions. Although our analysis is mostly based on data from one study area and one lemming cycle, our study provides strong support for the occurrence of both short-term and long-term indirect effects mediated by shared predators in an arctic tundra community.

Short-term indirect effects and behavioural mechanisms

Several mechanisms can generate short-term indirect effects among prey. Constraints on predator foraging such as the time required to handle prey may lead to mutually positive indirect effects because time spent handling one prey may reduce the time available for capturing other prey (Holt 1977). In addition, changes in predator behaviour that affect its relative and/or absolute effort in capturing different prey may generate apparent mutualism (Abrams and Matsuda 1993). An example of this type of indirect effect is the well-known prey-switching behaviour of predators (Lawlor and Maynard Smith 1976). Prey-switching may occur in response to changes in the relative abundance of prey and the resulting changes in relative profitability of foraging on those prey (Murdoch and Oaten 1975).

In arctic foxes, we showed that the overall frequency of attack on prey (either lemming or goose nest) when visiting the goose colony remained relatively constant among years despite fluctuations in prey availability. Therefore, it appears that attacks directed on eggs are at the expense of those directed on lemmings, and vice versa. Our results also suggest that lemming availability primarily drives foraging decisions in arctic foxes and that predators increase their foraging effort on goose nests when lemmings, their preferred prey, are not as abundant. These observations indicate that predators attacked prey selectively and that changes in foraging behaviour during the lemming cycle could be part of a prey-switching behavioural response. Even though there is much evidence in favour of switching behaviour in invertebrate predators (Murdoch and Oaten 1975), very few studies have demonstrated this in vertebrate predators under field conditions (O'Donoghue et al. 1998).

The most profitable foraging strategy for a predator is often to maximize the trade-off between energy reward and foraging costs rather than to maximize energy gain alone (Stein 1977). Foraging costs may include risk of injury, energy expenditure or missed foraging opportunities. The risk of injury can be an important cost for predators foraging within colonies of birds that perform active defence (Gilchrist, Gaston & Smith 1998). Therefore, predators foraging in snow goose colonies may be facing a trade-off between energy gain and foraging costs (e g. Samelius & Alisauskas 2001), and lemming abundance may influence the fitness benefits of eggs (see Schmidt 1999). The increase in attack rate when geese were in a position of defending their nest (i.e. a more costly and potentially risky situation) indicates that predators increased their foraging effort on nests at low lemming abundance.

We suggest that the indirect effect resulting from these behavioural mechanisms is a reciprocal positive-positive apparent mutualism between lemmings and geese on a short time scale (e.g. within a single predator generation). Nevertheless, intensive predator studies with marked individuals would be required to better evaluate the inter-individual variations in behavioural responses under fluctuating prey availability.

Numerical response of predators

A time lag in the increased activity of arctic foxes and parasitic jaegers in the goose colony with respect to the lemming peak may result from a delayed increase in predator population due to improved reproduction at high lemming densities (reproductive numerical response). Alternatively, or additionally, these fluctuations may be due to aggregative movements of predators to more profitable foraging areas with decreasing lemming abundance (aggregative numerical response). We suggest that both of these mechanisms occurred at our study site.

Generally, arctic foxes numerically track rodent populations with a time lag of one year in areas where rodent populations cycle (Macpherson 1969). Variation in reproductive rates is thought to be the main factor generating time lag between lemming and arctic fox population densities (Angerbjörn et al. 1999). Our results are consistent with previous reports showing that reproductive output of foxes is good when lemming abundance is high and negligible when lemming populations crash (e.g.

Macpherson 1969, Tannerfeldt and Angerbjörn 1998). Breeding arctic foxes are generally territorial with little overlap among neighbouring foxes (Anthony 1997). Therefore, local density of foxes may be limited by territoriality, thereby limiting the number of individuals foraging in a local food patch such as in a bird colony. However, an increase in the number of non-territorial foxes (i.e. non-breeders and wanderers) following lemming population decline may contribute to an increase in fox densities in bird nesting areas (Underhill et al. 1993).

Despite the availability of an abundant and predictable food source during the summer (i.e. large goose colony), our results suggest that arctic foxes primarily relied on lemmings to breed successfully. Nevertheless, the use of an additional food source such as birds during the summer may contribute to the breeding success of foxes and may be important for the maintenance of arctic fox populations in the low phase of the rodent cycle for several reasons (see also Macpherson 1969). First, the survival of pups is related to summer food availability (Tannerfeldt et al. 1994). Second, food caches made during the summer can be used in the fall, and even during the winter and the following spring (Bantle and Alisauskas 1998). In goose colonies, most eggs depredated by foxes are cached for future consumption (>80%; Stickney 1991, Bêty and Gauthier unpubl. data). Cached food may enhance winter survival of adult foxes (Macpherson 1969) and the number of young born in the following year (Angerbjörn et al. 1991). Consequently, the resulting indirect interaction mediated by the reproductive numerical response of foxes is most likely a negative-negative long-term apparent competition between lemmings and geese.

In contrast to foxes, the intense foraging activity of parasitic jaegers in the goose colony in the low phase of the lemming cycle may mostly result from an aggregative rather than a reproductive numerical response. The high mobility of avian predators allows them to migrate seasonally and they can aggregate rapidly in the most profitable foraging patches (e.g. Korpimäki 1994). Nonbreeding avian predators may also concentrate in areas of relatively high prey density (Norrdahl and Korpimäki 2000). Thus, a low breeding effort and/or a high breeding failure rate because of intraguild predation may lead to the concentration of avian predators in the vicinity of bird nesting areas in the low phase of the lemming cycle. If we assume that the indirect interaction with parasitic jaegers is mediated by an aggregative response, the resulting effect would be a short-term (within a single predator generation) apparent mutualism between lemmings and geese.

Rodent cycles and predation on birds

The foraging decisions made by shared predators will influence the resulting indirect interactions among prey (Holt 1977). In general, prey selection by a predator will depend on its preference hierarchy (e.g. Fairweather 1985), the ability of alternative prey to resist predation (e.g. Schmitt 1982), and the relative abundance of alternative prey (e.g. Murdoch 1969). The relative vulnerability of birds should therefore influence the optimal foraging decision of egg predators (Schmidt 1999), which in turn should affect the outcome of indirect interactions between cyclic rodents and birds.

If bird eggs are temporarily abundant and easy to catch, they may become the primary prey item in the summer diet of foxes in spite of a high abundance of rodents (e.g. in waterfowl nesting areas, Stickney 1991). In this case, the impact of predation should depend more on the ratio of predator/alternative prey than on the abundance of rodents (Norrdahl & Korpimäki 2000). In contrast, if the alternative prey is relatively difficult to capture, predators should concentrate their foraging activity on this prey only if the abundance of the main prey is low, and the impact of predators should depend primarily on the density of rodents (Norrdahl & Korpimäki 2000).

Our results support the latter scenario. Predators of lemmings and snow goose eggs appeared to primarily target rodents, and increased their foraging effort on eggs when rodent population declined. Active nest defence by geese was the primary factor limiting foraging success of predators. The high intensity of egg predation at low lemming abundance was not due to a higher success rate of attacks by predators but to a much higher frequency of attacks on goose nests.

Shared predators and arctic-nesting birds

Our results indicate that both short-term, positive effects and long-term, negative effects occurred between lemmings and geese. This conflict between indirect interactions has also been found in other systems (see Holt 1977, Holt and Lawton 1994), but the outcome of these antagonistic indirect interactions is difficult to predict in natural ecosystems (Abrams and Matsuda 1996). Mathematical models predict that cyclic population fluctuations may weaken apparent competition because the variability in prey abundance reduces the average density of predators (Abrams et al. 1998). In arctic ecosystems, it has been suggested that rodent populations could have an overall long-term positive effect on birds, especially those more vulnerable to arctic foxes (e.g. ducks and waders; Larson 1960).

In some areas devoid of lemmings, arctic fox populations are generally dependent on abundant localized prey such as large seabird colonies or dead carcasses of large mammals (e.g. Angerbjörn, Hersteinsson and Lidén 1994). However, in most terrestrial arctic regions, foxes act as specialist lemming predators and probably none or little alternative prey can maintain fox populations (Macpherson 1969, Angerbjörn et al. 1999). Consequently, we suggest that apparent competition mediated by the long-term numerical response of predators may be the dominant indirect interaction between lemmings and most terrestrial arctic-nesting birds. Large-scale empirical and experimental studies of the long- and short-term responses of predators to changes in prey availability are required to better highlight indirect trophic interactions in Arctic tundra.

Our main conclusion is that shared predation has considerable effects on the nesting production of greater snow geese, although other factors (e.g. food availability and climatic conditions) may also influence their breeding success (Gauthier et al. 1996, Skinner et al. 1998). In some arctic goose populations, egg and gosling predation may significantly limit population growth (e.g. Summers 1986), but this is apparently not a general phenomenon (e.g. Cooke et al. 1995). Theory of food chains dynamics (exploitation ecosystem hypothesis: Oksanen and Oksanen 2000) predicts that predators do not control herbivores in unproductive arctic environments and that the plant-herbivore interaction should be the dominant trophic interaction. However, the properties of each community may depend largely on the unique adaptations of the component species (Krebs et al. 1999). Our study provides direct evidence that birds nesting in a high arctic region can experience high, though variable, predation pressure. These observations are in accordance with previous suggestions that the distribution and the reproductive success of some terrestrial arctic-nesting birds could be strongly influenced by co-existing prey like cyclic lemmings via the response of shared predators. Therefore, predator-prey interactions may be more important than previously thought in structuring some arctic communities.

TABLE 1. Breeding production of arctic foxes on Bylot Island from 1994 to 2000. Litter sizes (mean ± 1SE) are minimum estimates of the number of cubs.

Year	Relative lemming abundance	No. of dens monitored	No. of breeding dens	Breeding dens per 100 km^2	Litter size	Breeding production (cubs per 100 km^2)
1994	MODERATE	11	0	0	-	0
1995	LOW	11	0	0	-	0
1996	HIGH	18	3	2.6	5.7 ± 0.8	14.6
1997	MODERATE	23	3	2.0	5.0 ± 0.3	10.0
1998	MODERATE	31	8	4.0	2.9 ± 0.2	11.5
1999	LOW	35	2	0.9	2.0 ± 0.7	1.8
2000	HIGH	37	5	2.1	3.6 ± 0.3	7.5

TABLE 2. Annual variation in snow goose nesting parameters on Bylot Island from 1996 to 2000. Daily nest mortality rates (Mayfield estimate) were calculated for two periods: Early (laying and first seven days of incubation) and Mid/late (8th day of incubation until hatching). Nest mortality rate (NMR) for the entire nesting period was calculated using the Product Method (Johnson 1979). Years accompanied by different letters indicate significant differences in NMR (α = 0.005, Bonferroni correction). Mean ± 1SE.

			Clutch size		Daily nest mortality rate			Nesting production[c]	
Year	n	Density[a]	TCL[b]	CSH[b]	Early	Mid/late	NMR	Potential	Real
1996	237	50	4.0 ± 0.1	3.6 ± 0.1	0.023 ± 0.003 a	0.014 ± 0.002 a	0.38 ± 0.03 a	200	112
1997	284	132	4.2 ± 0.1	4.0 ± 0.1	0.011 ± 0.002 b	0.002 ± 0.001 b	0.15 ± 0.02 b	554	450
1998	326	179	4.0 ± 0.1	3.7 ± 0.1	0.009 ± 0.002 b	0.006 ± 0.001 b	0.18 ± 0.02 b	716	544
1999	179	55	3.1 ± 0.1	2.4 ± 0.2	0.094 ± 0.010 c	0.048 ± 0.006 c	0.85 ± 0.03 c	171	20
2000	198	82	3.5 ± 0.1	3.3 ± 0.1	0.008 ± 0.002 b	0.006 ± 0.001 b	0.17 ± 0.03 b	287	224

[a] Nests per 50 ha

[b] TCL = Total clutch size, and CSH = Clutch size at hatching

[c] Estimated nesting production (eggs per 50 ha): Potential = Nest density * TCL, Real = Nest density * (1-NMR) * CSH

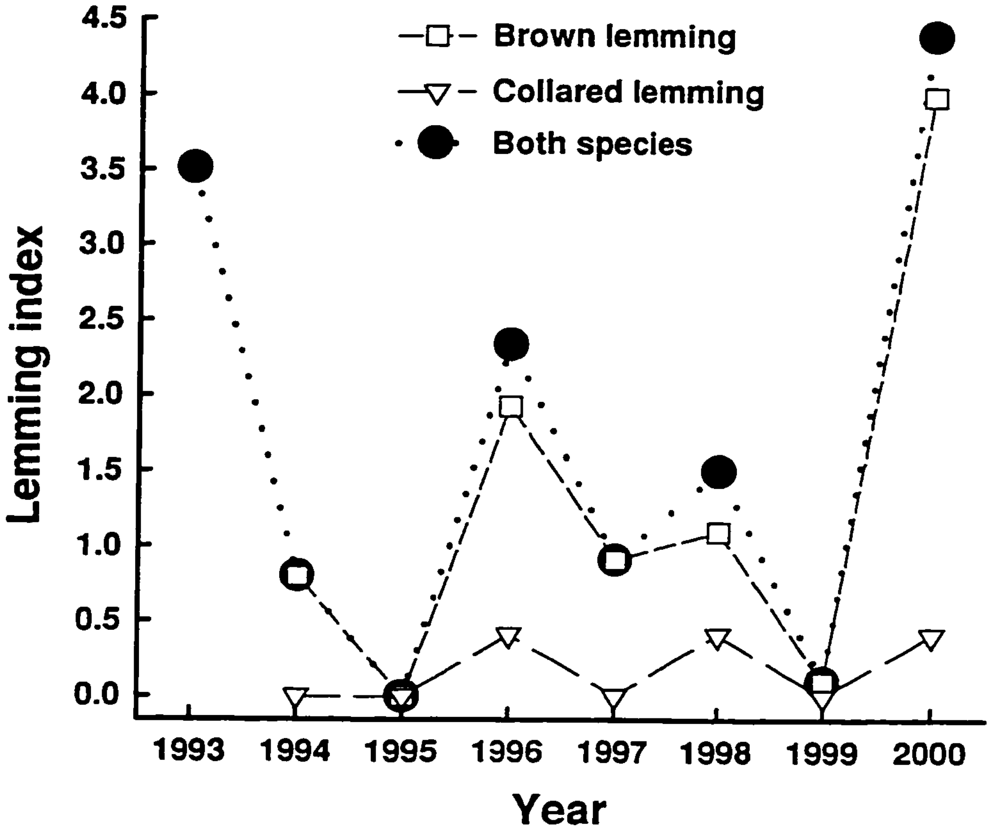

FIGURE 1. Index of lemming abundance (number caught per 100 trap-nights) in July on Bylot Island from 1994 to 2000. Lemming index in 1993 was estimated using lemming nest surveys (see Chapter 2 for details).

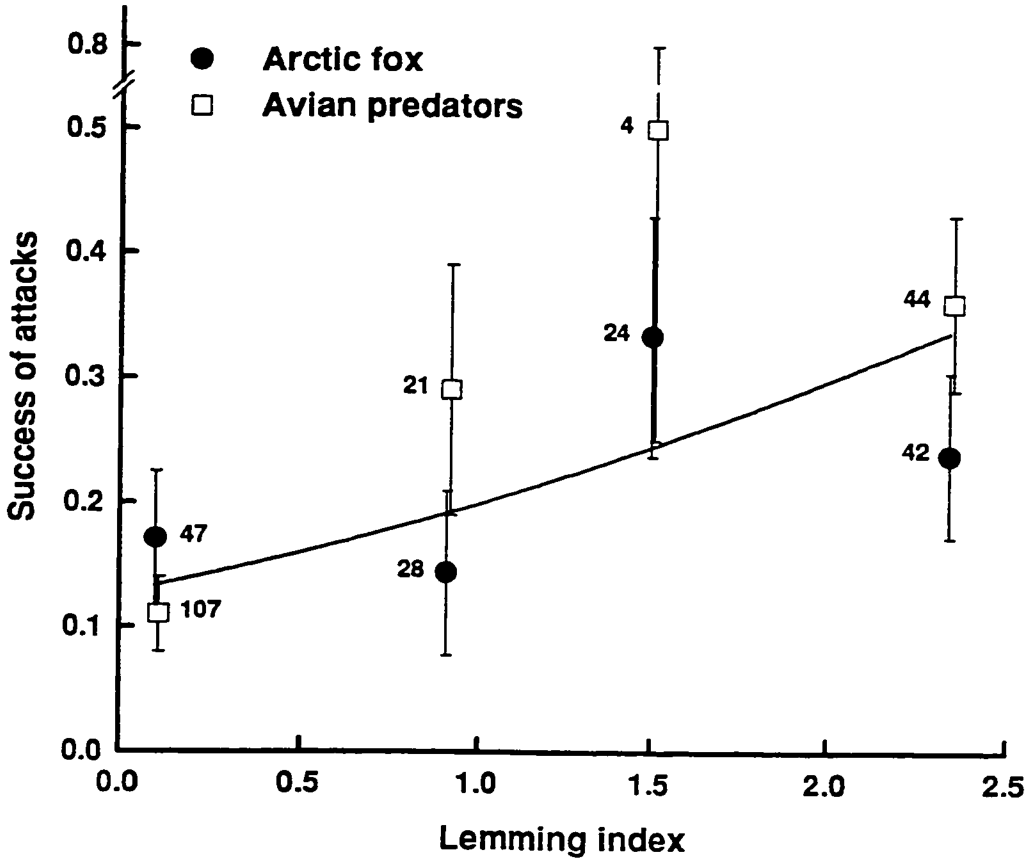

FIGURE 2. Proportion of nest attacks by predators that were successful in relation to the index of lemming abundance (both species), Bylot Island (1996 to 1999). To illustrate the adequacy of the model, annual success of predators are given for the two types of predators (arctic fox or avian predators). Number of attacks is shown and error bars are 1SE. GEE: lemming index, $\chi^2 = 12.7$, df = 1, $P = 0.0004$; nest density ($\chi^2 = 1.51$, $P = 0.22$), type of predators (arctic fox or avian, $\chi^2 = 0.53$, $P = 0.46$), and interaction terms ($P > 0.20$) were removed from the final model (df = 1 in all cases).

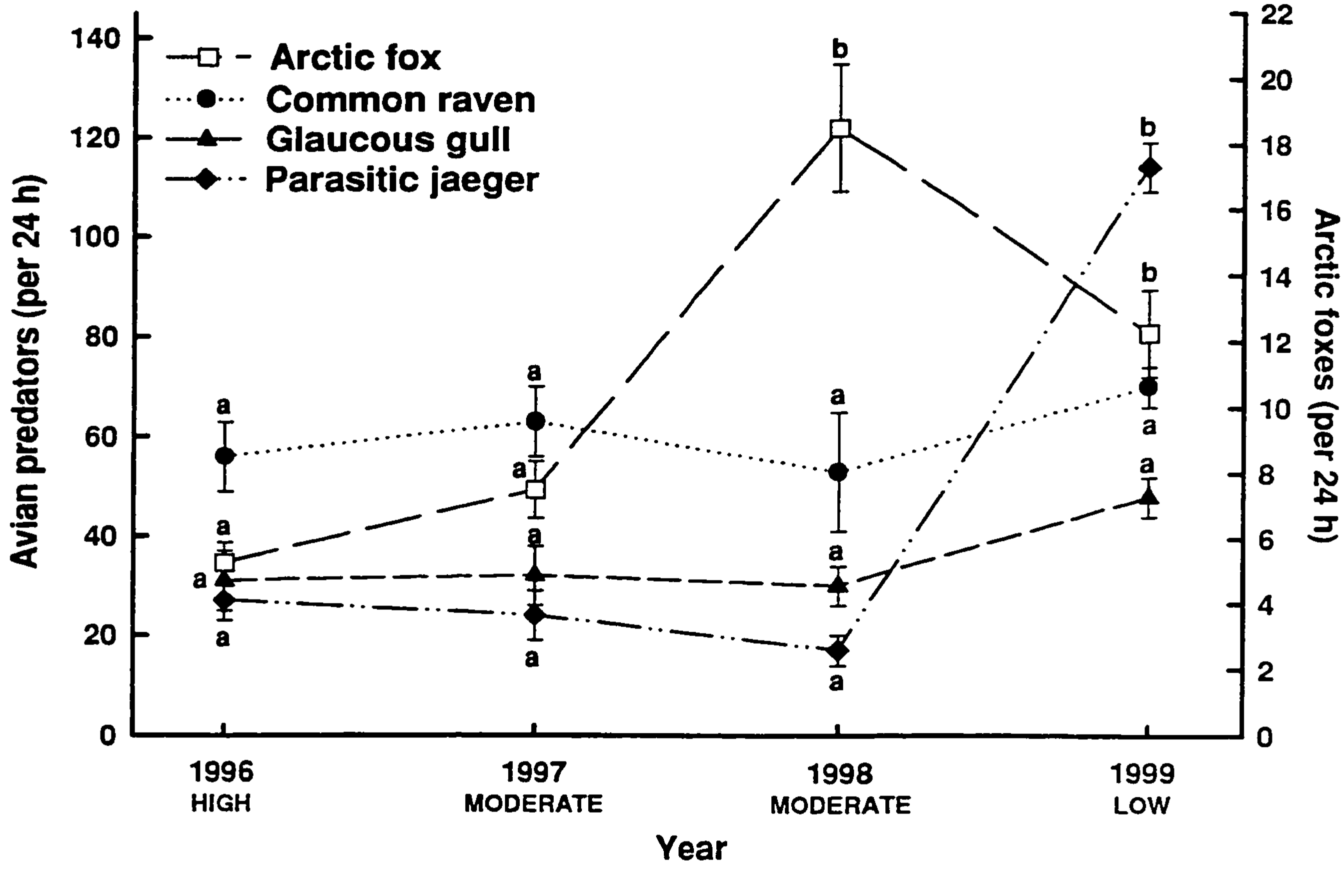

FIGURE 3. Annual variations in activity rate of nest predators in a snow goose colony during one complete lemming cycle on Bylot Island (mean ± 1SE, n = 4 complete 24-h cycle for each data point). Years accompanied by different letters differed significantly within species (A posteriori multiple comparisons with Tukey's adjustment, $p < 0.05$). Relative lemming abundance is indicated under corresponding years.

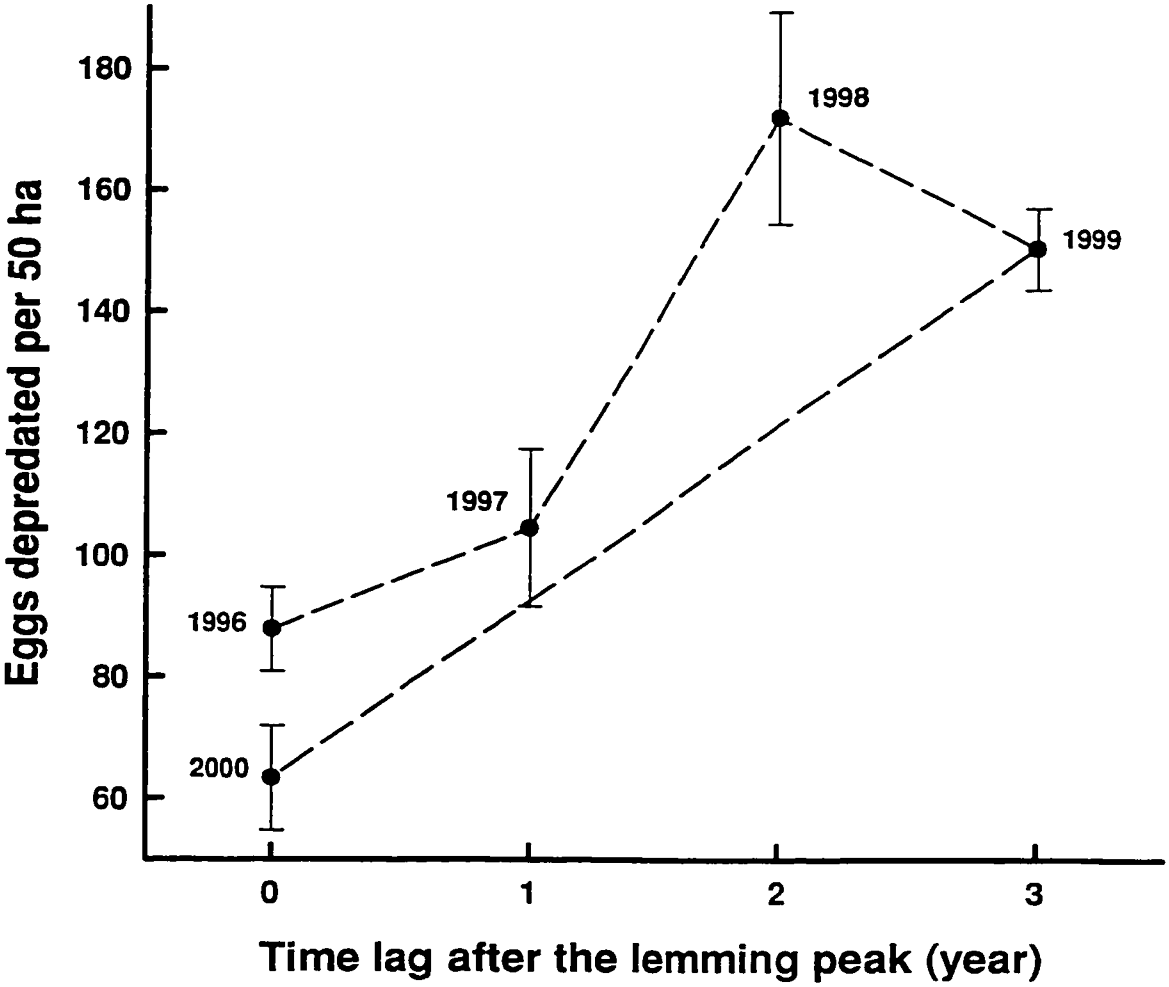

FIGURE 4. Annual variations in the number of goose eggs depredated (total response of predators) with respect to the phase of the lemming population cycle on Bylot Island. Years are indicated near each data point (mean ± 1SE).

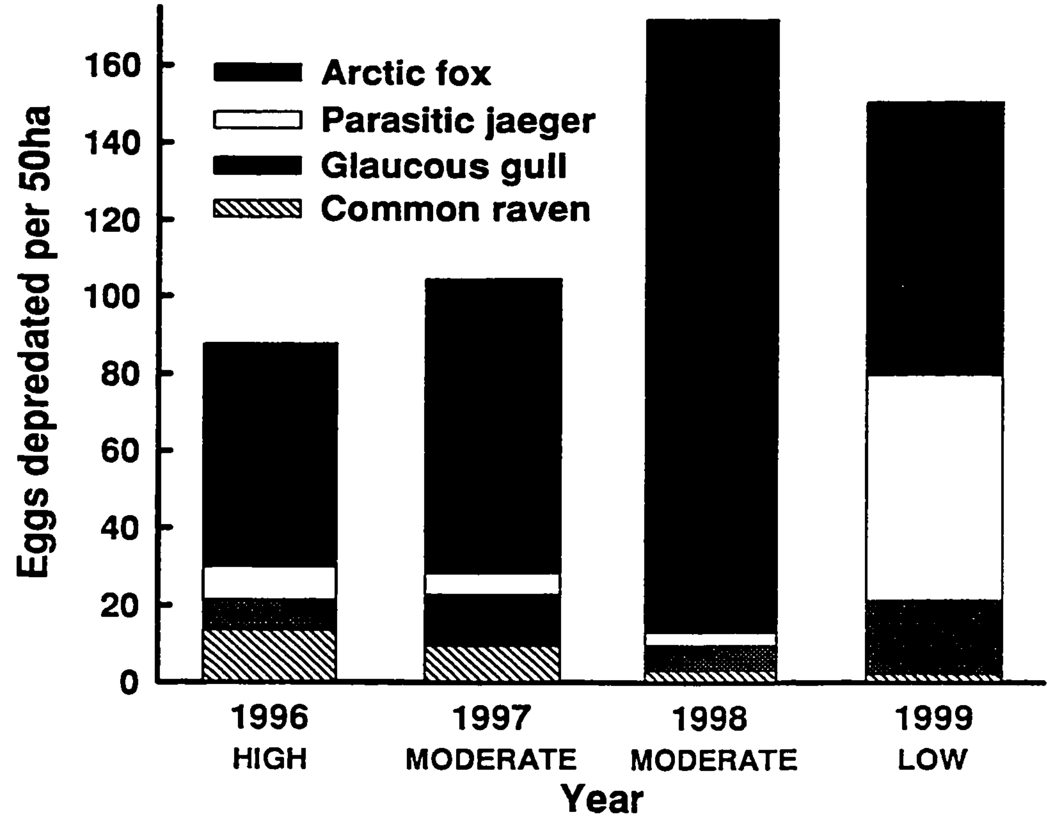

FIGURE 5. Estimated relative contribution of each predator species to the total number of goose eggs depredated during one lemming cycle on Bylot Island. These estimates were calculated using the relative nest attack rates (n = 317 attacks) and the total response of predators (see Methods). Relative lemming abundance is indicated under corresponding years.

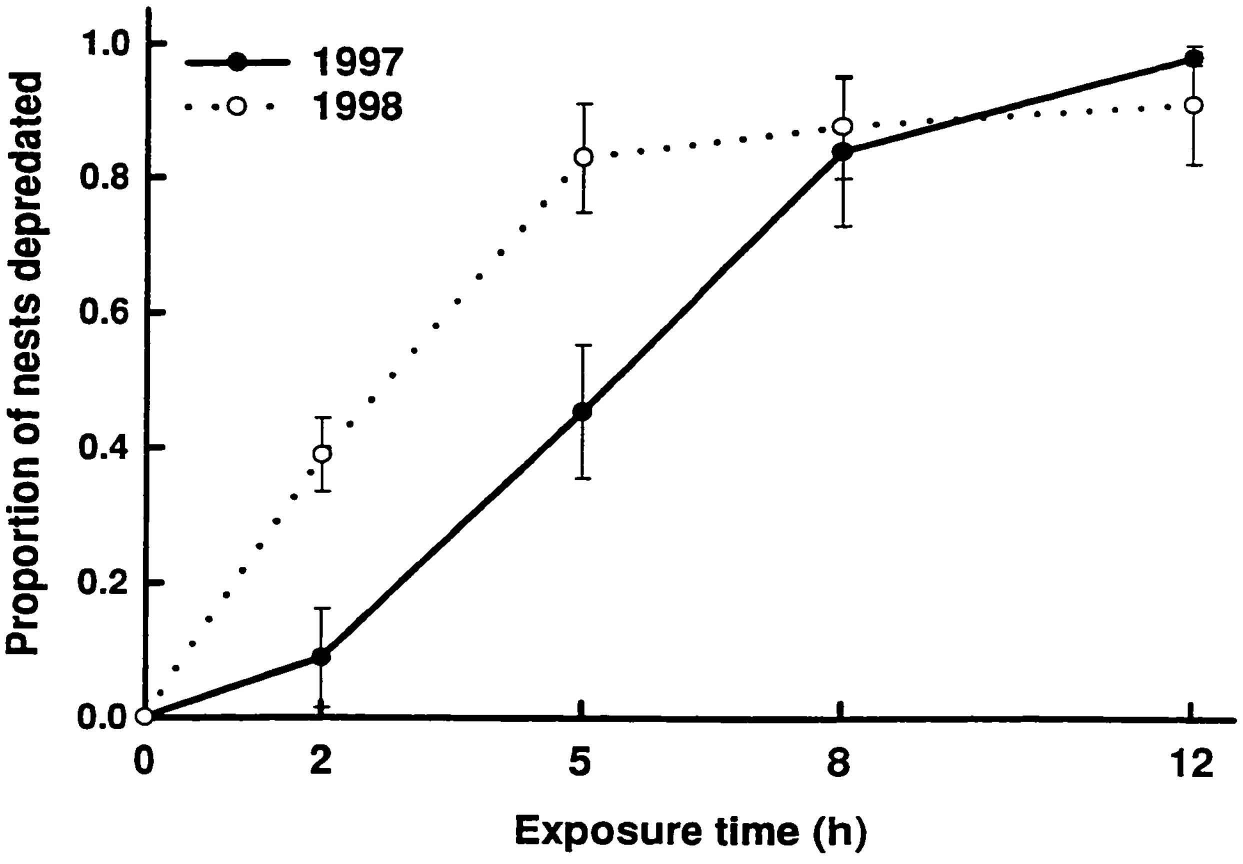

FIGURE 6. Predation rate on artificial nests in relation to the time that nests were exposed to predators in a snow goose colony one (1997) and two (1998) years after a peak of lemming abundance (mean ± 1SE, n = 3 plots for each data point).

Chapitre 4

BODY CONDITION, MIGRATION AND TIMING OF REPRODUCTION IN SNOW GEESE: A TEST OF THE CONDITION-DEPENDENT MODEL OF OPTIMAL CLUTCH SIZE

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Résumé

Le déclin saisonnier de la taille de ponte chez les oiseaux pourrait résulter du conflit entre les avantages de pondre tôt (augmentation de la qualité des jeunes) et les avantages d'un délai du moment de la ponte (augmentation de la condition corporelle et ainsi de la taille de ponte). Nous avons testé, chez une espèce migratrice nichant dans l'Arctique, des prédictions d'un modèle de décisions individuelles optimales dépendantes de la condition fondé sur cette prémisse générale (Rowe et al. 1994). Lors de leur halte migratoire principale (au sud du Québec), nous avons d'abord déterminé la condition corporelle pré-migratrice (basée sur les profils abdominaux) et la date de départ relative de femelles Grandes Oies des neiges (*Chen caerulescens atlantica*) marquées avec un radio-émetteur. Nous avons ensuite déterminé la date d'arrivée sur l'aire de reproduction dans l'Arctique canadien, 3000 km plus au nord, ainsi que la date et la taille de ponte subséquentes des femelles marquées. La date de départ était bien synchronisée entre les individus et la durée de migration était fortement corrélée avec la date d'arrivée. La date d'arrivée n'était pas significativement reliée à la date de départ ni à la condition pré-migratrice. Le délai entre l'arrivée et la date de ponte (pré-ponte) a varié considérablement entre les individus (estimations minimales variant de 0 à 10 jours, n = 30). Tel que prédit par le modèle de décisions optimales, les premières femelles arrivées sur l'aire de reproduction ont eu une pré-ponte plus longue et ont initié la ponte plus tôt que les dernières arrivées. De plus, en contrôlant statistiquement pour la date d'arrivée, la date de ponte était négativement reliée à la condition pré-migratrice. Finalement, la taille de ponte n'était pas reliée à la condition pré-migratrice en contrôlant pour le déclin saisonnier. Notre étude suggère que les oies ajustent leur stratégie de reproduction (date et taille de ponte) en fonction de leur condition corporelle et la chronologie de leur migration de façon à optimiser leur succès reproducteur attendu.

Abstract

The seasonal decline of clutch size in birds may result from the conflict between the advantage of early breeding (greater offspring value) and the advantage of a delay in laying date (improved body condition and hence clutch size). We tested some predictions of the condition-dependent individual optimal model based on this trade-off (Rowe et al. 1994) in a long-distant migrant breeding in the Arctic. We first determined the relative pre-migratory body condition (based on abdominal profile indices) and departure date of 49 radio-marked female greater snow geese (*Chen caerulescens atlantica*) from their main staging area (southern Quebec). Then, we determined their arrival date on the breeding ground in the Canadian Arctic, 3000 km further north, and their subsequent laying date and clutch size. Departure date was well synchronized among individuals and migration duration was highly correlated with arrival date. Arrival date was not significantly related to departure date or pre-migratory condition. Delay between arrival and laying date (pre-laying) was greatly variable among females (minimum estimates ranging from 0 to 10 days). As predicted by the optimal model, early-arriving females had longer pre-laying period and initiated their nests earlier than late ones. Also, after controlling statistically for arrival date, laying date was negatively related to pre-migratory condition. Finally, clutch size was not related to pre-migratory condition after controlling for the seasonal decline. Our study indicates that geese adjust their breeding strategy (laying date and clutch size) relatively to their body condition and migration chronology in order to optimize their expected reproductive success.

Introduction

The timing of breeding is critical for a successful reproduction in seasonal environments (Schultz 1991, Einum and Fleming 2000, Thomas et al. 2001). Therefore, parents should time their reproductive effort to maximize the number of surviving offspring (Perrins 1970). Yet, in most bird species, individuals that reproduce early in the breeding season lay a larger clutch size and reach a higher reproductive success than those that breed late (e.g. Daan et al. 1988, Rohwer 1992, Smith 1993).

Theory of life history strategy predicts that reproductive decisions of an individual should be adapted to environmental conditions (e.g. food availability, predation risk or weather condition) and intrinsic properties (e.g. body size and foraging efficiency). If individuals are able to perceive these differences, then their life history traits are expected to follow an optimal reaction norm with respect to the relevant circumstances (Kisdi et al. 1998). In birds, the seasonal decline in clutch size is generally associated with a seasonal decline in offspring survival prospects (e.g. Perrins 1966, Daan et al. 1990, Hochachka 1990). The relationship between timing of breeding and clutch size may be the outcome of a conflict between the advantage of breeding early (greater offspring value) and the advantage of a delay in breeding (improved body condition and hence potential clutch size). This idea, referred to as the cost-of-delay hypothesis (Drent and Daan 1980), predicts that birds in poor condition have more to gain from a delay in breeding than birds in good condition.

Rowe et al. (1994) formalized this hypothesis into a dynamic model of condition-dependent individual optimal strategy (Figure 1). Their model predicts optimal combinations of clutch size and timing of breeding based on the initial condition of individuals and the onset of condition gain (e.g. their arrival date on breeding grounds; Rowe et al. 1994). Assuming that there are differences among individuals in their condition at the start of the breeding season or in their onset of condition gain, the model predicts a seasonal decline in clutch size.

There is a growing body of evidence that the energetic requirement of laying plays an important role in determining optimal breeding decisions in birds (Monaghan and Nager 1997, Stevenson and Bryant 2000). In precocial species such as migratory wildfowl, it is generally recognized that clutch size limitation can operate at the egg-laying stage (Rohwer 1992, Cooke et al. 1995). In arctic-nesting geese, endogenous reserves acquired prior to arrival on breeding grounds were traditionally considered the primary source of nutrients for egg formation (Ryder 1970, Ankney and MacInnes 1978). However, recent studies showed that exogenous nutrients acquired on the breeding grounds during the pre-laying and laying period could be as important for egg formation as endogenous reserves acquired on staging areas (Bromley and Jarvis 1993, Choinière and Gauthier 1995, Ganter and Cooke 1996, Carrière et al. 1999). As a result, the nutrient reallocation hypothesis, originally proposed to explain the seasonal decline in geese (Ryder 1970), was rejected and the condition-dependent individual optimal model has been invoked to explain why late-nesting geese lay fewer eggs (see Ganter and Cooke 1996, Lepage et al. 2000).

Several predictions of this individual optimal model with respect to both the migratory behaviour and body condition of individuals have nonetheless never been tested. First, the model predicts that early-arriving birds should experience a longer delay on the breeding grounds and lay earlier than late arriving ones after controlling for their initial condition (individual A vs. C in Figure 1). Second, birds in better condition should have a shorter delay on the breeding grounds and thus lay earlier than individuals in poor condition after controlling for their arrival date (individual A vs. B in Figure 1). Third, after controlling for the effect of laying date, we expect no residual effect of initial condition on clutch size.

Our goal was to test these predictions in the greater snow goose (*Chen caerulescens atlantica*), a long distance migrant that breed in the High Arctic. This species exhibits a strong seasonal decline in clutch size (Lepage et al. 2000) and a steep seasonal decline in gosling survival due to environmental factors (Lepage et al. 1998, Lepage et al. 1999). Greater snow geese accumulate large amount of fat and protein on their main staging area in southern Quebec prior to their 3000-km spring migration to the Arctic (Gauthier et al. 1984, 1992). However these reserves are depleted during migration (up to 50%, Gauthier et al. 1992) and exogenous nutrients acquired through feeding on the breeding grounds make a significant contribution to egg formation, allowing pre-laying birds to improve their body condition (Gauthier and Tardif 1991, Choinière and Gauthier 1995). Because greater snow geese breed in a highly seasonal environment, they are good candidates to test predictions of the condition-dependent optimal model of reproductive decisions.

The originality of this study was our ability to relate events occurring during the spring migration at a distant staging area to the subsequent reproductive decisions of individuals once on the breeding grounds. We accomplished that by radio-tracking females at their spring staging area where we determined their pre-migratory body condition and departure date, and on their breeding grounds where we established their arrival date, laying date and clutch size.

Materials and methods

We captured female greater snow geese in August at the Bylot Island migratory bird sanctuary (73° 08', 80° 00'; Figure 2) during their moulting period (see Blouin et al. 1999 for details). In 1996 and 1997, we fitted 131 adult females with a radio transmitter affixed to a neck collar engraved with 2-alphanumeric codes (total weight 59 ± 9 g, 2.50 ± 0.02% of bird body mass) (Demers 2000). Only family groups were captured, and thus all birds were at least two years old or more because snow geese do not breed as yearlings and few do so successfully at two years of age (Cooke et al. 1995). Longevity of radios was about 16 to 24 months. On the staging area, the range was generally 1-3 km on the ground and 4-5 km in the air but reach 5-10 km and 10-20 km respectively in the open arctic habitat, respectively (see also Hughes et al. 1994). Transmitters had no significant effect on activity budget of individuals during the spring following marking but negatively affected some reproductive parameters (slight delay in laying date and decrease in clutch size; Demers 2000). We assumed that these effects were similar among marked females and that transmitters did not bias comparisons among them.

In 1997 and 1998, we radio-tracked geese on their spring staging area along the St-Lawrence River in southern Quebec and on their breeding ground in Nunavut (Figure 2). From the end of March to the departure of the last radio-marked birds at the end of May, we tracked birds on the staging area daily using vehicle-mounted receiving systems. Aerial tracking by plane was also conducted every week. On the breeding ground, we tracked birds during the pre-laying, laying and early incubation periods (27 May to 20 June) in two main nesting areas located 30 km apart on Bylot Island (see Chapter 2 for description of the goose colonies; Figure 2). We conducted tracking sessions (1 to 4 h) every one or two days from towers located on elevated ground at each area. We also used a receiving system mounted on a snowmobile to track birds in the surroundings of these nesting areas (<15 km; 26 May to 10 June). Finally, aerial tracking by helicopter was conducted every week over the south plain of Bylot Island (c.a. 1600 km^2, Figure 2) starting in early June. During laying and early incubation, we searched by foot the nests of females whose signal had been detected.

We defined departure date as the date of the last radio detection on the staging area, and arrival date as the date of the first radio detection on the breeding ground. Daily detection probability (DDP) was 80% after 10 May on the staging area and 74% on the breeding ground during the pre-laying period (e.g. for calculation: DDP on staging area = 100 × number of days individuals were detected from 10 May to their departure date / total number of days from 10 May to departure date of individuals). The probability of missing an individual for 2 days was thus 4% and 6% on staging area and breeding ground, respectively. Consequently, we are confident that our observations provided reliable estimates of departure and arrival dates of individuals relative to each others. The migration duration was defined as the difference between arrival and departure dates. For birds whose nests were found, we determined laying date (date of first egg laid, see Lepage et al. 1999) and clutch size (maximum number of eggs found in a nest after the start of incubation). Geese do not renest after a clutch failure (Lepage et al. 2000). The pre-laying duration was the difference between the onset of laying and arrival dates. Because DDP of nesting birds was 83% during the pre-laying period, pre-laying durations are thus minimum estimates.

To estimate body condition of geese on spring staging area, we used the abdominal profile index, which provides an estimate of stored energy by scoring the roundness of the abdominal region (Owen 1981, Brown 1996). In geese, the abdominal cavity is a site of fat deposition and abdominal fat is a good indicator of overall body fat (Gauthier and Bédard 1985). Profiles were scored subjectively from a distance using a scope (20-60X) and a 6-category scale with an intermediate level between categories. In greater snow geese, abdominal profile indices are linearly related with body mass corrected for body size (PC1) although there is considerable variation among individuals assigned to the same category (Féret, Bêty, Gauthier and Giroux, ms in preparation). Variability in abdominal profile score (see Brown 1996) was reduced for radio-marked birds by having four experienced and well-calibrated observers for most observations (>75%).

The pre-migratory condition of marked females was defined as the latest condition index observed <10 days prior to the annual median departure date from the staging area. Restricting this interval to a shorter period would force us to discard too many birds. We standardized their body condition scores using the seasonal changes in abdominal profile of the geese population. Seasonal change was characterized throughout the staging period by determining the abdominal profile of random samples of adults. We made observations in four regions located throughout the staging area. In each region, we scored the profile of about 50 randomly selected unmarked adults in general every 5 days. Although we could not reliably distinguish sexes in those birds, males and females store similar amount of fat during the staging period (Gauthier et al. 1992). We used the difference between the abdominal profile measured in radio-marked female and the value predicted from the year-specific linear relationship between date and abdominal profile for the whole population as an index of body condition for radio-marked females.

Data analysis

The GLM procedure of SAS (1999) was used to perform least-square multiple linear regressions. We visually inspected residuals to detect violation of the assumptions required for analysis. Variables were transformed as the deviation from the yearly median for statistical analyses at the individual level. All models included year as a covariate and interaction terms. Terms for which SAS Type III SS had $P >$ 0.05 were dropped sequentially from full regression models. Medians were compared using Kruskal-Wallis tests (Siegel and Castellan 1988). We calculated a Pearson correlation coefficient between migration length and arrival date. Unless otherwise indicated values provided are the mean ± SE.

Results

In 1997 and 1998, a total of 49 radio-marked females with known pre-migratory body condition were subsequently tracked on the breeding ground, and 30 of them were found nesting. The median departure date was earlier in 1998 than in 1997 (Kruskal-Wallis, $\chi^2 = 31.6$, df = 1, $P < 0.001$; Figure 3). Departure from staging area was synchronized within a year, with virtually all birds leaving over an 8-day period. Migration duration varied considerably among individuals and was longer in 1998 (median = 25, range 11 to 31) than in 1997 (median = 18, range 11 to 28; Kruskal-Wallis, $\chi^2 = 13.6$, df = 1, $P =$ 0.0002). Arrival on the breeding ground was less synchronized than departure, being spread over a 13 to 15-day period each year, but median arrival date was similar in both years (Kruskal-Wallis, $\chi^2 = 0.66$, df = 1, $P = 0.42$; Figure 3). Median laying date was earlier in 1998 than 1997 (11 June, n = 28 and 14 June, n = 21, respectively, $\chi^2 = 5.2$, df = 1, $P = 0.02$). The delay between arrival and laying date (pre-laying) was highly variable among birds but did not differ between years (1997, median = 2.5 days, n = 12, range 0 to 9, and 1998, median 2 days, n = 18, range 0 to 10; Kruskal-Wallis, $\chi^2 = 0.02$, df = 1, $P =$ 0.88).

Seasonal change in body condition of geese on the staging area was similar over the two years of the study, although daily rate of condition increase was slightly higher in 1997 relative to 1998 (0.039 ± 0.001 vs. 0.030 ± 0.001 API per day, $F_{1,1395} = 17.06$, $P < 0.0001$; Figure 4). Pre-migratory condition index varied considerably among marked birds and spread over 2.5 abdominal profile score. Departure date of individuals from the staging area was not related to their pre-migratory body condition (linear regression: $r^2 = 0.001$, $n = 49$, $P = 0.77$). Similarly, arrival date of individuals on the breeding ground was not related to their departure date or pre-migratory body condition index (Figure 5).

Since departure was well synchronized, migration length of individuals was highly correlated with their arrival date (Figure 6). Thus, assuming that the energetic balance of migration is similar for birds with the same duration of migration, the post-migratory body condition of individuals arriving at the same time on the breeding ground should be related to their pre-migratory body condition. Therefore, after controlling statistically for the effect of arrival date (i.e. energetic balance of migration), relative pre-migratory body condition should reflect the relative post-migratory condition for birds with similar migration duration. Based on this assumption, we then tested our three predictions of the condition-dependent optimal model. First, early-arriving females had longer pre-laying period than late ones (Figure 7) and initiated their nests earlier than late-arriving ones after controlling statistically for their pre-migratory body condition (Figure 8A). This supports the first prediction. Second, laying date was negatively related to the pre-migratory body condition of females after controlling statistically for arrival date (Figure 8B), thus supporting the second prediction. Finally, clutch size of marked females declined with laying date ($\beta = -0.21$ 95% CI: -0.35 to –0.07, $r^2 = 0.26$, $n = 27$, $P = 0.006$) but was not related with pre-migratory body condition after controlling statistically for laying date ($\beta = -0.08$ 95% CI: -0.76 to 0.60, $P = 0.82$; year and interaction terms $P > 0.19$), thus supporting our third prediction.

Discussion

Our results support all three predictions of the condition-dependent optimal model of clutch size and laying date in an arctic-nesting goose species. Individuals appeared to simultaneously adjust their laying date and clutch size according to their pre-migratory body condition and migratory behaviour in order to optimize their expected reproductive success. To our knowledge, this is the first field study that integrates body condition, migration patterns and reproductive decisions at the individual level to test predictions of the condition-dependent optimal model. By incorporating both proximate and ultimate mechanisms, the dynamic optimal model based on the cost-of-delay hypothesis (Drent and Daan 1980) explains the seasonal decline in clutch size without invoking a cost of reproduction. According to this model, variations among individuals in initial condition and onset of condition gain on breeding grounds, combined with the seasonal decline in offspring value, explain the breeding delay of some individuals and their subsequent reduced clutches (Rowe et al. 1994).

Migration and optimal reproductive decisions

Our observations indicate that radio-marked geese breeding on Bylot Island did not migrate directly from their main staging area in southern Quebec to their breeding grounds in the Canadian High Arctic. The timing of departure and arrival was similar for radio-marked and unmarked birds, as showed by daily counts on staging and breeding grounds (Béchet et al. in prep., Bêty, Gauthier and Giroux, unpubl. data). Thus, we cannot ascribe the observed migration pattern to the presence of a radio-transmitter effect on marked birds (see also Ward and Flint 1995). The 2 to 3-week long migration indicates that most geese spent some time at one or several other staging areas before arrival on their breeding site. Although the observations of Le Hénaff et al. (1995) indicate that the central Ungava peninsula in northern Quebec may be one of those areas, feeding opportunities at such final stopovers are still unknown. However, it is possible that geese stopping in such areas were able to feed and thus spare or even increase their endogenous reserves for the remaining part of the migration, especially for birds with the longest migration duration. Consequently, these birds may have arrived on breeding grounds in better condition relative to early arriving ones (see also Tombre et al. 1996). This does not affect our conclusions about the relationship between pre-migratory body condition and reproductive decisions because we controlled statistically for arrival date (and thus migration duration). However, arrival date of individuals might be related to body condition upon arrival on breeding grounds. Our data do not allow us to evaluate the independent potential effect of arrival date and post-migratory body condition per se on individual breeding strategy and this will need further investigations. Nevertheless, our general conclusion that snow geese adjust their reproductive decisions (laying date and clutch size) in a condition-dependent optimal fashion remains well founded.

Our study indicates that the migratory behaviour may play a major role in the overall breeding strategy of an individual. The migration of many species, particularly waders and geese, consist of a series of long-distance flights and stopover periods where nutrient reserves are accumulated. During migration, foraging and departure decisions may be influenced by numerous factors. Dynamic modelling showed that the predictability of the environment at the current and future stopover sites (e.g. social environment, food supply, temperature and wind speed) and the trade-off between energy accumulation and predation risk may cause uncertainty in the costs and benefits of different migratory decisions (Weber et al. 1998). For instance, high variance in condition gain at a target staging site may result in a delay of departure date from a site allowing birds to increase body condition to a higher level before departure (see Weber et al. 1998). Properties of individuals such as high social status and experience may reduce the variance in foraging opportunities and explain the rapid migration of some individuals. These factors could thus generate additional individual variations in arrival date, condition at arrival and subsequent optimal reproductive decisions of goose females.

Recent models of optimal avian migration assume that reproductive success is determined by arrival date and nutrient reserves at arrival (e.g. Alerstam and Hedenstrom 1998, Farmer and Wiens 1998). This is in accordance with our observations for greater snow geese. However, factors that determine the arrival date of individuals on the breeding grounds remain unknown in greater snow geese, as we detected no association with pre-migratory body condition or departure date. Few studies have linked the migratory behaviour and subsequent reproductive decision of individuals in long distance migrants (Sandberg and Moore 1996), and most observations are limited to the arrival date without information on condition of individuals. In greater snow geese, we showed that early arriving birds lay earlier and thus achieve higher expected reproductive success than late ones (Lepage et al. 2000), which is consistent with other studies (e.g. Petersen 1992, Nilsson and Persson 1994, Dalhaug et al. 1996). However, there is still little empirical data on the fitness costs and benefits of different migratory decisions in birds (Møller 1994, Palomino et al. 1998, Madsen 2001).

In a highly seasonal environment such as the Arctic, birds should not arrive on the breeding grounds too early before snowmelt because extreme weather and lack of food may threaten their survival, increase prohibitively maintenance costs and constraint nutrient accumulation before breeding (Farmer and Wiens 1998). Birds must nonetheless arrive on the breeding grounds as early as possible in order to initiate laying early and maximize their reproductive success. If too much time is devoted to nutrient accumulation on staging areas, individuals may lose time and arrive later than the optimal arrival date on the breeding grounds (Sandberg and Moore 1996). They may thus face a trade-off between arrival date and energy reserves at the onset of breeding.

Condition and seasonal decline in clutch size

The rate of nutrient acquisition on the breeding grounds, and hence of condition gain, should influence the trade-off between laying date and clutch size (Rowe et al. 1994). In the Arctic, food becomes more readily accessible as snowmelt progresses and new plant growth is initiated (e.g. Gauthier 1993, Carrière et al. 1999). Thus, if the rate of nutrient acquisition increases during the pre-laying period, early arriving birds should have, on average, a lower rate of condition gain than late arriving ones (i.e. the slope of the condition gain line increases, Figure 1). Although this modification could be added to the model in order to improve biological reality, its qualitative predictions will remain the same (Rowe et al. 1994). In addition, variations in the foraging efficiency of individuals should also influence the rate of condition gain, and thus subsequent individual optimal decisions. If individuals of highest quality were among early arriving birds, this would attenuate the difference in rate of condition gain compared to late ones due to improved feeding conditions. All these factors likely contribute to generate additional variation in nest initiation dates and clutch sizes.

In capital breeders such as arctic-nesting geese, previous studies showed that body reserves accumulated on spring staging areas influenced subsequent reproductive success (e.g. Teunissen et al. 1985, Ebbinge and Spaans 1995). However, the early suggestion that this was largely because endogenous reserves at arrival on the breeding ground was a direct determinant of clutch size (e.g. Ryder 1970, Ankney and MacInnes 1978) needs to be revised. As in many other species, late nesting snow goose parents perform more poorly than early ones in most components of reproductive success, which globally shows a very steep seasonal decline (Cooke et al. 1995, Lepage et al. 2000). Our study indicates that individuals in better condition prior to spring migration reach optimal combinations of laying date and clutch size earlier than birds in poor condition and this may be the main reason why they may achieve higher reproductive success. Our pre-migratory body condition index had, however, a low predictive power of laying date (partial $r^2 = 0.07$). This may partly reflect the low precision of our index due to large variation in the predicted nutrient reserves among individuals assigned to the same profile score (see also Bowler 1994, Scott et al. 1995, Wiersma and Piersma 1995, Féret et al., ms in preparation). Unfortunately, direct manipulations of marked goose females on staging area was unfeasible in our study due to field constraints and large flock sizes. Moreover, variable conditions (biotic and abiotic) encountered during the final migration bout after leaving the main staging area may also increase the variance in body condition upon arrival among geese that had similar amount of endogenous reserves upon departure.

Radio-marked birds may experience higher energetic cost of migration relative to unmarked birds. Radio transmitter may increase aerodynamic drag and overall flight cost due to extra load and, consequently, negatively affects the body condition of marked females at arrival on the breeding grounds (Demers 2000). The condition-dependent optimal model predicts that females in lower condition should lay later and smaller clutches than females in higher condition independently of their migration pattern (see Introduction). The slight delay in laying date and decrease in clutch size observed in marked birds relative to unmarked birds (Demers 2000) are in accordance with this prediction. We are thus confident that our comparisons among radio-marked birds are acceptable to test predictions of individual optimization model.

According to the condition-dependent individual optimization, birds would appear to be under persistent directional selection, i.e. individuals in high condition lay earliest and largest clutches and achieve highest fitness. Thus, phenotypic variation in clutch size and laying date may be maintained by environmentally-induced variation in initial nutritional condition and onset of condition gain on the breeding grounds independently from the genetic component (see Rowe et al. 1994, Price et al. 1988, Price and Liou 1989). Finally, females may also vary in their timing of reproduction for reasons other than body condition and arrival date (e.g. habitat quality and availability of a mate or nest site; see Winkler and Allen 1996, Kelly and VanHorne 1997).

Conclusion

Individual optimization hypothesis of reproductive decisions have been tested for few species but was supported in most studies (see Murphy 2000, Pettifor et al. 2001). Our study indicates that individual greater snow geese adjust their breeding decisions relative to their migration chronology and pre-migratory body condition in order to optimize their expected reproductive success. However, although the simple theoretical model used in this study is useful to generate qualitative predictions, our study indicate that biological observations could not easily be at variance with its predictions due to numerous factors (environmental conditions and intrinsic properties) that may affect optimal decisions of individuals. Finally, despite its potential importance for understanding reproductive patterns, our knowledge of factors causing intraspecific variations in timing of migration is poor. Further empirical and experimental work is required to better link migration, body condition and reproductive decisions in birds and see how strategies change in response to environmental conditions and the type of reproductive investment (i.e. relative contribution of endogenous and exogenous nutrients).

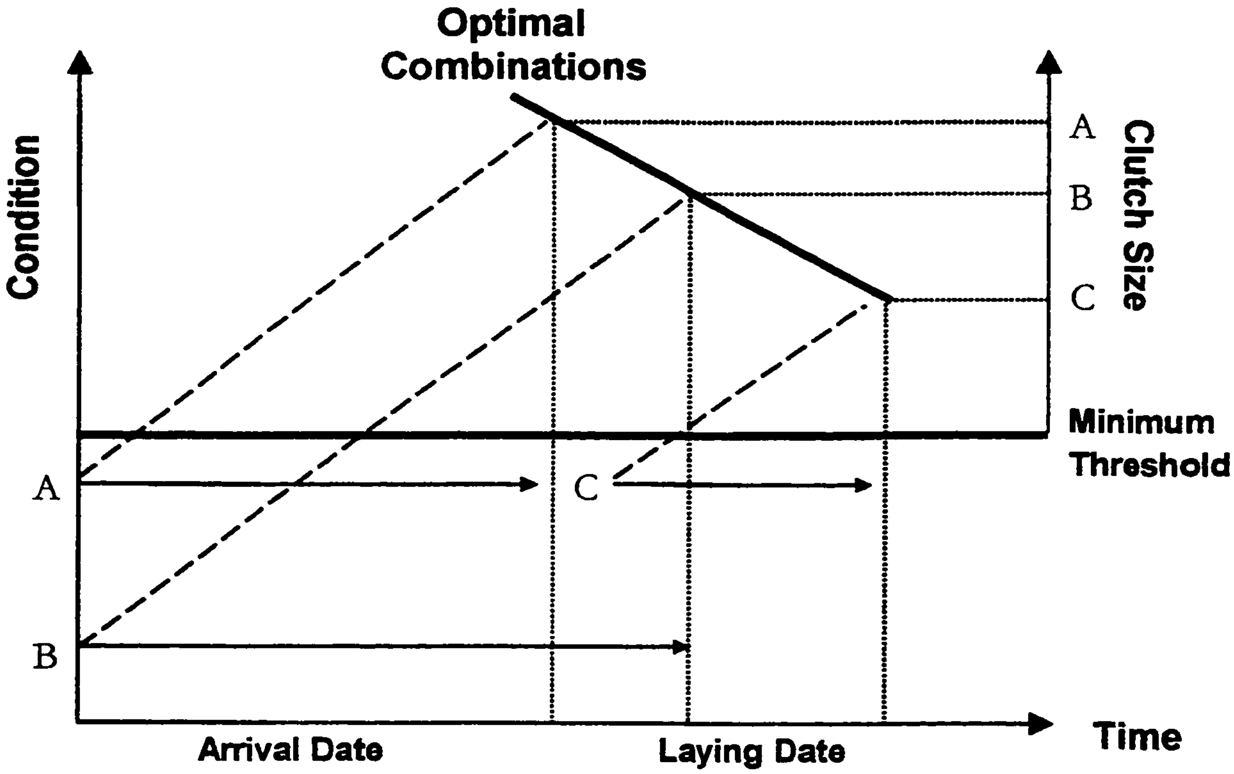

FIGURE 1. Graphical representation of the condition-dependent optimal model of clutch size vs. laying date (modified from Rowe et al. 1994). The line showing the optimal combinations of clutch size and laying date assumes a trade-off between the cost (decreasing offspring value) and the benefit (increasing condition and, consequently clutch size) of a delay in laying date (see Rowe et al. 1994 for details on calculations and assumptions). Letters represent individuals with different initial condition or arrival date on the breeding grounds. Dashed lines illustrate the increase in condition. Individuals should first reach the minimum threshold condition before producing a clutch and then delay laying until the optimal curve is crossed. Dotted lines connect the resulting laying date and clutch size for individuals reaching the optimal curve at different time. Arrows indicate the pre-laying duration (delay between arrival and laying date).

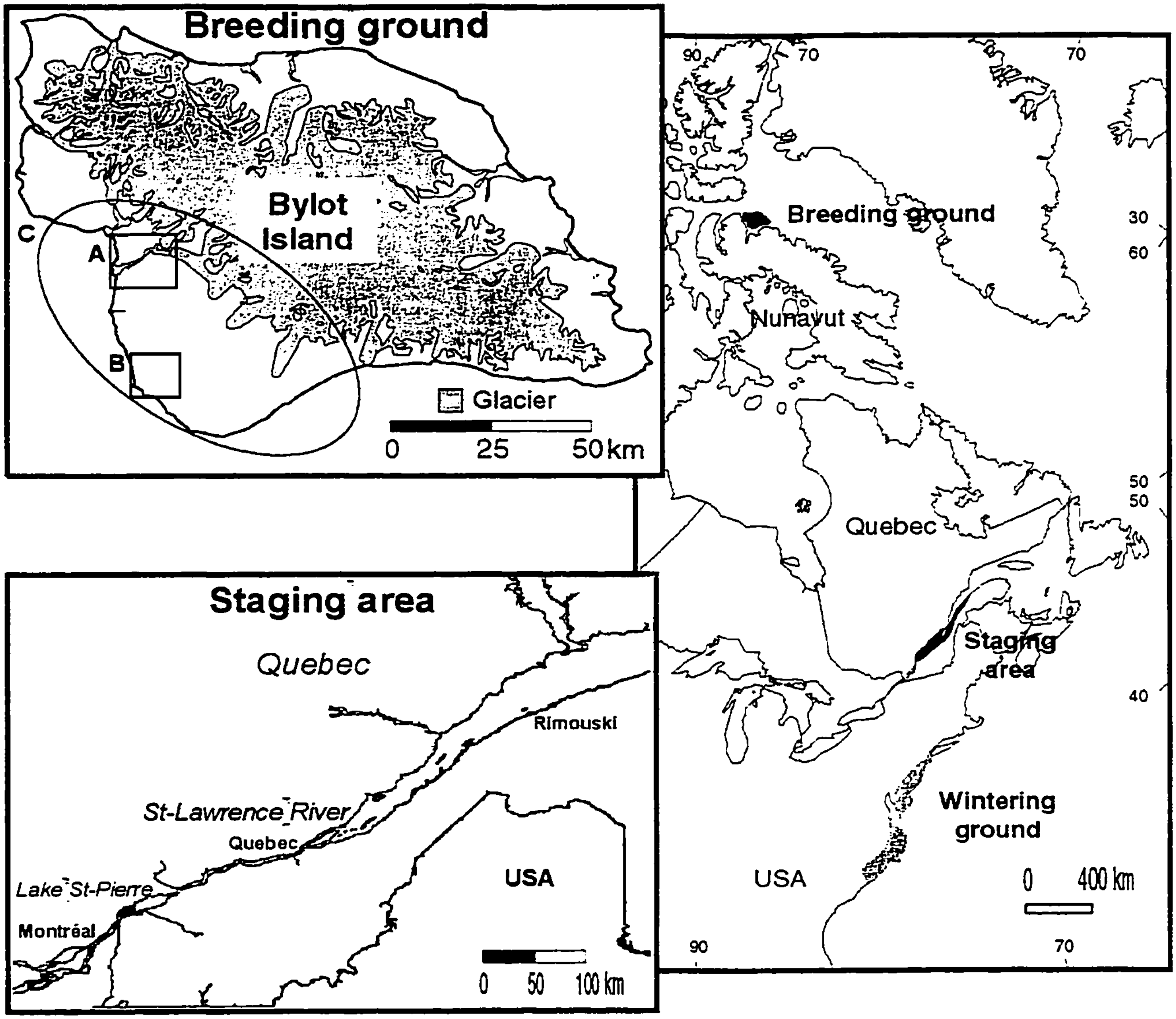

FIGURE 2. Study areas and detailed map of the staging area and the breeding ground of radio-marked greater snow geese. Birds were tracked along the St-Lawrence River (mostly from Lake St-Pierre to Rimouski) and on Bylot Island, Nunavut, at two nesting areas (A and B) and over the south plain of the island (C).

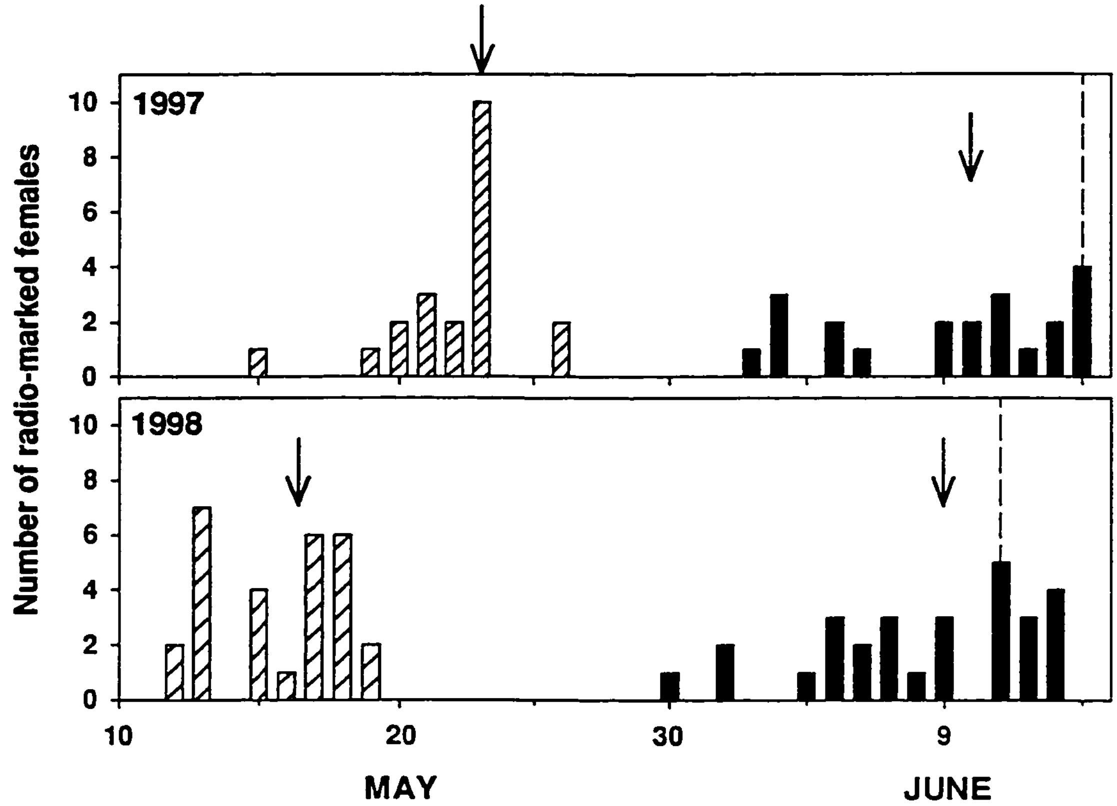

FIGURE 3. Frequency histograms showing the migration chronology of radio-marked female greater snow geese in 1997 (n = 21) and 1998 (n = 28). Departure date (hatched bars) is from staging area in southern Quebec, and arrival date (solid bars) is on the breeding ground of Bylot Island in the Canadian High Arctic. Arrows indicate yearly median for each variable and stippled lines indicate the median laying date.

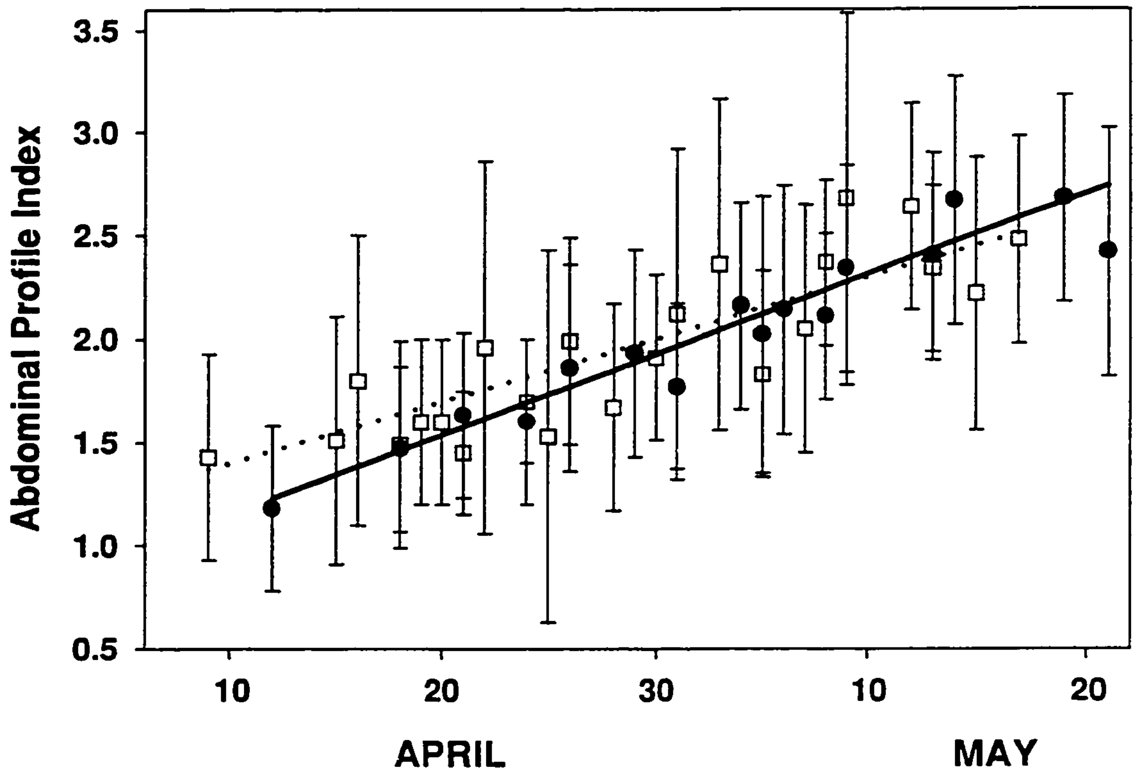

FIGURE 4. Seasonal change in abdominal profile index (API) of greater snow geese during the spring staging period along the St-Lawrence River, southern Quebec, in 1997 (black circles, plain line) and 1998 (white squares, dotted line). Values are mean ± 1 SD (each dot represents 49 to 189 individuals). Multiple linear model: API = -1.633 + 0.030 (Date) – 1.096 (Year) + 0.008 (Date*Year); $F_{3, 3195} = 406.1$, $P < 0.0001$, $r^2 = 0.27$, n = 3199 (Year: 1997 = 1, 1998 = 0; Julian date, 1 = 1 January).

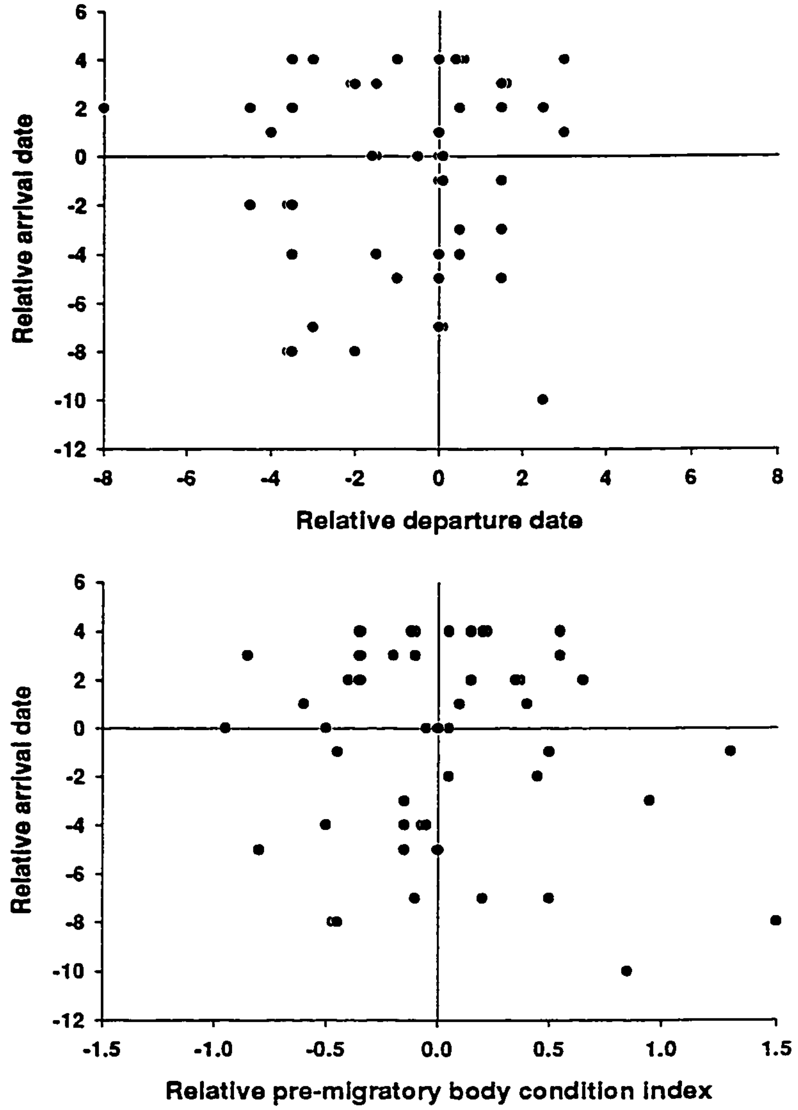

FIGURE 5. Relationship between arrival date and a) departure date or b) pre-migratory body condition of radio-marked greater snow geese. Values are standardized relative to the yearly median. Multiple linear regression including variables departure date and body condition: $r^2 = 0.02$, $P = 0.64$.

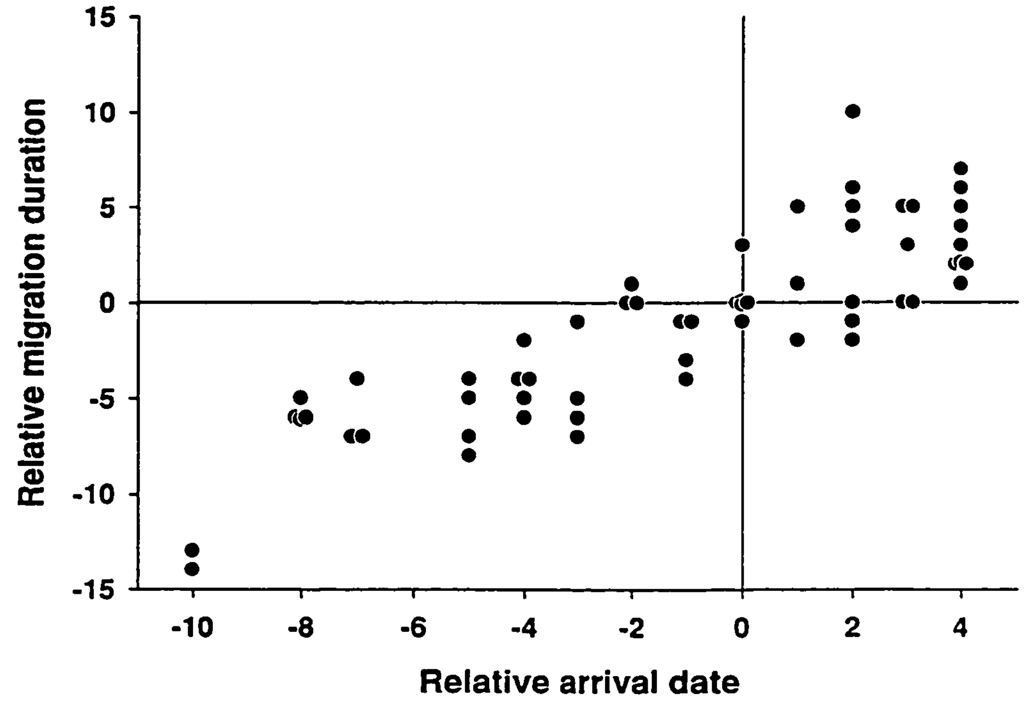

FIGURE 6. Relationship between migration duration and arrival date on the breeding ground of radio-marked female greater snow geese. Values are standardized relative to the yearly median: $r = 0.85$, $P < 0.0001$, $n = 49$.

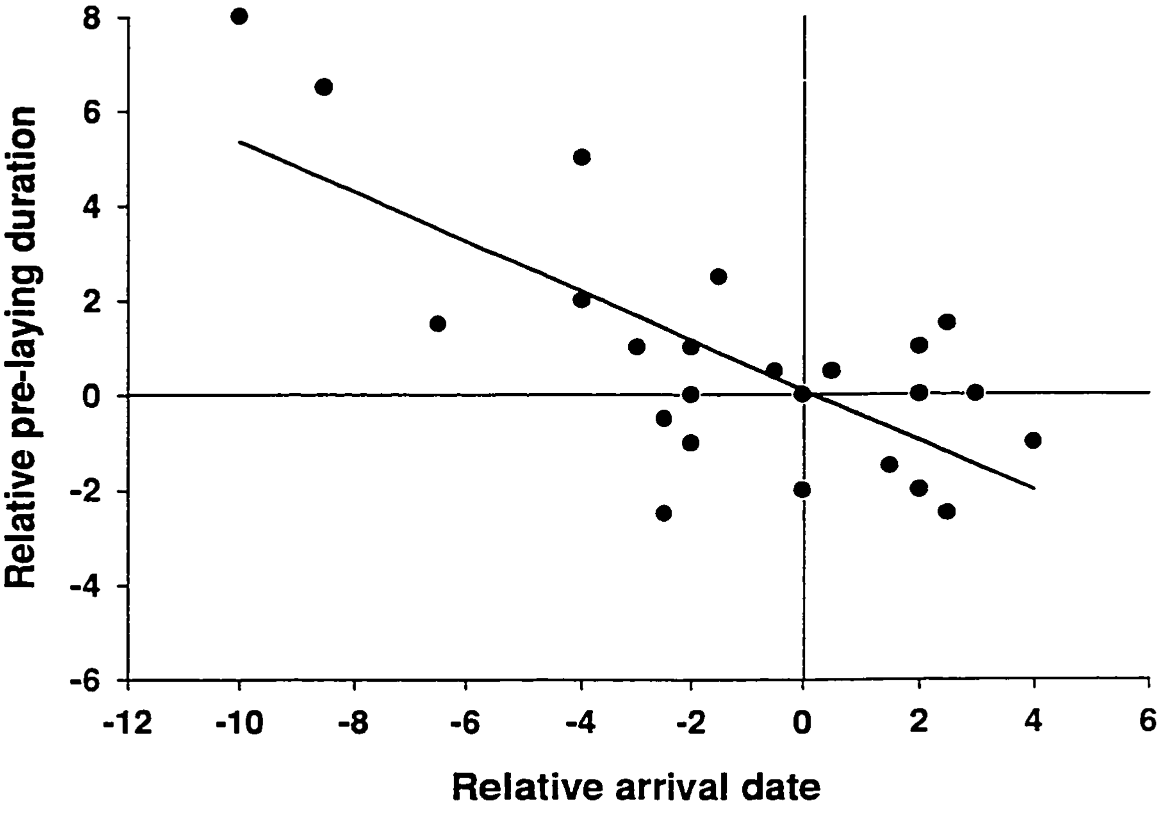

FIGURE 7. Relationship between pre-laying duration and arrival date on the breeding ground of radio-marked greater snow geese. Values are standardized relative to the yearly median. Linear regression: $r^2 = 0.55$, $P < 0.0001$.

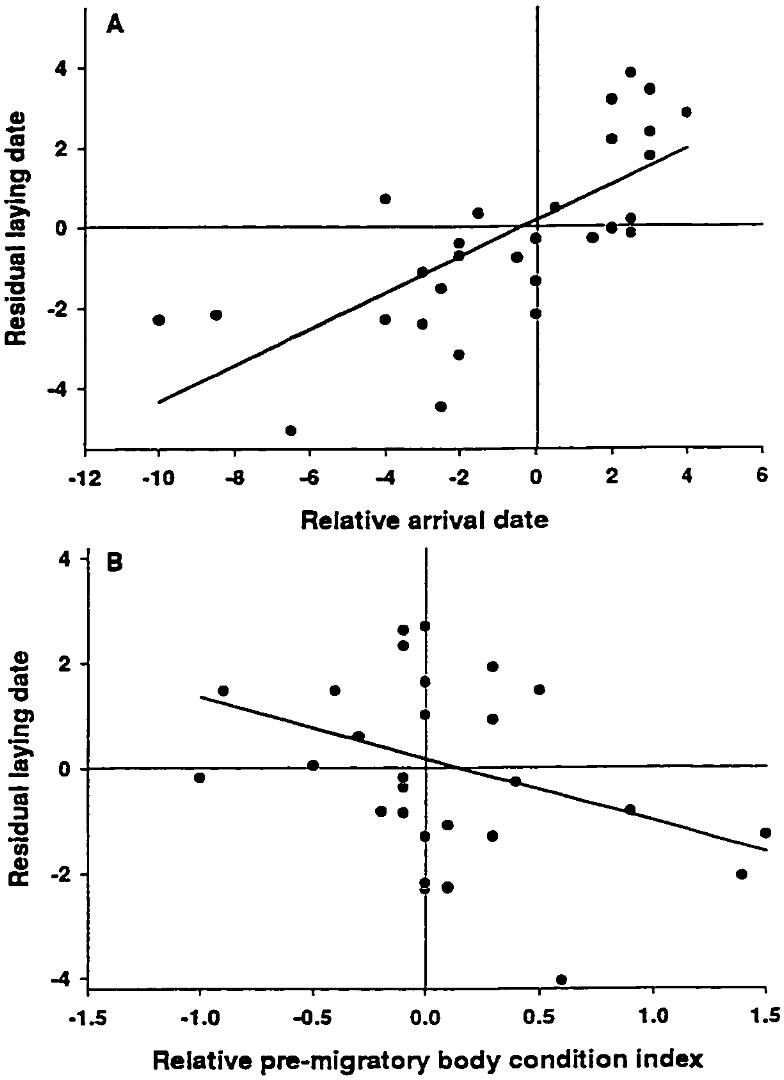

FIGURE 8. Relationship between laying date and a) arrival date on the breeding ground or b) pre-migratory body condition of radio-marked greater snow geese. Values are standardized relative to the yearly median. Multiple linear regression: arrival date, semi-partial r^2 = 0.44, P < 0.0001; body condition, semi-partial r^2 = 0.07, P = 0.04. Residuals were calculated after controlling for the significant effect of the other variable in the model.

Conclusion générale

Dans le cadre de ma thèse, j'ai abordé différents aspects associés aux interactions trophiques et aux stratégies de reproduction susceptibles d'influencer la performance des individus et, en conséquence, la productivité des populations d'oiseaux herbivores. Dans un premier temps, j'ai tenté de mettre en lumière les effets indirects associés à la réponse des prédateurs aux fluctuations cycliques d'une proie principale présente dans le système à l'étude. Ensuite, l'examen des variations interindividuelles dans la chronologie de la migration et la condition corporelle m'a permis de tester certaines prédictions d'un modèle de décision optimale d'allocation des ressources dans la reproduction. J'ai intégré dans cet ouvrage un contexte évolutif et des composantes clés d'un écosystème, soit les niveaux trophiques, les populations et les individus, tous indispensables à la compréhension de la dynamique des populations et la dynamique trophique des écosystèmes.

Prédation et interactions trophiques

Le débat actuel portant sur la dynamique trophique des écosystèmes terrestres implique généralement trois principaux points de vue. Une première hypothèse met l'accent sur la diversité des stratégies de défense des plantes et des herbivores (*defence diversity hypothesis*). Cette hypothèse soutien qu'en présence de tels mécanismes de défense, les niveaux trophiques supérieurs sont rarement capables de réguler les niveaux trophiques inférieurs dans des écosystèmes riches en espèces (ex.: Strong 1992, Polis 1999). Au contraire, un second concept soutient que l'effet combiné des niveaux trophiques supérieurs comme les carnivores limite considérablement la densité des herbivores et, en conséquence, les plantes sont rarement surexploitées en dépit de leur vulnérabilité (Hairston et al. 1960). L'hypothèse « d'exploitation des écosystèmes » (*exploitation ecosystems hypothesis*) ajoute à ce dernier la productivité des écosystèmes et propose que les herbivores seraient généralement contrôlés par les prédateurs sauf dans les habitats à faible productivité comme la toundra arctique et les régions alpines (Oksanen et al. 1981, Oksanen et Oksanen 2000). Finalement, un troisième point de vue se distingue des deux premiers et propose que l'effet des interactions trophiques sur les herbivores serait essentiellement dépendant des caractéristiques propres aux espèces qui forment les communautés (Krebs et al. 1999). Les résultats de cette étude contribuent en partie à ce débat très actuel.

Plusieurs facteurs sont susceptibles d'influencer la dynamique des populations d'herbivores, soit la prédation, la disponibilité et la qualité de la nourriture, les maladies, les parasites et les conditions climatiques. Chez les oies nichant dans les milieux arctiques, la disponibilité et la qualité de la nourriture sur les haltes migratoires ainsi que les conditions climatiques rencontrées durant la migration et sur l'aire de reproduction ont été identifiées comme des facteurs clés (ex.: Lemieux 1959, Owen 1987, Boyd 1987, Ebbinge 1989, Cooke et al. 1995, Gauthier et al. 1996, Skinner et al. 1998; voir aussi Chapitre 2 et 4). Une des conclusions majeures de mon étude est que la prédation peut aussi considérablement influencer la productivité de la Grande Oie des neiges nichant dans le Haut-Arctique (Chapitre 2 et 3). Bien que cette proposition avait été soulevée par le passé chez d'autres espèces d'oiseaux de l'Arctique (ex.: Summers 1986, Summers et Underhill 1987, Martin et Baird 1988, van Impe 1996), les résultats empiriques et expérimentaux présentés dans ma thèse permettent de clairement identifier les principaux mécanismes responsables des variations inter-annuelles du succès de nidification de ces espèces. Les changements d'intensité de prédation observés dans cette étude ont été nettement associés à des effets indirects résultant de fluctuations cycliques d'une autre proie dans le système, soit les populations de lemmings. En effet, les observations supportent les prédictions des deux hypothèses non-exclusives permettant d'expliquer cette interaction trophique indirecte, soit l'hypothèse d'association avec des rapaces et l'hypothèse de proies alternatives (voir Introduction générale).

Dans le système étudié, la réponse comportementale et numérique des prédateurs de nids aux cycles de lemmings apparaît comme étant le principal mécanisme générant des fluctuations d'intensité de prédation (Chapitre 2 et 3). Bien que l'effet d'association avec des rapaces semble plutôt local, ces observations démontrent néanmoins le rôle de la stratégie de reproduction des individus dans une interaction trophique indirecte. De plus, le choix de nicher à faible ou forte densité semble jouer un rôle important pour expliquer la synchronie des oscillations d'abondance de rongeurs et la performance des individus (Chapitre 2). Ceci reflète bien l'importance de considérer la variabilité inter-individuelle et les adaptations évolutives d'une espèce pour comprendre la dynamique d'une population. Dans l'ensemble, ces observations suggèrent que les communautés aviaires des régions arctiques peuvent être soumises à une pression de prédation intense, quoique très variable.

Chez les oies et les canards, la prédation des œufs et des jeunes peut limiter considérablement la croissance des populations (ex.: Pehrsson 1986, Summers 1986), mais ce phénomène ne semble pas être généralisé (Krebs et al. 1999). Dans l'ensemble, le rôle de la prédation dans la dynamique de ces populations demeure obscur (Johnson 1992, Karr et al. 1992). Chez des espèces plus vulnérables à la prédation, la saturation des habitats de nidification de haute qualité (faible risque de prédation) pourrait devenir le principal facteur limitant (Ebbinge 2000). Chez la Grande Oie des neiges, l'effet de la prédation sur la croissance de la population était probablement plus important dans le passé, avant l'explosion démographique observée au milieu du vingtième siècle. En effet, les résultats du Chapitre 2 mettent en évidence la présence d'une forte synchronie entre les cycles d'abondance de lemmings et les taux de prédation à faible densité de nids. Au contraire, les taux de prédation sont inversement reliés à la densité dans les colonies denses où le nombre d'œufs prélevés semble limité par la densité des prédateurs. Ainsi, l'augmentation récente de la densité d'oies sur les aires de reproduction associée à l'augmentation globale de la population (Reed et al. 1998) a certainement eu comme conséquence de réduire l'impact relatif de la prédation sur la productivité annuelle de cette population.

Contrairement au modèle de dynamique trophique qui prédit que l'interaction plante-herbivore devrait être dominante dans les milieux arctiques (voir ci-haut l'hypothèse d'exploitation des écosystèmes), nos observations suggèrent que l'interaction prédateur-proie pourrait jouer un rôle non-négligeable dans la structure et la composition des communautés arctiques. Les modèles théoriques qui regroupent les espèces sous forme de niveaux trophiques distincts ne considèrent pas les caractéristiques propres aux espèces qui les composent. Le fait de considérer homogène les espèces d'une catégorie (ex.: herbivores et carnivores) est probablement trop simpliste pour énoncer des prédictions valables et utiles à la compréhension des communautés écologiques. À la lumière de mon étude et des récentes revue de littérature (ex.: Persson 1999, Chase 2000), il m'apparaît essentiel de considérer les adaptations spécifiques aux espèces qui composent une communauté pour en comprendre les propriétés (voir aussi Krebs et al. 1999). Les stratégies anti-prédateurs, les stratégies de reproduction et les propriétés des individus (ex.: taille corporelle et vulnérabilité) sont tous des éléments susceptibles d'influencer l'effet de la prédation sur la dynamique de population d'oiseaux herbivores même dans des milieux peu productifs comme l'écosystème arctique.

De nombreuses questions relatives à l'interaction indirecte lemming-oie demeurent sans réponse. À l'échelle des populations, il serait très pertinent d'étudier la synchronie dans les oscillations d'abondance de lemmings et la synchronie dans l'intensité de prédation à travers l'aire de reproduction des oies. Ceci permettrait, entre autres, de mieux évaluer l'effet indirect global des cycles de lemmings sur la productivité de la population d'oies. De plus, des études plus détaillées de la réponse des prédateurs (comportementale et numérique) incluant des réplications spatiales, des individus marqués et des expériences en milieu naturel permettraient d'approfondir et généraliser les conclusions du Chapitre 3. D'autre part, cette étude, comme bien d'autres, démontre l'importance des petits rongeurs dans la chaîne trophique des écosystèmes nordiques. La cause des cycles de lemmings demeure évidemment un thème d'étude fascinant qui doit être étudié plus en détail.

Les facteurs qui influencent les variations inter-individuelles dans la stratégie de nidification chez les Grandes Oies des neiges demeurent aussi inconnus. Pourquoi et comment certains individus, qui représentent un faible pourcentage de la population, sélectionnent-ils un site de nidification dans des aires à faible densité de nids (petites colonies) ou à proximité de rapaces? Quels sont les caractéristiques (age, expérience ou statut social) de ces individus? Pour aborder ces questions, il est indispensable de faire un bilan des coûts et des bénéfices associés au choix du site de nidification en intégrant les conséquences des différentes décisions sur les autres composantes du succès reproducteur. En effet, chez les espèces nidifuges comme les oies, les conditions environmentales (ex.: risques de prédation et qualité des sites d'alimentation) auxquelles sont soumis les jeunes après l'éclosion peuvent avoir un impact majeur sur le taux de croissance, de survie et de recrutement (Cooke et al. 1995, Lepage et al. 1998). En somme, pour optimiser leur succès reproducteur, les parents devraient entre autre faire un compromis entre la qualité du site de nidification (ex.: risque de prédation des oeufs) et la proximité d'un site d'élevage de qualité.

Investissement des ressources dans la reproduction.

Les modèles théoriques développés grâce aux mathématiques n'ont pas pour objectif de décrire parfaitement la réalité, mais visent plutôt à donner une représentation cohérente avec les informations que la réalité veut bien nous dévoiler. La qualité première d'un modèle est donc de s'ajuster aussi bien que possible aux observations. Au Chapitre 4, le modèle de décisions optimales basé sur l'hypothèse du coût-du-délai de Drent et Daan (1980) et formalisé de façon mathématique par Rowe et al. (1994) est un bel exemple d'approche théorique qui intègre différentes composantes susceptibles d'influencer les traits d'histoire de vie des individus. Ce type de modèle d'optimisation nous permet d'améliorer considérablement notre compréhension des adaptations des individus. Il est aussi important de mentionner que l'approche d'optimalité n'est pas utilisée pour démontrer que la sélection naturelle produit des solutions optimales, mais bien pour mettre à l'épreuve notre connaissance des contraintes biologiques qui influencent le résultat de l'évolution (voir Parker et Maynard Smith 1990).

L'originalité des observations rapportées au Chapitre 4 est sans aucun doute celle de lier la stratégie de reproduction d'individus marqués avec des évènements pré- et post-migratoires, et ce dans un contexte théorique d'optimalité. Bien que ces résultats soient cohérents avec les prédictions du modèle d'optimalité, d'autres études seront nécessaires pour bien démontrer la relation entre la migration, la condition corporelle et les décisions reproductives subséquentes. Mes travaux sont, à mon avis, un bon tremplin pour l'étude des causes immédiates (*proximate mechanisms*) qui influencent les décisions reproductives des individus et des compromis auxquels ceux-ci font face durant la période pré-reproductrice.

Plusieurs thèmes de recherche reliés au modèle de décisions optimales mériteraient une attention particulière. Premièrement, les causes de la variabilité inter-individuelle de condition corporelle pré-migratrice n'ont pas été abordées dans cet ouvrage. La variabilité des conditions environnementales rencontrées par les individus sur les haltes migratoires (ex.: disponibilité de nourriture, environnement social, dérangement) et les caractéristiques des individus à l'intérieur de la population (efficacité de quête alimentaire, âge, statut social, rang social) sont tous des facteurs susceptibles d'influencer l'accumulation des réserves endogènes.

Deuxièmement, les observations indiquent que le comportement migratoire est une partie intégrante de la stratégie de reproduction globale des individus. Chez la Grande Oie des neiges, une meilleure intégration de cette période critique nécessiterait, entre autres, une bonne connaissance des opportunités d'alimentation au-delà de la halte migratoire principale située au sud du Québec. À mon avis, l'étude des variations inter-individuelles dans le comportement de migration représente un thème de recherche crucial qui permettra de mieux définir la stratégie reproductive globale chez les oiseaux.

Finalement, il serait important de tester les prédictions du modèle d'optimalité chez des espèces ayant différentes stratégies d'utilisation des ressources endogènes et exogènes. De plus, des manipulations expérimentales seront nécessaires pour bien établir les liens de cause à effet pouvant survenir entre la phénologie de migration, la condition corporelle et la stratégie reproductive des individus. À ma connaissance, aucune manipulation expérimentale de la date d'arrivée et du taux d'alimentation durant la période de pré-ponte n'a été réalisée en milieu naturel de façon combinée. D'autre part, des manipulations physiologiques, par exemple du système endocrinien des femelles, permettraient de mieux comprendre les conséquences de la production d'œufs supplémentaires sur la performance des individus et évaluer comment les parents peuvent réajuster leur investissement énergétique au cours des différentes phases de la reproduction (ex.: ponte, incubation et élevage des jeunes; voir aussi Monaghan et Nager 1997).

De la théorie à la pratique

Les résultats présentés dans cet ouvrage peuvent sans aucun doute contribuer à améliorer notre compréhension de la dynamique de population de la Grande Oie des neiges et, en conséquence, améliorer la qualité des décisions de gestion entourant cette espèce. Certains résultats sont particulièrement pertinents relativement aux récentes mesures adoptées par les gestionnaires fauniques. En effet, dans le but de stabiliser la population, une chasse printanière de conservation a été instaurée au Québec depuis 1999. De plus, un programme d'effarouchement à grande échelle à été mis en place de façon à réduire les dommages aux récoltes subits par les agriculteurs. Ces actions exceptionnelles prennent place durant une période critique du cycle de reproduction des oies, soit durant la période pré-migratoire d'accumulation de réserves énergétiques (Gauthier et al. 1984, Chapitre 4). Des observations effectuées avant et après l'instauration de ces mesures spéciales indiquent que les oiseaux soumis à ces nouvelles sources de dérangements accumulent moins de réserves avant leur départ vers l'Arctique (Féret et al. ms en préparation).

Quels sont les impacts à cours et à long terme de telles méthodes de gestion sur la performance des individus et la productivité de la population? Plusieurs prédictions peuvent être faites sur les bases du modèle théorique d'allocation optimale des ressources appuyé par nos observations au Chapitre 4. Par exemple, le modèle prédit qu'une réduction de la condition corporelle des individus avant la reproduction devrait se traduire par un délai du moment de la reproduction (date de ponte), une réduction de la taille de ponte et, en conséquence, du nombre de jeunes produits. Bien que ces décisions reproductives soient possiblement optimales au niveau individuel, les jeunes produits plus tard en saison seront de moins bonne qualité (diminution des taux de croissance, de survie et de recrutement : Cooke et al. 1995, Lepage et al. 1998, Lepage et al. 1999). De plus, le modèle suppose qu'une condition corporelle minimale doit être atteinte avant d'investir dans la reproduction. Ce seuil minimal doit être atteint avant une certaine date au-delà de laquelle l'investissement dans la reproduction n'est plus bénéfique étant donné le déclin saisonnier de la valeur des jeunes. Puisque le déclin saisonnier de la valeur des jeunes est très marqué chez les oies nichant dans l'Arctique, on peut s'attendre à ce que tout facteur qui réduit la condition moyenne des individus provoque une diminution notable de la proportion des individus qui atteignent le seuil critique, et donc qui vont nicher. Cette réduction dans l'effort de reproduction devrait se refléter par une faible densité de nids et, en conséquence, une augmentation des taux de prédation dans les colonies où la prédation est inversement reliée à la densité (Chapitre 2). Ainsi, des évènements qui se produisent à 3000 km du site de reproduction peuvent influencer les décisions reproductives des individus et, en conséquence, la productivité de la population.

Nos premières observations tendent à supporter ces prédictions et suggèrent que les méthodes de gestion utilisées durant la période pré-migratoire pourraient avoir des effets négatifs marqués sur la reproduction (Mainguy et al. sous presse). Ainsi, certains outils de gestion dont l'objectif initial était de diminuer la survie des oiseaux adultes (Gauthier et Brault 1998, Giroux et al. 1998a) peuvent aussi diminuer indirectement et de façon non-négligeable la fécondité des oies. Évidemment, ces effets indirects peuvent contribuer à atteindre certains objectifs de gestion et doivent être pris en compte dans les modèles de population de façon à améliorer les décisions de gestion. Les prévisions entourant ces effets indirects seraient certainement améliorées si l'on pouvait intégrer aux modèles les stratégies individuelles reliées au comportement et à l'investissement des ressources dans la reproduction.

D'autre part, on peut s'interroger sur les conséquences à long terme d'une augmentation des populations d'oies sur l'écosystème arctique. Il est bien démontré que les oies sont des herbivores clés qui influencent grandement les communautés végétales (Gauthier et al. 1996, Giroux et al. 1998b). En conséquence, les premières préoccupations soulevées par l'accroissement des populations étaient reliées presque essentiellement à l'intégrité des communautés de plantes et des habitats. Cependant, peu d'attention a été apportée aux impacts potentiels d'une augmentation de proies (surtout les œufs et les jeunes oies) sur les niveaux trophiques supérieurs et les effets indirects potentiels sur les autres proies qui partagent un ou des mêmes prédateurs. L'exposé fait au Chapitre 3 permet d'apporter certains éléments de réponse. Cette section illustre l'importance d'intégrer les niveaux trophiques supérieurs et interactions directes et indirectes dans l'écosystème arctique. Les résultats présentés suggèrent qu'une compétition apparente à long terme pourrait survenir entre les proies (oies et lemmings) par l'intermédiaire de la réponse des prédateurs. Dans un tel contexte, l'augmentation de la densité des oies pourrait éventuellement résulter en une augmentation de la densité de prédateurs et, en conséquence, une diminution de la densité moyenne des autres proies présentes dans le système. Par ailleurs, les probabilités de colonisation et de maintien d'autres espèces dans le système peuvent être réduites à cause d'une augmentation de la pression de prédation causée indirectement par la présence d'une autre proie abondante dans le système (Holt et Lawton 1994). À l'inverse, ces effets indirects pourraient être bénéfiques (ex.: mutualisme apparent) si, par exemple, la densité des populations de prédateurs serait limitée par des facteurs indépendants de l'abondance de proies (ex.: territorialité ou disponibilité de site de reproduction). Voilà une question qui mérite, selon moi, beaucoup plus d'attention et qui souligne l'importance d'une vision qui englobe l'ensemble des interactions trophiques d'un écosystème lors d'intervention de gestion et de conservation.

Conclusions

En conclusion, les résultats présentés dans ce travail démontrent l'importance d'une intégration des niveaux trophiques supérieurs et des effets directs et indirects dans un milieu à faible productivité comme la toundra arctique. De plus, il est bien démontré que les recherches empiriques au niveau des individus peuvent sensiblement améliorer la compréhension des niveaux supérieurs tels la régulation des populations et les interactions trophiques (voir Mooij et DeAngelis 1999). Ma thèse intègre cette dernière composante essentielle et représente une contribution susceptible d'encourager et faciliter l'incorporation de composantes individuelles dans des modèles de population. En somme, mes travaux ouvrent la voie à de nouveaux projets de recherche traitant des interactions trophiques en milieu arctique et peuvent servir de base à des études traitant des modèles d'optimalité dans l'allocation des ressources au moment de la reproduction.

L'écosystème arctique est un laboratoire de recherche unique pour l'étude des interactions trophiques et des stratégies d'histoire de vie des organismes vivants. C'est aussi un environnement très sensible qui fait maintenant face à des défis sociaux, physiques et environnementaux sans précédent. Malheureusement, notre niveau de compréhension de ce système écologique est encore bien inférieur à celui qui est requis pour en assurer l'intégrité et la pérennité. J'estime que ma thèse représente une contribution non-négligeable aux connaissances de cet écosystème et j'espère sincèrement qu'elle facilitera et stimulera la poursuite de futurs travaux de recherche en écologie terrestre arctique.

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