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CHAPITRE 1 : INTRODUCTION GÉNÉRALE

L'identification des principaux facteurs et mécanismes qui influencent la dynamique des populations animales est un des aspects fondamentaux de l'écologie. Les phénomènes démographiques qui déterminent le taux de croissance des populations (succès reproducteur, taux de survie et mouvements des individus) peuvent être influencés par de nombreux facteurs environnementaux ou intrinsèques aux populations (Krebs, 1994). D'une part, il y a les facteurs dépendant de la densité de la population. Ces facteurs peuvent être biotiques ou abiotiques (disponibilité en nourriture et en espace, prédation, compétition, parasitisme, etc.; Krebs, 1994). D'autre part, il y a les facteurs qui peuvent altérer les taux de natalité et de mortalité sans égard à la densité des populations. Ces facteurs, typiquement abiotiques, peuvent influencer le taux d'accroissement d'une population sans toutefois la réguler (Akçakaya & al., 1999). Les deux types de facteurs peuvent avoir des effets importants et peuvent interagir pour déterminer l'abondance des populations (Saether, 1997; Gaillard & al., 2000).

EFFET DU CLIMAT, DES RELATIONS TROPHIQUES ET DE LA DENSITÉ SUR LA DYNAMIQUE DES POPULATIONS

Actuellement, dans un contexte de réchauffement climatique planétaire, les écologistes cherchent particulièrement à comprendre les processus qui lient le climat à la structure et à la taille des populations afin de mieux prévoir le devenir et la vulnérabilité des populations et des écosystèmes naturels (Begon & al., 1996; Saether & al., 2000; McCarty, 2001; Saether & al., 2004; Ims & Fuglei, 2005). Les premières études traitant de l'effet du climat sur les animaux portaient surtout sur des paramètres météorologiques locaux telles que la température, les précipitations et la couverture neigeuse (Namias & Cayan, 1981). Récemment, les travaux ont porté une attention particulière aux phénomènes climatiques à grande échelle afin d'intégrer les paramètres locaux dans un système climatique global de régulation (Aanes & al., 2002; Saether & al., 2004). D'ailleurs, des études ont révélé que l'utilisation des phénomènes climatiques à grande échelle pouvait être un avantage lorsque les réponses écologiques devaient être interprétées sur de grandes échelles spatiales (Forchhammer & al., 1998; Forchhammer & Post, 2004; Stenseth & Mysterud, 2005). C'est notamment le cas lorsque l'on s'intéresse aux populations qui vivent sur de vastes étendues géographiques, comme les oiseaux migrateurs. Le phénomène climatique à grande échelle le plus étudié et documenté dans la région Euro-Atlantique est l'Oscillation Nord-Atlantique (ONA ou NAO en anglais pour North Atlantic Oscillation; Saether & al., 2004). L'ONA est parfois décrit comme étant une manifestation régionale d'un autre phénomène climatique à grande échelle, soit l'Oscillation Arctique (OA; Thompson & Wallace, 1998). L'ONA représente les fluctuations de pressions entre l'anticyclone des Açores et la dépression d'Islande. Ces fluctuations de pressions créent des mouvements d'air au-dessus de l'Atlantique et sont indirectement responsables de la plupart des variations inter-annuelles des précipitations et des températures hivernales dans une partie de l'hémisphère Nord (Hurrell, 1995; Hurrell, 2000). L'ONA peut influencer directement ou indirectement la dynamique des populations animales et végétales par son influence sur les phénomènes climatiques locaux (Post & Stenseth, 1999; Mysterud & al., 2001; Ottersen & al., 2001; Huppop & Huppop, 2003; Almaraz, 2004; Welker & al., 2005).

Le climat peut influencer la dynamique des populations animales par des effets directs sur la physiologie des individus (coûts de thermorégulation, coûts de locomotion), ou par des effets indirects qui agissent sur la nature des interactions biologiques (compétition, relations prédateurs-proies, accès à la nourriture). Le climat prévalant durant la saison hivernale, par exemple, peut être directement et indirectement associé aux taux de mortalité chez certaines populations d'ongulés. Entre autres, chez les orignaux (*Alces alces*) de l'île Royale (É.U.), des hivers rigoureux associés à une forte accumulation de neige conduisent à une augmentation de la mortalité des individus suite à l'augmentation des coûts de thermorégulation et de déplacement (causé par une plus grande accumulation de neige au sol, effet direct du climat; Parker & Robbins, 1985; Post & Stenseth, 1999). Une forte accumulation de neige peut également influencer indirectement le taux de mortalité de ces ongulés par le biais des interactions trophiques. En effet, suite à l'accumulation de neige au sol, les prédateurs peuvent augmenter leur efficacité de chasse en se regroupant (Post & Stenseth, 1999).

Comme le suggère l'exemple précédent, les populations ne vivent pas isolées les unes des autres. Différentes espèces peuvent interagir à l'intérieur d'un même réseau trophique notamment par le biais de la compétition pour les ressources et la prédation (Krebs, 1994). Dans un système à plusieurs niveaux trophiques, des interactions indirectes peuvent s'établir entre deux espèces d'un même niveau (ex.: deux espèces consommées par un même prédateur peuvent être en compétition ou partager une relation de mutualisme).

Chaque espèce peut ainsi voir son abondance modifiée par les effets du climat et ceux dépendant de la densité, autant que par une modification des interactions trophiques directes ou indirectes (Figure 1.1; Krebs, 1994).

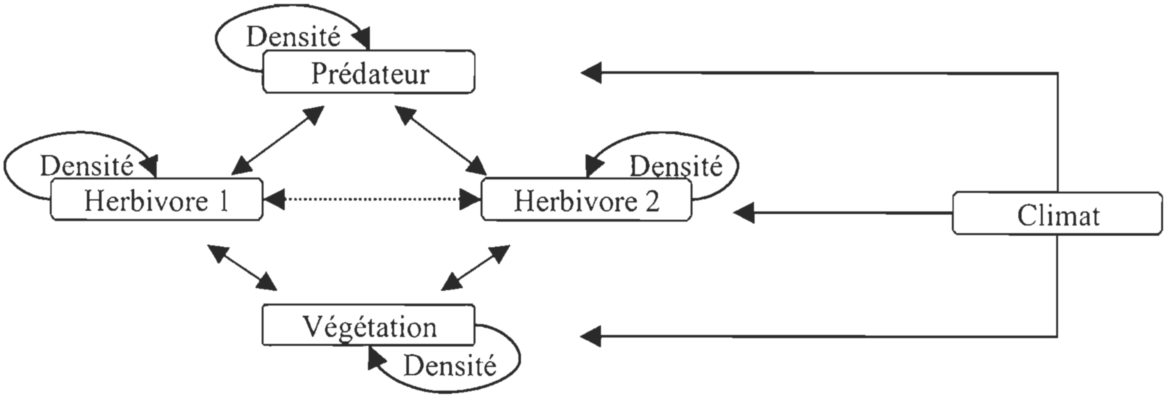

Figure 1.1 Schématisation d'un réseau trophique simple (chaîne trophique à trois niveaux). Les végétaux représentent les producteurs primaires alors que les herbivores et les prédateurs représentent les consommateurs. Les lignes pleines représentent des liens directs et la ligne pointillée un lien indirect. Tous les liens indirects ne sont pas inclus dans la figure afin de la simplifier. Le climat a un effet direct et/ou indirect sur chacun des niveaux trophiques et les interactions entre les espèces peuvent aussi être influencées par les fluctuations climatiques.

Par ailleurs, à l'intérieur d'un réseau trophique, les espèces peuvent interagir entre-elles par le biais de relations ascendantes (« bottom-up ») ou descendantes (« top-down »). Un système peut être contrôlé par des relations ascendantes via la disponibilité des ressources nutritives. Ces relations ont particulièrement été étudiées dans les milieux lacustres où, par exemple, le rôle des éléments nutritifs dans l'eutrophisation des lacs est bien connu (Downing & al., 2001). Un système peut également être contrôlé par des relations descendantes via la prédation. En reprenant l'exemple des lacs, l'augmentation du nombre de poissons prédateurs peut entraîner la diminution du zooplancton herbivore et, par un effet en cascade, l'augmentation du phytoplancton (les producteurs primaires; Caraco & al., 2006). Il est maintenant reconnu que dépendamment de la productivité du milieu et des conditions climatiques, un écosystème peut être dominé par des relations ascendantes ou descendantes et que ces deux types de relations peuvent avoir simultanément une influence significative sur les réseaux trophiques d'un écosystème (Gauthier & al., 2004; Holmgren & al., 2006).

Puisque le climat peut affecter les populations animales de plusieurs façons (effets directs et/ou indirects via les réseaux trophiques), il devient rapidement difficile de comprendre tous les mécanismes qui mettent en lien le climat et la dynamique des populations. Puisqu'il est pratiquement impossible de manipuler le climat, mener des expériences contrôlées devient presque irréalisable lorsqu'on s'intéresse aux effets du climat à grande échelle. La majorité du progrès accompli dans ce domaine est réalisé à partir d'observations ou d'expériences naturelles (non planifiées). L'un des désavantages de cette approche à grande échelle est qu'elle ne permet pas de distinguer les mécanismes de causes à effets entre les paramètres puisqu'elle se base généralement sur des corrélations (Krebs & Berteaux, 2006). D'un autre côté, les conclusions tirées des études à petites échelles, qui permettent de montrer plus facilement les relations de causes à effets, sont généralement limitées à des sites d'étude particuliers et sont difficilement extrapolables (Petersen & Hastings, 2001; Peters & Herrick, 2004). C'est pourquoi une approche qui alterne les études à petite et à grande échelles devrait être favorisée. Ce type d'approche permettrait de mettre en évidence des liens de causes à effets et ensuite de faire des prédictions à plus grande échelle (Root & Schneider, 1995). La compréhension des effets du climat sur la dynamique des populations est importante si l'on veut prévoir le devenir et la vulnérabilité des espèces, des communautés et des écosystèmes dans le contexte de réchauffement climatique actuel. Elle est aussi très importante pour réagir de façon appropriée aux corrélations observées entre changements climatiques et changements écologiques.

DYNAMIQUE DES POPULATIONS AVIAIRES NICHANT EN ARCTIQUE

Prédire les facteurs qui influencent la dynamique des populations aviaires est particulièrement difficile puisque plusieurs espèces migrent sur de très grandes distances. En effet, l'abondance des populations d'oiseaux migrateurs peut être influencée par les conditions climatiques rencontrées dans différentes parties du monde (Sherry & Holmes, 1996; Newton, 2004). Selon l'hypothèse « du robinet » (*tap hypothesis*), la dynamique des populations d'oiseaux se reproduisant en milieux arides, tel l'Arctique, serait plus fortement influencée par les conditions climatiques en saison de reproduction qu'en période d'hivernage puisque la reproduction serait possible uniquement lorsque les conditions climatiques sont favorables (Grant & al., 2000; Martin, 2001; Saether & al., 2004). Les conditions climatiques prévalant durant la période de reproduction auraient ainsi un impact plus marqué sur les juvéniles que sur les adultes (Blomqvist & al., 2002). Chez les espèces dites « longévives » (grande durée de génération), le taux de survie des adultes est considéré comme étant le paramètre démographique influençant le plus fortement la dynamique des populations (Gaillard & al., 2005). Toutefois, puisque le taux de mortalité naturelle est assez faible et relativement constant chez les adultes (peu affecté par les variations environnementales), la survie des juvéniles, plus vulnérable aux conditions climatiques, peut devenir un paramètre important dans la dynamique des populations (Gaillard & al., 1998).

Plusieurs études ont analysé l'effet des variations climatiques sur la dynamique des populations d'oiseaux (variations de la taille ou de la productivité; Franklin & al., 2000; Grant & al., 2000; Thompson & Ollason, 2001; Saether & al., 2003). La température en juin serait, par exemple, positivement corrélée à la productivité de jeunes chez l'Oie rieuse (*Anser albifrons*; Zöckler & Lysenko, 2000), la Bernache du Canada (*Branta canadensis*; Sheaffer & Malecki, 1996) et la Bernache cravant (*Branta bernicla*; Boyd, 1987). Les variations climatiques pourraient même expliquer jusqu'à 97% de la variabilité inter-annuelle de certains aspects de la phénologie et du succès reproducteur de la Petite Oie des neiges (*Chen caerulescens caerulescens*; Skinner & al., 1998). Les phénomènes à grande échelle tels l'ONA ou El Niño (oscillation australe équivalente à l'ONA) semblent également expliquer une proportion importante des variations annuelles de la taille de certaines populations d'oiseaux (Barbraud & Weimerskirch, 2001; Loison & al., 2002; Barbraud & Weimerskirch, 2003). En Norvège, par exemple, l'ONA est positivement associée au taux de recrutement et au taux de croissance d'une population de Cincle plongeur (*Cinclus cinclus*; Saether & al., 2000). Par contre, les mécanismes qui expliquent les relations entre les variations climatiques et les populations sont souvent moins bien documentés (Krebs & Berteaux, 2006).

D'autre part, il a été démontré que les interactions trophiques pouvaient également avoir un impact sur la dynamique des populations aviaires nichant en Arctique. En effet, des corrélations ont entre autres été rapportées entre les cycles de lemmings et le succès reproducteur de plusieurs espèces d'oiseaux, spécialement chez les oies et les échassiers nichant dans la toundra (*Calidris ferruginea*, Cramp & Simmons, 1983; *Branta b. bernicla* et *Calidris canutus*, Summers & Underhill, 1987; *Calidris alba*, Underhill, 1987; *Arenaria interpres,* Underhill & al., 1989; Underhill & al., 1993; Spaans & al., 1998). Selon l'hypothèse « oiseau-lemming», les années de forte abondance de lemmings seraient généralement associées à un succès reproducteur élevé et, à l'inverse, un échec de reproduction survient les années de très faible abondance de lemmings (Summers & Underhill, 1987; Summers & al., 1998). Cette hypothèse suggère que les prédateurs modifient leur comportement d'alimentation lors d'années de faible abondance de lemmings en s'alimentant davantage d'œufs et de jeunes oiseaux que de lemmings. Les prédateurs peuvent également montrer une réponse numérique aux variations d'abondance de lemmings en se reproduisant lors d'années de grande abondance ou en s'agglomérant près des colonies d'oiseaux les années de faible abondance de lemmings. La variation annuelle de pression de prédation suite aux réponses comportementale et numérique des prédateurs pourrait ainsi être le facteur dominant générant des fluctuations cycliques dans la reproduction de ces oiseaux (Blomqvist & al., 2002).

Par ailleurs, plusieurs populations d'anatidés (bernaches, oies et canards) ont considérablement augmenté au cours des 50 dernières années, causant des effets dépendant de la densité chez certaines populations. Chez la Bernache nonnette, par exemple, le taux de mortalité adulte était approximativement de 2% par année lorsque la population comptait 5 000 individus alors qu'il a augmenté à 10% par année lorsque la population a atteint la taille de 10 000 individus (Owen & Black, 1991). L'augmentation de la taille de la population aurait causé une compétition plus importante pour les ressources alimentaires sur les aires de reproduction, ce qui a conduit à une diminution du taux d'accumulation des graisses nécessaires à la migration automnale et, conséquemment, à une augmentation de la mortalité adulte durant cette période (Owen & Black, 1991). D'autres effets dépendants de la densité ont été répertoriés sur divers paramètres de reproduction chez la sauvagine (taille de couvée, croissance et survie des juvéniles; Cooch & al., 1989; Francis & al., 1992; Williams & al., 1993; Reed & Plante, 1997).

DYNAMIQUE DE LA POPULATION DE LA GRANDE OIE DES NEIGES

La Grande Oie des neiges (*Chen caerulescens atlantica*) est un oiseau migrateur qui niche principalement dans l'Est du Haut-Arctique canadien. Elle parcourt au moins 4 000 km entre ses aires d'hivernage, situées sur la côte Est des États-Unis, et ses aires de reproduction, situées principalement du nord de l'île de Baffin à l'île d'Ellesmere. La plus importante colonie d'oies nicheuses est située sur l'île Bylot (20 000 couples, représentant approximativement 15% de la population; Reed & al., 2002). L'écosystème terrestre arctique de l'île Bylot est relativement simple (peu d'espèces) comparativement aux écosystèmes tempérés ou tropicaux. Outre la Grande Oie des neiges, la communauté d'herbivores vertébrés est majoritairement composée de Lemmings bruns (*Lemmus sibiricus*) et de Lemmings variables (*Dicrostonyx groenlandicus*). Le Lagopède alpin

(*Lagopus mutus*) et le Lièvre arctique (*Lepus arcticus*) sont aussi présents, mais en très faibles nombres (Gauthier & al., 1996). Les principaux prédateurs des oies ou des lemmings sont le Renard arctique (*Vulpes lagopus*), le Labbe parasite (*Stercorarius parasiticus*), le Goéland bourgmestre (*Larus hyperboreus*) et le Grand corbeau (*Corvus corax*; Bêty & al., 2001). Le Harfang des neiges (*Nyctea scandiaca*), la Buse pattue (*Buteo lagopus*), le Labbe à longue queue (*Stercoraris longicaudus*) et l'Hermine (*Mustela herminea*) sont essentiellement des prédateurs de lemmings (Gauthier & al., 2004). Contrairement aux lemmings, les oies sont présentes seulement l'été puisqu'elles arrivent majoritairement au début juin et quittent au début septembre. Elles sont d'importants brouteurs de la toundra et peuvent fortement influencer la dynamique de la chaîne trophique arctique, incluant les communautés végétales ainsi que la distribution et la productivité des prédateurs (Gauthier & al., 1996; Szor & al., 2007). Les oies n'ont qu'une seule couvée par année et ne pondent pas à nouveau s'il y a un échec de reproduction (Lepage & al., 2000). La prédation est la principale cause d'échec de nidification sur l'île Bylot (Bêty & al., 2001; Lecomte & al., 2008).

La phénologie de la reproduction

À leur arrivée sur le site de reproduction, les oies doivent acquérir d'importantes quantités de nourriture nécessaires à la production des œufs. Les nutriments accumulés localement représentent en effet plus de 70% des protéines et des graisses nécessaires à la formation des œufs (Gauthier & al., 2003). Les conditions climatiques prévalant durant la période d'arrivée, de pré-ponte et de ponte des oies sont donc cruciales puisqu'elles vont influencer le taux d'accumulation de réserves en modulant la disponibilité de la nourriture (Bêty & al., 2003). Le climat lors de cette période est d'ailleurs considéré comme le principal facteur déterminant l'effort et la phénologie de la reproduction des oies. Des conditions printanières rigoureuses (basses températures et fort couvert neigeux) sont associées à un faible effort de reproduction, des dates de ponte tardives et des tailles de couvée réduites (Bêty & al., 2003; Reed & al., 2004; Dickey & al., 2008). La date de ponte est un paramètre déterminant puisqu'elle influence la phénologie des étapes subséquentes de la reproduction (incubation, éclosion, élevage des jeunes) et affecte fortement le succès reproducteur des individus (Lepage & al., 2000).

Durant l'incubation, les oies passent jusqu'à 94% du temps sur leur nid, ne le quittant que pour s'alimenter et s'abreuver (Reed & al., 1995). Puisque la vulnérabilité des œufs à la prédation augmente considérablement lorsque les femelles s'éloignent à plus de 10 mètres du nid, ces absences régulières peuvent être directement liées aux risques de prédation des œufs (Bêty & al., 2002). Les besoins énergétiques et hydriques des femelles en incubation et l'accessibilité des ressources peuvent varier selon les conditions environnementales. Des précipitations abondantes peuvent, par exemple, diminuer la distance qu'une femelle doit parcourir pour s'abreuver lorsque les dépressions naturelles de la toundra se remplissent d'eau, réduisant ainsi le risque de prédation (Lecomte, 2007).

La croissance des oisons s'effectue sous des conditions difficiles dans l'Arctique. Étant exclusivement herbivores, les oisons disposent d'une nourriture de faible qualité pour assurer leur croissance (en comparaison avec des tissus animaux; Sedinger & Raveling, 1986). De plus, étant incapables de digérer les fibres contenues dans les plantes, les oies n'absorbent qu'environ le tiers de leur contenu (Manseau & Gauthier, 1993). Les oisons doivent donc ingérer une grande quantité de nourriture afin d'assurer un haut gain énergétique permettant un développement rapide avant le début de la migration automnale. Leur croissance est ainsi fortement influencée par la quantité et la qualité (spécialement la disponibilité en azote) des plantes qu'ils consomment. Par ailleurs, afin d'assurer une croissance maximale, les jeunes ont avantage à se nourrir plus tôt en saison puisque la qualité des plantes diminue avec la maturation des végétaux (Manseau & Gauthier, 1993; Piedboeuf & Gauthier, 1999; Cadieux & al., 2005). De plus, la disponibilité peut être réduite par la compétition avec les autres oisons (Gauthier & al., 1995; Lepage & al., 1998). Un retard de croissance peut avoir un impact majeur sur la survie future des oisons et sur leur chance de recrutement dans la population (Lindholm & al., 1994; Sedinger & al., 1995; Reed & al., 2003; Menu & al., 2005).

Pression de prédation et abondance de lemmings

Les variations de la pression de prédation exercée sur les oies sont principalement le résultat d'interactions indirectes entre les oies, les lemmings, les renards et les Labbes parasites. Les prédateurs peuvent consommer jusqu'à 90% de tous les œufs d'oies produits en une année et le Renard arctique représente le principal prédateur (Bêty & al., 2002). Lorsque l'abondance de lemmings est relativement élevée, les attaques de renards sur les nids d'oies sont moins fréquentes que lorsque l'abondance de lemmings est faible (Gauthier & al., 2004). Alors que les Renards arctiques semblent montrer une réponse numérique reproductive, les Labbes parasites semblent davantage présenter une réponse numérique agrégative à l'abondance de lemmings (Bêty & al., 2002). Les réponses numérique et comportementale de ces deux prédateurs aux variations d'abondance de lemmings expliquent en grande partie l'association entre l'abondance de lemmings et le succès reproducteur des oies (Gauthier & al., 2004; Lecomte & al., 2008).

Pour certaines espèces d'oiseaux de l'Arctique, la productivité annuelle est cyclique et fortement corrélée avec les cycles de lemmings (Summers & Underhill, 1987; Summers & al., 1998). Par contre, les fluctuations du succès de nidification des oies semblent être synchronisées avec les cycles de lemmings seulement à l'intérieur des colonies de très faibles densités (Bêty & al., 2001; Gauthier & al., 2004). Pour les oies nichant à fortes densités, le taux annuel d'échec est inversement relié à la densité de nids en raison des effets de dilution (l'augmentation du nombre d'oeufs disponibles diminue les chances qu'un oeuf soit consommé par les prédateurs; Bêty & al., 2001). Les variations annuelles de densité de nids sont indépendantes des cycles de lemmings et semblent surtout déterminées par les conditions climatiques printanières dans l'Arctique (Reed & al., 2004; Dickey & al., 2008).

Croissance de la population

La taille de population de la Grande Oie des neiges a augmenté considérablement, passant d'approximativement 165 000 à plus d'un million d'individus entre 1976 et 2006 (période couverte par la présente étude; données provenant du Service canadien de la faune). Cette augmentation est en partie expliquée par un changement d'alimentation chez les oies qui ont délaissé les littoraux et les marais pour s'alimenter davantage sur les terres agricoles nouvellement disponibles sur les aires d'hivernage et les haltes migratoires (Reed & al., 1998; Menu & al., 2002; Gauthier & al., 2005). Afin de limiter la croissance de la population, une récolte printanière a été instaurée au Québec depuis 1999. Des études ont démontré que cette récolte, en plus d'augmenter la mortalité chez les adultes, affecte négativement l'accumulation de réserves endogènes sur les haltes migratoires (Féret & al., 2003; Béchet & al., 2004a). En arrivant sur le site de reproduction, les femelles se trouvent ainsi avec une moins bonne condition corporelle ce qui diminue la probabilité de nicher, retarde la date de ponte et diminue la taille des couvées (Mainguy & al., 2002; Bêty & al., 2003; Reed & al., 2004).

OBJECTIF ET PLAN DE L'ÉTUDE

Des études réalisées à l'île Bylot ont souligné l'importance des conditions climatiques locales sur certains paramètres de la reproduction de la Grande Oie des neiges (Lepage & al., 1996; Bêty & al., 2003; Reed & al., 2004; Menu & al., 2005; Dickey & al., 2008), des effets indirects des populations de lemmings sur la pression de prédation (Gauthier & al., 2004) et des effets dépendants de la densité sur la croissance des juvéniles durant la période d'élevage des oisons (Reed & Plante, 1997). Toutefois, aucune étude n'a tenté d'estimer l'effet simultané et relatif de ces facteurs sur la productivité globale de cette population, ni sur d'autres populations d'oiseaux de l'Arctique. Dans notre étude, nous analysons les variations de productivité annuelle des oies afin de déterminer si les liens de causes à effets suggérés à petite échelle spatiale affectent la productivité à plus grande échelle, soit au niveau de la population.

La productivité annuelle des oies est estimée à partir du pourcentage de juvéniles observés dans la population d'oies à l'automne lors de sa migration dans le sud du Québec. Même si les variations de pression de chasse ont généralement un impact considérable sur la dynamique des populations chassées intensivement (Hestbeck, 1994; Gauthier & al., 2001), la variation de productivité annuelle peut significativement influencer la dynamique des populations (Gaillard & al., 1998). Nous allons tout d'abord vérifier cette prémisse en déterminant si la productivité annuelle de la Grande Oie des neiges explique une partie de la variabilité du taux de croissance de la population. Nous voulons ensuite estimer de quelle façon la productivité globale des oies est affectée par i) les conditions climatiques, mesurées par l'Oscillation Nord Atlantique (ONA) et certains paramètres météorologiques locaux à différentes périodes du cycle reproducteur des oies, ii) les variations de la pression de prédation causées par les cycles d'abondance de lemmings et iii) les effets dépendants de la densité de la population d'oies. Nous allons également étudier l'effet potentiel de l'implantation, sur les haltes migratoires, de la récolte printanière de conservation sur la productivité des oies.

Cette étude s'étend sur une longue échelle temporelle (31 années) et les hypothèses suivantes seront testées:

1) les conditions climatiques printanières déterminent le niveau de productivité annuelle maximal de la population d'oies
2) les cycles de lemmings modulent la proportion d'oisons qui est consommée par les prédateurs au cours de l'été

3) la taille de la population d'oies influence négativement la productivité annuelle en affectant l'effort de reproduction (compétition entre les individus en période pré-reproductrice) et la survie des juvéniles (compétition entre les individus durant la période d'élevage).

Nous voulons également vérifier si les phénomènes climatiques à grande échelle (ONA/OA) peuvent être de bons indicateurs des conditions climatiques rencontrées par les oies sur l'aire de reproduction.

Globalement, ce projet offre l'opportunité d'examiner l'importance relative des relations ascendantes et descendantes sur une composante majeure d'un écosystème peu diversifié et relativement peu productif, soit la toundra arctique. De plus, en intégrant les effets des conditions climatiques à grande et petite échelles, les effets des interactions trophiques indirectes et les effets de la densité dans un même modèle, ce projet permettra de mieux comprendre les facteurs qui influencent la dynamique des populations animales.

CHAPITRE 2: CLIMATE, INDIRECT TROPHIC INTERACTIONS AND DENSITY-DEPENDENT EFFECTS: WHICH FACTORS DRIVE HIGH ARCTIC SNOW GOOSE PRODUCTIVITY?

Manuscrit en préparation pour une publication

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M. Morrissette, J. Bêty, G. Gauthier, A. Reed and J. Lefebvre. Climate, indirect trophic interactions and density-dependent effects: which factors drive high arctic snow goose productivity?

Identifying and understanding the factors driving the productivity of animal populations is difficult because a large number of parameters can interact. Previous studies have highlighted the importance of local weather conditions, the indirect impact of lemming population cycles, and the effects of density dependence on some key reproductive components of arctic-nesting birds. Based on causal links previously documented at small spatial scales, we investigated the relative importance of various parameters on the annual productivity of the greater snow goose (*Chen caerulescens atlantica*), a migratory species nesting in the Canadian High-Arctic. Using a 31-year time series, we determined the extent to which the annual productivity of the whole population, defined as the percentage of juveniles in the fall flock, was affected by i) climatic conditions, ii) fluctuations in predation pressure caused by rodent cycles and iii) density-dependent effects via goose population size. We also investigated the potential carry-over effects caused by human disturbance associated with spring harvest on the main staging sites. Spring climatic conditions in the Arctic seemed to determine the maximum potential goose productivity as they explained about 29% of the variation in the annual breeding productivity. The spring North Atlantic Oscillation (NAO) index and the spring snow depth were the key climatic parameters affecting inversely the production of juveniles, likely through their effects on food availability during goose pre-laying and laying periods (bottom-up processes). Lemming population cycles explained 19% of the variation in the annual goose productivity (positive relationship) through indirect trophic interactions via shared predators (top-down processes). We also found evidence that the strength of these top-down processes was dependent on the climatic conditions, being weaker when spring conditions were unfavourable for geese. Mean temperature during goose brood-rearing period, spring harvest on staging sites and the fall NAO index were, in decreasing order of importance, the other factors affecting goose productivity (total of 21% of explained variation). No density-dependent effects were detected despite a major population increase (6-fold) over the study period. Hence, climate and indirect trophic interactions via shared predators appeared to be the primary driver of productivity in high arctic snow geese during the study period.

INTRODUCTION

Identifying and understanding what factors drive animal population dynamics is still a central and difficult ecological question because a large number of environmental parameters such as climate, trophic interactions and density-dependence can interact. It has long been recognized that climatic factors may have a profound influence on population dynamics. The effect of climate on individuals may be direct through effects on locomotion (Telfer & Kelsall, 1984; Post & al., 1999) and thermoregulation (Parker & Robbins, 1985; Putman & al., 1996) or indirect by affecting species interactions (Post & Stenseth, 1999; Lenart & al., 2002; Hebblewhite, 2005). These effects often interact with density (Milner & al., 1999; Coulson & al., 2001). Since we cannot manipulate climate on a large scale, controlled experiments are virtually impossible when studying climate effects on vertebrate populations. Most progress in this field is achieved by observational science or natural (unplanned) experiments (Krebs & Berteaux, 2006). Recent studies revealed that using large-scale climatic phenomena rather than local weather conditions may be advantageous when relating climate to population dynamics, because the former integrate multiple weather components and can capture sources of variations in local weather that are not present in analysed local weather variables (Stenseth & al., 2003). This is especially true when ecological responses have to be interpreted on a large spatial scale (Forchhammer & al., 1998; Forchhammer & Post, 2004), which is the case for migrating populations living in spatially extensive areas. Of course, climatic indices, such as the North Atlantic

Oscillation (NAO), can explain variations in biological systems only if they are a good proxy for local weather conditions (Hurrell, 1995).

Variations in annual productivity can be a major factor affecting population dynamics in long lived species where variation in adult mortality is generally low (Gaillard & al., 1998). According to the *tap-hypothesis*, the population dynamics of arctic-nesting birds should be most influenced by climatic conditions during the breeding period as reproduction is only possible when climatic conditions are favourable (Saether & al., 2004). Empirical evidence suggests that climatic conditions, indirect trophic interactions mediated by predators and density-dependent effects are all potential forces that can affect the productivity of arctic-nesting birds. Indeed, their reproductive success appears to be mostly affected by climatic conditions observed early in the breeding season via changes in food and nest site availability (bottom-up processes; Boyd, 1987; Sheaffer & Malecki, 1996; Zöckler & Lysenko, 2000). Higher temperatures in spring are typically associated with earlier laying date, higher clutch and brood size, and thus higher breeding success (Moss & al., 2001; Madsen & al., 2007; Dickey & al., 2008). Also, it has been shown that fluctuations in small mammal populations in the tundra can indirectly affect the abundance and breeding success of some bird species through indirect interactions mediated by shared predators (top-down processes; Bêty & al., 2002; Krebs & al., 2003; Brook & al., 2005; Ims & Fuglei, 2005). Therefore, the dynamics of arctic wildlife populations can be significantly influenced by both bottom-up and top-down processes (Gauthier & al., 2004). Density-dependence is another pervasive force in ecology; for instance several goose populations, which have increased considerably during the last 50 years, have exhibited a density-dependent response in some reproductive components (clutch size, brood size, juvenile growth and survival; Cooch & al., 1989; Francis & al., 1992; Williams & al., 1993; Reed & Plante, 1997). Although all these potential driving forces are well known, few studies have attempted to simultaneously investigate the relative importance of these factors at the whole population level.

We investigated this question in the greater snow goose (*Chen caerulescens atlantica*), a migratory species nesting in the Canadian High Arctic. This species is an important herbivore in the arctic tundra and can strongly affect food web dynamics (including plant communities and predator distribution; Gauthier & al., 2004; Szor & al., 2007). We used a 31-year time series to investigate the relative importance of various environmental parameters (biotic and abiotic) on the annual goose productivity (percentage of juveniles in the fall population). Previous studies in greater snow geese have highlighted the importance of local climatic conditions on some key reproductive components. Spring climatic conditions, for instance, are considered a major factor affecting goose breeding propensity, which is an important determinant of annual productivity (Reed & al., 2004; Dickey & al., 2008). Other studies have also looked at the importance of indirect effects linking lemming population cycles to predation rates (Gauthier & al., 2004) and density-dependent effects on gosling growth (Reed & Plante, 1997). As proposed by Krebs and Berteaux (2006), we essentially based our study on mechanisms previously proposed or documented at a small spatial scale, to investigate simultaneously the effects of key factors at the population level. The main goal of our study was to examine to what extent annual goose productivity was affected by i) climatic conditions at different periods of goose breeding cycle (analysed through variations of large-scale phenomena (NAO/AO) and local weather parameters), ii) fluctuations in predation pressure caused by rodent cycles, and iii) density dependence via goose population size. We also investigated the impact of human disturbance (i.e., spring harvest) on the main staging sites as it can generate carry-over effects on breeding propensity and success (Mainguy & al., 2002; Reed & al., 2004).

Our main hypothesis was that spring climatic conditions are the primary factor determining the maximum potential annual goose productivity and that rodent abundance indirectly influences the proportion of goose productivity consumed by predators over the summer. As nest predation rates are inversely density dependent (Bêty & al., 2001), we expected that lemming abundance would have a stronger effect on annual goose productivity when spring climatic conditions are unfavourable for goose reproduction (i.e., low nest density). In addition, the increase in population size that took place over the last 30 years (6-fold increase; Menu & al., 2002) was expected to influence annual goose productivity.

METHODS

STUDY POPULATION

The greater snow goose is one of the northernmost breeding goose species in North America, nesting principally in the Eastern Canadian High Arctic, from North Baffin Island to North Ellesmere Island, with some birds also breeding in West Greenland (Gauthier & al., 2005). In fall, birds migrate from the Arctic to their main staging areas in south-eastern Canada (Québec) and then to their wintering grounds on the mid-Atlantic coast of the

United States (New Jersey to North Carolina). The largest breeding colony (representing ~ 15% of the world breeding population) is located on Bylot Island, Sirmilik National Park of Canada, Nunavut Territory, Canada (73° 08' N, 80° 00' W; Reed & al., 2002). Bylot Island is situated within the southern part of the breeding range of the greater snow goose (Fig. 2.1). Other important concentrations of breeding birds are mainly located within 500 km of Bylot Island (i.e. Jungersen Bay, 71°25'N, 84°40'W and Creswell Bay, 72°45'N, 93°30'W). To our knowledge, only one significant breeding colony can be found outside this range (Bathurst Island, 75°42'N, 97°21'W; Reed, unpublished data).

The greater snow goose is a strict herbivore and an important grazer in arctic wetlands (Gauthier & al., 1996). Nest initiation occurs in June and is typically highly synchronized (about 90% of nests initiated within 8 days; Lepage & al., 2000). Females nesting earlier achieve the highest reproductive success (lay more eggs and have higher gosling survival; Lepage & al., 2000). Geese are single-brooded and do not renest after clutch failure (Lepage & al., 2000). Nest desertion is rare (estimated at < 2%) and predation is the main cause of nest failure on Bylot Island (Bêty & Gauthier, 2001; Lecomte & al., 2008).

STUDY DESIGN

We estimated the annual goose productivity using the percentage of juveniles (i.e., young of the year) in the fall population. This was determined from age ratio counts of flocks during the fall migration at several sites in southern Québec, their main staging area (47°04'N, 70°47'W, Fig. 2.1). Juveniles are grey in fall allowing them to be easily identified among the white adults. Data were collected by the Canadian Wildlife Service from 1976 to 2006 with > 9,500 birds counted each year (Calvert & al., 2007; Lefebvre, unpl. data). Because fall harvest removes a higher percentage of juveniles than adults (Reed & al., 1998), surveys were conducted early in the hunting season (mostly prior to 15 October) to minimize underestimation of productivity.

The main potential mechanisms linking the studied environmental factors to annual goose productivity are summarized in Figure 2.2 and reflect bottom-up processes, top-down processes, carry-over effects and density-dependent effects. Details concerning each process and selected parameters are outlined below.

Climatic effects

It has been shown that local climatic conditions encountered during the breeding cycle on Bylot Island have strong and variable influences on several components of reproductive success (e.g., breeding propensity, laying date, nesting success, gosling growth and survival; Table 2.1). Based on previous studies, we separated the goose breeding cycle into five periods in order to investigate the relative impacts of climatic conditions on the annual goose productivity for each period independently (Table 2.2). Finally, we chose local and large-scale climatic variables that were previously shown to be linked with some components of goose reproductive success and we formulated specific hypotheses (Table 2.1).

The North Atlantic Oscillation (NAO) is a major source of atmospheric mass balance measured as the mean deviation in average sea level pressure between the subarctic and subtropical Atlantic (Hurrell, 1995). This large-scale climatic phenomenon is sometimes described as a regional manifestation of a hemispheric-wide pattern of variability referred to as the Arctic Oscillation (AO; Thompson & Wallace, 1998). By influencing the speed and direction of westerly surface winds across the North Atlantic from North America to Northern Europe, the NAO has an impact on local weather in the Arctic (Hurrell & al., 2003). Although the NAO is commonly viewed as a winter phenomenon, recent atmospheric pressure reductions have also been observed during spring, summer and fall months, partly reflecting the same nature as the NAO winter index but with less vigorous variation (Hurrell & al., 2003). In the North Baffin area, a high winter NAO index value is generally associated with reduced temperatures and precipitation (Hurrell, 1995). We obtained daily values of the NAO and AO indices from the Climate Prediction Center of the National Weather Service (http://www.cpc.ncep.noaa.gov).

From 1994 to 2006, we used climatic data from an automated weather station installed on Bylot Island (20 m above sea level). As mentioned above, Bylot Island is located within 500 km of other important breeding colonies in the Arctic and thus likely represents climatic conditions met by a majority of breeding geese. Accordingly, mean temperatures on Bylot Island are strongly correlated with others sites in the Arctic (i.e. spring mean temperature; $r > 70$ with Pond Inlet, Resolute Bay and Clyde River; Picotin, 2007). Air temperature was measured 2 m above ground using a shielded temperature probe and mean hourly values were recorded. From these data, we calculated daily mean temperatures and then mean temperatures for the selected periods (Table 2.2). We recorded total daily rainfall (mm) manually from 3 June to 15 August using a rain gauge. We visually estimated the percentage of snow cover on Bylot Island on 5 June each year and measured snow depth (cm) at 50 stations along two 250 m transects at two day intervals during snow-melt. We used data from the Environment Canada weather station located at the Pond Inlet airport (72°41'N, 77°59'W), approximately 60 km from the Bylot Island goose breeding colony, to cover the period preceding the installation of the weather station on Bylot Island (1976-1993). The weather data from the two stations (Bylot Island and Pond Inlet) were highly correlated (see Appendix 1). Predictive equations were used to estimate climatic parameters on Bylot Island for the period 1976-1993. Because Pond Inlet snow cover was not available, we used mean daily snow depth (1 to 13 June; longest time series available on Bylot Island) as snow condition index. Snow cover and snow depth data from Bylot Island were positively correlated ($r = 0.64$, $P = 0.006$, $n = 17$). There was a gap in local climatic data (i.e., no data available from either Bylot or Pond Inlet) for the year 1994 and this year was not considered in the analyses.

To estimate climatic conditions during the goose fall migration, we used local mean temperature recorded at the Environment Canada weather station located at the airport in Cape Dorset (64°13'N, 76°31W; Fig. 2.1). This village is located along the first leg of the migration route, where climatic conditions seem to affect juvenile survival (Menu & al., 2005).

Predation pressure effects

Two lemmings species coexist on Bylot Island, the brown (*Lemmus sibiricus*) and the collared (*Dicrostonyx groenlandicus*) lemming. Annual variation in predation pressure on geese (mostly eggs and goslings) is mainly due to complex interactions between geese, arctic foxes (*Vulpes lagopus*), parasitic jaegers (*Stercorarius parasiticus*), snowy owls (*Nyctea scandiaca*) and lemmings (Bêty & al., 2001; Wilson & Bromley, 2001; Bêty & al., 2002). In years of low lemming abundance, predators partially switch prey and focus more on goose eggs (Bêty & al., 2002; Gauthier & al., 2004; Lecomte & al., 2008). Arctic fox also show a reproductive numerical response to rodent densities, whereas parasitic jaegers appear to show an aggregative numerical response (more abundant around goose colonies in low lemming years; Bêty & al., 2002). Numerical and behavioural responses of these two predators (via rodent cycles) generate fluctuations in goose nesting success. Beneficial nesting associations of geese with snowy owls can also occur on Bylot Island during years of high lemming abundance (Gauthier & al., 2004). However, it is probably used by a small proportion of the nesting geese and this positive association is not suspected to be significant at the population level (Bêty & al., 2001). Since the impact of predation on nesting success is strongly dependent on lemming population fluctuations, we expected a positive association between lemming abundance and overall goose productivity. We also tested for a potential interaction between climatic conditions and lemming abundance.

An index of lemming abundance on Bylot Island was obtained in July from 1994 to 2006 with snap-trap censuses and in 1993 with a lemming winter nest survey. From 1994 to 2006, trapping was carried out at the main goose brood-rearing area and from 1997 to 2006 a second site was monitored in the main goose nesting colony (30 km south of the first site). Trapping was carried out in two study plots (wet lowland and dry upland) in the brood-rearing area and in one study plot (dry upland) in the colony. In each plot, 50 baited traps were set for 10-11 days (see Gruyer, 2007). From 1997 to 2006, we used mean abundance from both sites to better estimate lemming abundance at large spatial scale. Lemming abundance index was calculated as the number of lemmings killed per 100 trap-nights over the whole trapping period (Beauvais & Buskirk, 1999). Overall, this index encompass about 1000 trap-nights, which is adequate to track trends in lemming abundance at a regional scale (Gauthier & al., 2004).

Raptor winter irruptions can be a good indicator of population cycles in northern small mammals (Gauthier & Aubry, 1995; Cheveau & al., 2004). To estimate lemming abundance from 1976 to 1992, we used the Christmas Bird Count of snowy owls from the National Audubon Society (www.audubon.org/bird/cbc/). We constructed a predictive equation by linking lemming abundance on Bylot Island and the number of snowy owls observed in Manitoba, Ontario and Québec over the period 1993-2005 (Lemming index = -0.310 + 60.90 * snowy owl Christmas Bird Count index; $R^2 = 0.54$, n = 13, P = 0.004; see Appendix 2).

Carry-over effects

Carry-over effects (events occurring in one season that influence individual success the following season) may play an important role in migratory bird population dynamics (Norris & Taylor, 2006). Since 1999, a spring conservation harvest has taken place at the southern main goose staging area (Fig. 2.1). This spring harvest negatively affected accumulation of body reserves (Féret & al., 2003) and, consequently, negatively affected some goose reproductive parameters (breeding propensity, laying date and clutch size; Mainguy & al., 2002; Bêty & al., 2003; Reed & al., 2004). We accounted for this additional factor by adding a dummy variable in our statistical analyses (1 = spring harvest; 0 = no spring harvest). We also explored potential delayed effects (one to four year time-lags) of annual goose productivity on subsequent production. Indeed, favourable breeding output in a given year may influence goose productivity in following years as geese usually start breeding at three years of age (Reed & al., 2003).

Density-dependent effects

The greater snow goose population has been surveyed every spring since 1965 by the Canadian Wildlife Service on the main staging areas using photo inventory (for details see Béchet & al., 2004b). The population has increased considerably over the study period, from 165,000 in 1976 to about 1,000,000 in 2006 (Lefebvre, unpl. data), in part due to the food subsidy that birds receive while feeding on agricultural lands in wintering and staging areas (Menu & al., 2002; Gauthier & al., 2005). Population increases has resulted in higher densities on staging and breeding areas (Reed & al., 2002).

DATA ANALYSES

Relationship between small and large-scale climatic conditions

We examined the relationships between NAO and AO indices and local climatic conditions between 1976 and 2006 to determine the strength of the associations between large and small scales climatic conditions within the goose breeding and migratory range. We used Pearson correlations to relate annual NAO and AO indices to Bylot Island weather parameters for each period of the goose breeding cycle (spring to late summer), and to relate the fall NAO and AO indices to Cape Dorset local mean temperatures. Although the NAO and AO are the same physical entity and are highly correlated ($r = 0.95$, $P < 0.001$; Thompson & Wallace, 1998), the NAO was consistently more strongly associated with local parameters than the AO. We therefore used the NAO index in subsequent analyses. When NAO index and local temperatures were correlated, we used them in different statistical models in order to avoid multicollinearity.

Annual goose productivity

We used spectral analyses to determine if variability in the annual goose productivity (percentage of juveniles) followed regular cycles. The spectral density function is a natural tool to examine the properties of periodic processes (Priestley, 1981). We used Proc SPECTRA (SAS-Institute-Inc., 2002-2003). The Fisher Kappa statistic (k) tests the null hypothesis of no cycle. We used simple linear regression analysis to estimate the effect of the annual goose productivity on population dynamics (population growth rate, λ_t). We used estimates of spring population size to calculate annual growth rate:

$\lambda_t = N_{t+1} / N_t$

in which N_t is population size in year t.

We used linear multiple regression analyses to examine the effects of explanatory variables on annual goose productivity. A list of candidate models was selected *a priori* based on our predictions regarding the effects of climatic conditions, trophic interaction, density-dependence and carry-over effects. We used square terms to investigate potential non-linear effects (NAO and snow depth variables). Except for the interaction between spring climatic conditions and lemming abundance, no interactions between the variables were considered and all possible combinations of variables were not tested due to sample size constraints. The Akaike's Information Criterion adjusted for small sample size (AICc; Burnham & Anderson, 2002) was used to select the most parsimonious general linear model. The model with the lowest AICc value was considered to be the most parsimonious and those with differences of < 2 AICc units were considered well supported by the data (Burnham & Anderson, 2002). We calculated Akaike weights, which give an estimated probability that a model is the most parsimonious among the candidate models. We also provided the percentage of variation (R^2) explained by each candidate model. The individual contribution of independent variables entered in the most parsimonious model, while controlling for the effect of other variables, was depicted in partial residual plots. Inspection of residuals indicated no violation of the assumptions of normality and homogeneity of variance. We also verified correlations among all variables included in any given model and no correlation was higher than 0.50. Finally, we used temporal autocorrelation to investigate potential delayed effects of annual goose productivity on subsequent breeding events (Proc ARIMA, n lag = 1 to 4; SAS-Institute-Inc., 2002-2003). All analyses were run in software SAS 9.1 (SAS-Institute-Inc., 2002-2003).

RESULTS

RELATION BETWEEN SMALL AND LARGE-SCALE CLIMATIC VARIABLES

Bylot Island mean spring temperature (20 May to 20 June) was negatively correlated with the NAO spring index (1976 to 2006: r = -0.58, P = 0.002, n = 30) but the NAO spring index and snow depth were not correlated (r = 0.20, P = 0.284, n = 30). The fall NAO index was negatively associated with mean fall temperature at Cape Dorset (r = -0.61, P < 0.001, n = 30). Although slightly weaker, negative correlations between the NAO index and Bylot Island mean temperatures during the mid and late summer were also found (r = -0.42, P = 0.020, n = 30 and r = -0.37, P = 0.040, n = 30, respectively). Overall, results indicated that positive NAO indices were associated with cold temperatures on the breeding ground and the northern part of the migration route.

ANNUAL GOOSE PRODUCTIVITY

Annual goose productivity (percentage of juveniles) showed very strong annual variation, ranging from 2% in 1999 to 48% in 1993 (average = 24.2%, n = 31 SD = 12.06; Fig. 2.3e). No cyclic pattern in the percentage of juveniles was detected (k = 3.05, P = 0.390). The annual goose productivity was significantly related to the annual population growth rate (λ_t) and explained 28% of its variation (λ_t = 0.900 + 0.007 * proportion of juveniles, n = 30, R^2 = 0.28, P = 0.003).

The selected models explaining variation in annual goose productivity are shown in Table 2.3 and appendix 3. The most parsimonious model accounted for 69% of variation in the percentage of juveniles in the fall flock. However, three others models provided a similar fit to the data (ΔAIC < 2). Two of them included the interaction term between spring climatic conditions and lemming abundance (Table 2.3). The spring NAO quadratic term (*NAO^2_sp*) was retained in the third best model and spring harvest (*sp_harv*) was absent from the fourth model (Table 2.3). Below, we separately present the different effects included in the preferred models.

Climatic effects

Spring climatic conditions on the breeding grounds were the dominant climatic factors affecting annual goose productivity (spring NAO index partial, *NAO_sp*, R^2 = 0.16; snow depth partial, *snow*, R^2 = 0.13). Positive spring NAO index (i.e., low temperature) and high spring snow depth were associated with low goose breeding productivity (Fig. 2.3a). There was some evidence that very early spring (characterized by extreme negative NAO values) lead to a reduction in the annual goose productivity as the quadratic term of spring NAO index was selected in the third most parsimonious model (β = -4.53, SE = 4.40; Table 2.3). In most competitive models (ΔAICc < 4), large-scale climatic phenomena (i.e., spring NAO) was always selected over local temperature (Table 2.3). Mid-summer local temperature (*temp_ms*) and fall NAO index (*NAO_f*) were other climatic parameters present in the most parsimonious models, explaining respectively 11% and 4% of variation in annual goose productivity (Table 2.3). Annual goose productivity was positively related to mid-summer temperatures and was higher in years with positive fall NAO index values (Fig. 2.3a).

Predation pressure effects

The abundance of lemmings (*lem*) influenced positively goose annual productivity and explained about 19% of the annual variation (Table 2.3 & Fig. 2.3b). We also found some evidence for an interaction between NAO spring index and lemming abundance (2nd most parsimonious model, β = -4.63, SE = 3.49, Table 2.3). Variation in lemming abundance had a minor effect on goose productivity when spring climatic conditions were unfavourable to goose reproduction (i.e., cold temperatures, Fig. 2.4).

Snowy owl data from the Christmas Bird Count were used to estimate lemming abundance from 1976 to 1992. Since climatic conditions could also influence snowy owl reproduction, this could generate an overestimation of the genuine effect of lemmings on annual goose productivity. However, we found very similar results when restricting the analyses to the 13-year time series when lemming index was obtained directly by trapping (partial R^2 ranging from 25 to 40 %). We are thus confident that our estimates based on owl counts were adequate and that the observed relationship between lemmings and goose productivity mostly reflects variation in predation pressure.

Carry-over and density-dependent effects

Carry-over effect caused by spring conservation harvest was retained in the most parsimonious model (Table 2.3). Based on this model, the implementation of spring harvest on the main staging sites reduced goose productivity by about 7% on average. Spring harvest was included in six of the nine competing models and thus our results suggest that a reduction in pre-breeding body condition caused by human-induced disturbance negatively affected population productivity. Moreover, no delayed effects of annual goose productivity on subsequent year's productivity were detected (1 to 4 year time-lags; $r < 0.30$).

Finally, despite the strong population increase over the study period, we found no association between population size and annual goose productivity (ΔAICc > 27.6 for models including population size as covariate; Appendix 3).

Predictive power of the model

Using data from 2007, we tested the predictive ability of our most parsimonious model and found that the percent of juveniles observed in fall flocks (20%) was close to the predicted value (31% with spring NAO index = -0.34, spring snow depth = 10.36 cm, index of lemming abundance = 0.81, mean temperature mid-summer = 5.61°C, fall NAO index = 0.25 and presence of spring conservation harvest). Future observations will allow us to better evaluate the performance of the model under more extreme environmental conditions.

DISCUSSION

Annual greater snow goose productivity is strongly variable among years and we showed that goose productivity significantly affects annual population growth rate, and thus its population dynamics. This corroborates population models showing that the frequency of occurrence of "bad" and "good" breeding years has important consequences on population growth rate (Gauthier & Brault, 1998; Poysa & Pesonen, 2003).

Our approach, based on previously proposed or documented mechanisms, provides evidence for the strong influence of both climatic conditions and indirect trophic interactions on goose population productivity. While the effects of climatic conditions probably reflect bottom-up processes (food availability), indirect trophic interactions with small rodents reflects top-down processes (via shared predators). As expected, conditions encountered slightly prior to or at the start of the breeding season (spring NAO index and spring snow condition) were the main climatic factors determining the maximum potential annual goose productivity. Additionally, as a proxy for annual predation pressure (Bêty & al., 2002), rodent cycles indirectly influenced the proportion of the goose productivity consumed by predators during the summer. Results thus support our main hypothesis. Accordingly, major breeding failures observed in 1986, 1992 and 1999 (Fig. 2.3e) were characterized by extreme spring weather conditions. Inversely, lemming crashes were not necessarily associated with major goose breeding failures (Fig. 2.4). Interestingly, we found evidence suggesting that fluctuations in predation pressure caused very little variation in goose productivity when spring climatic conditions were unfavourable. This does not support our second hypothesis and further indicates that climate was the primary driver of the annual snow goose productivity.

ANNUAL GOOSE PRODUCTIVITY AND CLIMATIC CONDITIONS: BOTTOM-UP PROCESSES

The reduced productivity in years with positive spring NAO index values (i.e., low temperatures) and deep snow is consistent with previous findings indicating that spring climatic conditions are the main factors affecting snow goose reproductive effort and laying date (Lepage & al., 2000; Bêty & al., 2003; Reed & al., 2004; Dickey & al., 2008). By modulating local mean temperatures, the NAO presumably affects food availability (bottom-up process) as temperature influences the emergence, phenology and growth of arctic plants (Havstrom & al., 1993; Rustad & al., 2001; Aerts & al., 2006). Snow condition also has a major impact on food availability by determining accessibility of feeding sites to pre-breeding birds and timing of plant growth (Gauthier, 1993; Aerts & al., 2006). Females must feed intensively during the pre-laying and egg-laying periods, as most of the nutrients required for egg formation are acquired on the breeding grounds in this population (about >70% of egg protein and lipid; Choinière & Gauthier, 1995; Gauthier & al., 2003). Because of the very short arctic summer season, the optimal time period to breed is limited and a short delay in nesting can result in high costs in terms of reproductive success (the number of young surviving to winter declines by 90% over the span of laying dates, ~12 days; Lepage & al., 2000). Geese tend to reduce their clutch size or may not even attempt to breed in years with poor spring climatic conditions as an adaptive response to seasonally declining survival prospects of offspring (Lepage & al., 2000; Bêty & al., 2003). By influencing nutrient acquisition rates during critical pre-laying and laying periods and timing of breeding, spring climatic conditions affect the entire goose breeding productivity. Despite the beneficial effect of warm spring, we found evidence that extremely high temperatures associated to very negative spring NAO index values can reduce annual goose productivity. This could result from very high local temperatures that can lead to a reduction in gosling mass near fledging likely due to a mismatch between peak food quality and hatching date (Dickey & al., 2008).

The observed positive effect of summer temperatures on goose productivity could be through direct or indirect effects on gosling survival. Indeed, low temperatures can increase the probability of chick death due to cold exposure (Beintema & Visser, 1989; Schekkerman & al., 1998). Although goslings are fully competent homeotherms at a very young age (Fortin & al., 2000a), cold temperatures can increase their thermoregulatory costs, thereby reducing the amount of energy available for growth (Renaud, 1999). Alternatively, the positive effects of warm summer may be mediated through an effect on food availability (bottom-up process), as the biomass of plants grazed by goslings is enhanced during warm summers (Graham-Sauvé, 2007; Dickey & al., 2008). Several authors have shown that the seasonal decline in the growth of goslings is a consequence of declining plant quality and of density-dependent food depletion (Cooch & al., 1991; Sedinger & Flint, 1991; Lindholm & al., 1994; Lepage & al., 1998).

Menu et al. (2005) found a strong negative effect of cold local temperatures shortly after or at fledging time on gosling survival during the fall migration. Cold temperatures in late summer and at the beginning of migration may result in night frosts, which could accelerate plant senescence and thus reduce food quality. Precipitation, which is frequent at this time of the year, will fall as snow when temperature is below freezing, which should considerably reduce food availability for goslings (Menu & al., 2005). As positive fall NAO index values are associated with cold temperatures in northern regions, we expected to find a negative association between this index and the percentage of juveniles in the fall flocks. Surprisingly, we found the opposite. This may be partly explained by the influence of NAO on wind direction and speed, which could also affect goose fall migration. However, this association is hard to evaluate as we did not find any evidence in the literature indicating that positive fall NAO index values generate specific wind conditions along the goose migratory route. Although this parameter explained only a small proportion of the variance in goose productivity, it would be interesting to further investigate the potential mechanisms linking the fall NAO and the annual goose productivity.

Goose productivity was apparently not influenced by the amount of precipitation during the incubation and hatching periods ($\beta = -0.16$, SE = 0.13). The hypothesis that precipitations reduce nest predation rates and hence increase breeding productivity (via an increase in water availability for incubating females; Lecomte, 2007) is therefore not supported at the population level. Precipitation amounts recorded on Bylot Island may differ from those encountered at other breeding sites and that may explain why we did not detect an influence of this local climatic parameter on overall productivity. In addition, the reduction in predation rates resulting from increased precipitation rates may be counterbalanced by a negative effect on plant growth. Indeed, it has been shown that rainy summers (usually associated with cloudy conditions) may lead to reduced plant production, possibly because solar radiation required for photosynthesis is reduced (Chapin & al., 1995; Graham-Sauvé, 2007).

There are marked geographic and taxonomic biases in the literature on the effects of the NAO on terrestrial ecosystems. The majority of studies have been conducted in Western Europe and on large herbivores. Our study on greater snow geese, an herbivore breeding in the High Canadian Arctic, is one of the first to illustrate how NAO can influence key reproductive components and population dynamics of North American birds. Temperature measured at the main breeding site was a better predictor of goose productivity than climatic oscillations during mid-summer only, when total sea level pressure variability explained by the NAO reaches its minimum. Hence, the NAO index seems to adequately integrate local climatic conditions that affect geese during critical phases of their breeding cycle. Moreover, this large-scale climatic phenomenon likely represents conditions met by geese over a large part of their breeding range and may provide a more holistic account of the climate systems than local weather collected from only one site in the Arctic (i.e. Bylot Island). As suggested by other authors (Stenseth & Mysterud, 2005), using large-scale systems rather than local conditions appears to be advantageous when dealing with species living in spatially extensive areas.

ANNUAL GOOSE PRODUCTIVITY AND PREDATION PRESSURE: TOP-DOWN PROCESSES

Our results indicate that variation in predation pressure on goose eggs and young due to shared predators with lemmings (top-down processes; Bêty & al., 2002; Gauthier & al., 2004) is strong enough to be detected at the goose population level. Similar effects have been found in some populations of arctic-nesting waders and brent geese (*Branta b. bernicla*), in which breeding productivity follow three-year cycles associated with variations in lemming abundance (Summers & Underhill, 1987; Summers & al., 1998). Although the annual productivity of greater snow geese was clearly influenced by lemming abundance, there was no evidence of cyclic patterns. The effects of annual climatic variation on breeding propensity, timing of breeding and clutch size appears to be strong enough to obscure any cyclic patterns in predation pressure. This may explain why the overall goose productivity is not cyclic even though the predation intensity is largely dependent on the cyclic lemming population. Moreover, unlike most smaller tundra bird species, greater snow geese are a large bird that can adequately fight against the most important tundra predator, the arctic fox, to protect their eggs (Bêty & al., 2001; Lecomte, 2007) and goslings (J. Bêty, personal observations). They also nest in dense colonies were birds can benefit from a predator dilution effect during the laying period (Bêty & al., 2001), a critical phase during which nests are left mostly unattended (Poussart & al., 2000). Differences in the relative vulnerability to predators likely contribute to explain the disparity with other tundra bird species showing cyclic productivity.

CARRY-OVER EFFECTS

The body reserves accumulated by geese on spring staging areas are an essential fuel source for the northward migration and contribute to their breeding success (Gauthier & al., 1992; Bêty & al., 2003). As predicted, the spring conservation harvest occurring on the main staging area had a carry-over effect and negatively affected goose productivity, likely through an effect on the accumulation of pre-migration endogenous reserves (Féret & al., 2003; Béchet & al., 2004a). The previously documented negative effect on some components of reproductive success due to an increase in human-induced disturbance rates (Bêty & al., 2003) is thus strong enough to decrease the mean annual productivity by 7%, which is considerable for an average annual productivity of 25%. This result corroborates previous models suggesting that about 47% of the reduction in population growth rates due to the spring harvest was actually an indirect consequence of the concomitant reduction in fecundity, the remainder being due to increased mortality (Gauthier & Reed, 2007).

DENSITY DEPENDENCE

Despite a 6-fold increase in population size over 3 decades, we found no evidence of density-dependent effects on annual goose productivity. In greater snow geese, it has been proposed that a decline in body size, mass and condition of juveniles over the period 1975–94 was generated by increasing densities on the breeding grounds, leading to a reduced availability of per capita food for growing goslings during the summer (Reed & Plante, 1997). However, it appears that such a density-dependent effect has not yet affected population productivity (Reed, 1990; Menu & al., 2002). In 1996, when the total population was estimated at 670 000 birds, the Bylot Island breeding population was approximately at 46% of the estimated carrying capacity of the wetlands (Massé & al., 2001). This is likely near a long-term sustainable level (Reed & al., 1998) and may explain why no density-dependent effects have been detected on productivity. Increasing food availability on the main staging areas occurred at the same time as the population grew during the study period (Gauthier & al., 2005) and may have generated positive effects (i.e., better pre-breeding body condition) that compensated for potential negative density-dependent effects on the breeding grounds. Gauthier and al. (2005) reported an increase in pre-migration body stores between the late 1970's to the late 1980's, but the increase apparently levelled off in the 1990's. Increasing densities on the breeding grounds may also have generated positives effects on goose productivity as nest predation rate is inversely density dependent. This may also partly explain why no density-dependent effects have been detected on productivity. It is customary to regress annual productivity against population size of the same year to look for possible density dependence in reproduction (Newton, 1998). However, we must be cautious in our conclusions because our study is not experimental and this may result in a failure to detect density dependence (Fowler & al., 2006). Experimental studies addressing population dynamics and regulatory mechanisms directly are recommended, but in many species such experiments are not feasible and we have to be content with non-experimental approaches (Harrisson & Cappuccino, 1995). Moreover, very few studies have looked simultaneously at the long-term potential effects of density-dependence, climatic conditions and indirect trophic interactions generating fluctuations in predation pressure as we did.

CONCLUSION

Several factors may influence annual productivity in animal populations. Long term data sets allowing the integration of key environmental factors, such as those used in this study, remain scarce. By combining a rare and detailed data set with a mechanistic-based approach, we were able to illustrate that density-dependent effects on the productivity of an arctic nesting bird were apparently negligible relative to those of climate and indirect trophic interactions. In a context of global warming, the fate of the terrestrial arctic ecosystem is uncertain and it is imperative to have a good understanding of the effects of climate on the key components of the tundra food chain. Population models based on previously identified mechanisms will likely allow us to go one step further in our capacity to identify the relative importance of bottom-up and top-down processes, and the potential impacts of global warming on animal populations.

ACKNOWLEDGMENTS

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TABLES AND FIGURES

Table 2.1 Potential climatic effects (variables and mechanisms documented in previous studies, see reference in footnote) on the annual productivity of the greater snow goose according to different periods of the breeding cycle in the Arctic (Table 2.2). Variation through time of climatic effects can be captured by local measures of weather or by large-scale climatic indices (both categories of variables appear in the table). The right column details hypotheses.

Periods	Variables	Mechanisms	Hypotheses
Spring	Temperature Snow cover NAO/AO*	Influences breeding propensity[1,3], laying date[2,3], and gosling growth[3] mostly through food availability	A) Early spring (warm temperature and low snow cover) increases food availability and is thus positively associated with goose productivity (linear relationship) B) Very early spring causes a mismatch between peak food quality and hatch date, reducing goose productivity (quadratic relationship)
Early summer	Precipitations	Influences egg predation rate by affecting water availability and distance traveled from the nest by females during incubation recesses[3,4]	C) High precipitation increases water availability during incubation and is positively associated with goose productivity
Mid summer	Temperature NAO/AO*	Influences gosling survival and growth by affecting costs of thermoregulation[5,8], exposure to cold[3,6] and food availability[3,7]	D) Higher temperatures decrease costs of thermoregulation, reduce exposure to cold temperatures and increase the availability of food, and are thus positively associated with goose productivity
Late summer & Fall	Temperature NAO/AO*	Influences juvenile survival through food availability[9]	E) Higher temperatures extend the period of food availability and are thus positively associated with goose productivity

* Previous studies looked specifically for the effects of AO.

[1](Reed & al., 2004), [2](Bêty & al., 2003), [3](Dickey & al., 2008), [4](Lecomte, 2007), [5](Renaud, 1999), [6](Lindholm & al., 1994), [7](Lepage & al., 1998), [8](Fortin & al., 2000b), [9](Menu & al., 2005)

Table 2.2 Definition of the selected periods of the greater snow goose breeding cycle used for statistical analyses.

Periods (label)	Date	Stage
Spring (sp)	20 May to 20 June	Arrival and egg-laying
Early summer (es)	21 June to 15 July	Incubation and hatching
Mid summer (ms)	16 July to 15 August	Brood-rearing
Late summer (ls)	16 to 31 August	Fledging and early post-fledging
Fall (f)	1 to 30 September	Migration (northern regions)*

* The complete migration period is longer but we only considered the first part over the northern region because a large amount of migration mortality occurs shortly after fledging or at the beginning of fall migration (Menu & al., 2005).

Table 2.3 a) Variables, sign of the effect, the number of estimates parameters (k), log likelihood, ΔAICc, Akaike weights and proportion of variation explained by the nine most parsimonious candidate models of annual greater snow goose productivity (% of juveniles in the fall flight between 1976 and 2006; N=30). b) Slope parameters and standard error (SE) from the most parsimonious model.

a) Selected models

Variables	k	Log likelihood	Δ AICc	ω_i	R^2
-NAO_sp, -snow, +temp_ms, +NAO_f, +lem, +sp_harv	7	179.85	0.00	0.22	0.69
-NAO_sp, -snow, +temp_ms, +NAO_f, +lem, +sp_ harv, -NAO_sp*lem	8	173.77	0.63	0.16	0.72
-NAO_sp, -NA0^2_sp, -snow, +temp_ms, +NAO_f, +lem, +sp_harv	8	173.99	0.85	0.14	0.71
-NAO_sp, -snow, +temp_ms, +NAO_f, +lem, -NAO_sp*lem	7	181.42	1.57	0.10	0.67
-NAO_sp, -snow, + temp _ms, +NAO_f, +lem	6	187.87	2.73	0.06	0.64
-NAO_sp, -snow, + temp _ms, +NAO_f, +lem, +sp_harv, -NAO_ls	8	175.94	2.80	0.05	0.70
-NAO_sp, -snow, +lem, -NAO_sp*lem	5	192.38	2.91	0.05	0.57
-NAO_sp, -snow, + temp _ms, +lem, +sp_harv,	6	183.49	3.63	0.04	0.66
-NAO_sp, -snow, + temp _ms, +NAO_f, +lem, +sp_harv, + temp _ls	8	176.99	3.85	0.03	0.70
Null	1	229.52	27.84	0.00	0.00

b) Slope parameters of the most parsimonious model

Parameter	NAO_sp	snow	temp_ms	NAO_f	lem	sp_harv	Intercept
β	-9.27	-0.48	5.48	4.95	5.87	-6.65	-10.38
SE	2.90	0.17	2.11	3.03	1.67	3.36	12.68

Note: Except for the null model showed as reference, other alternative models rejected are not shown (ΔAICc values >4.0). See Appendix 3 for a full list of the alternative models.

NAO_sp = spring NAO index, snow = spring snow depth, temp_ms = mean temperature mid-summer, NAO_f = fall NAO index, lem = index of lemming abundance, sp_harv= spring conservation harvest, temp_ls = mean temperature late summer, NAO_ls = late summer NAO index

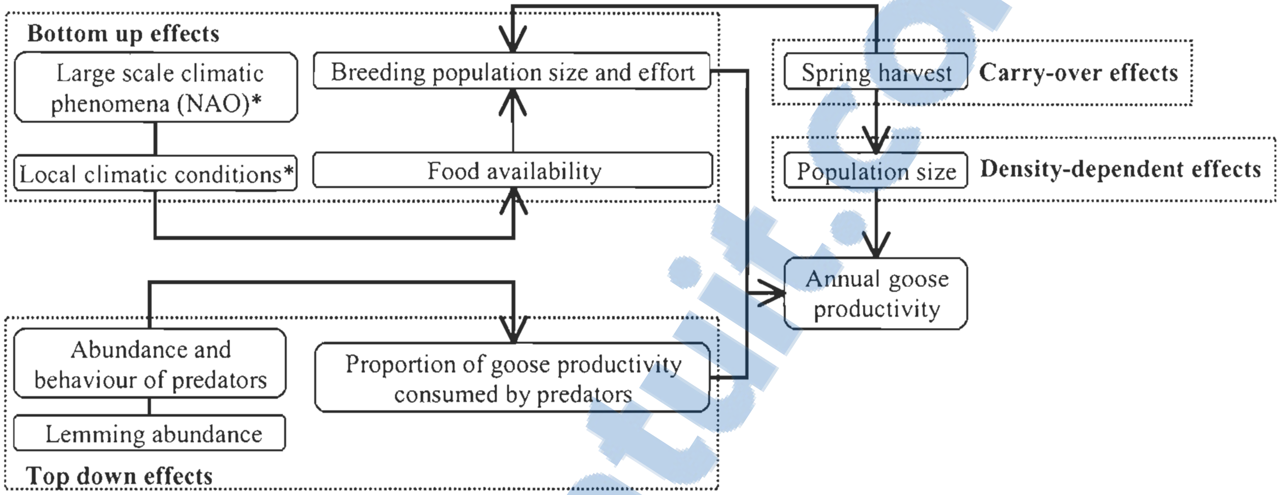
Figure 2.1 Map showing the breeding ground of greater snow geese (enclosed by a dotted line), including the locations of nesting colonies in grey, the main staging areas and the wintering ground.

Figure 2.2 Flow diagram summarizing the main mechanisms that are likely to link the annual greater snow goose productivity (% of juveniles in fall flock) and various environmental factors, including climatic conditions (mainly through bottom-up effects; see mechanisms in Table 2.1), fluctuations in predation pressure caused by rodent cycles, population size, and spring harvest on the main staging areas.

Figure 2.3 Relationships illustrating residual values for annual goose productivity (% of juveniles in fall flock) calculated for each variable included in the most parsimonious model (Table 2.3). b) Index of lemming abundance (pooled number of *Lemmus sibiricus* and *Dicrostonyx groenlandicus* caught per 100 trap-nights). d) Population size variation is also shown although not selected in the model.

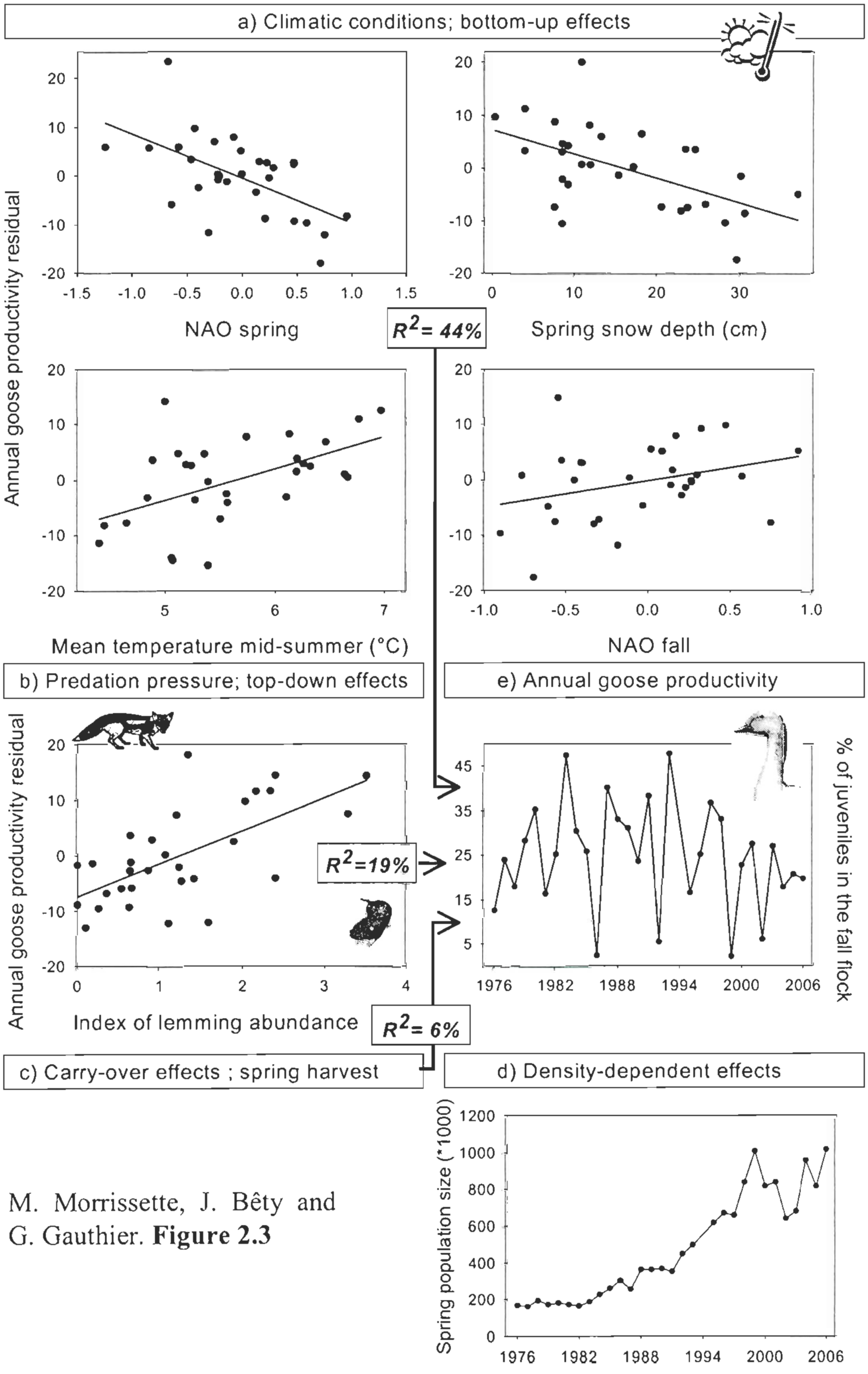
Figure 2.4 Illustration of the interaction between the effect of the NAO spring index and of the lemming abundance on the annual goose productivity (% of juveniles in fall flock). The regression curves were generated with the model including the interaction term (second most parsimonious model in Table 2.3) and using three values of NAO (-1.20, -0.40 and 0.95). To illustrate the adequacy of the model, each point represents the observed annual percentage of juveniles according to lemming abundance (0.0 to 3.5) and NAO index (grouped in three categories:○ > 0.25; • -0.40 to 0.25; ● < -0.40).

M. Morrissette, J. Bêty and G. Gauthier. **Figure 2.1**

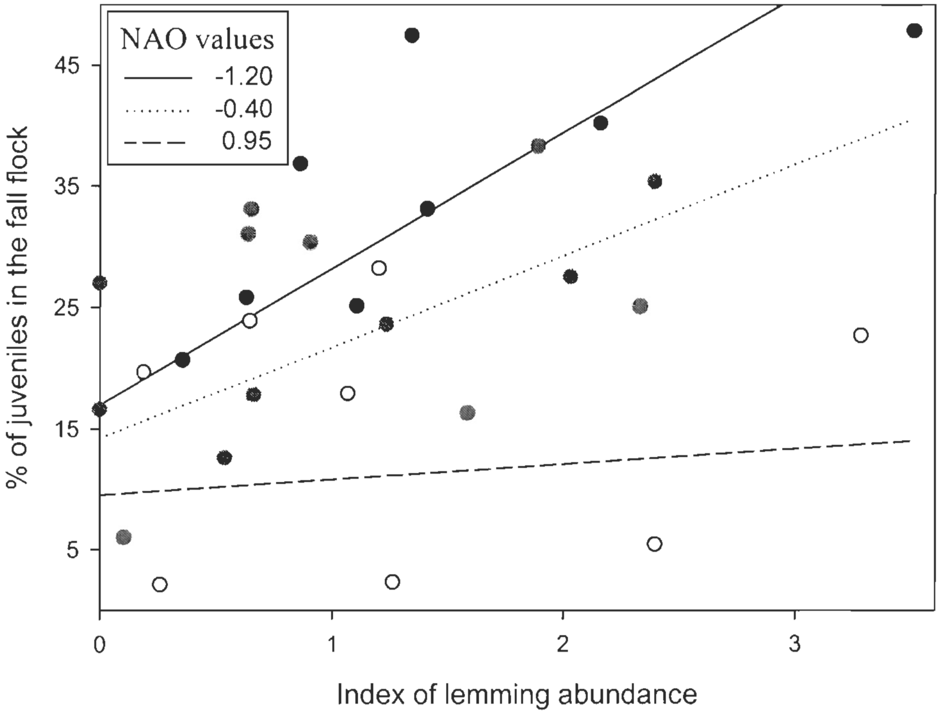


M. Morrissette, J. Bêty and G. Gauthier. **Figure 2.2**

* All climatic effects on annual goose productivity are not showed; see Table 2.1 for a complete list of possible effects



M. Morrissette, J. Bêty and G. Gauthier. **Figure 2.3**



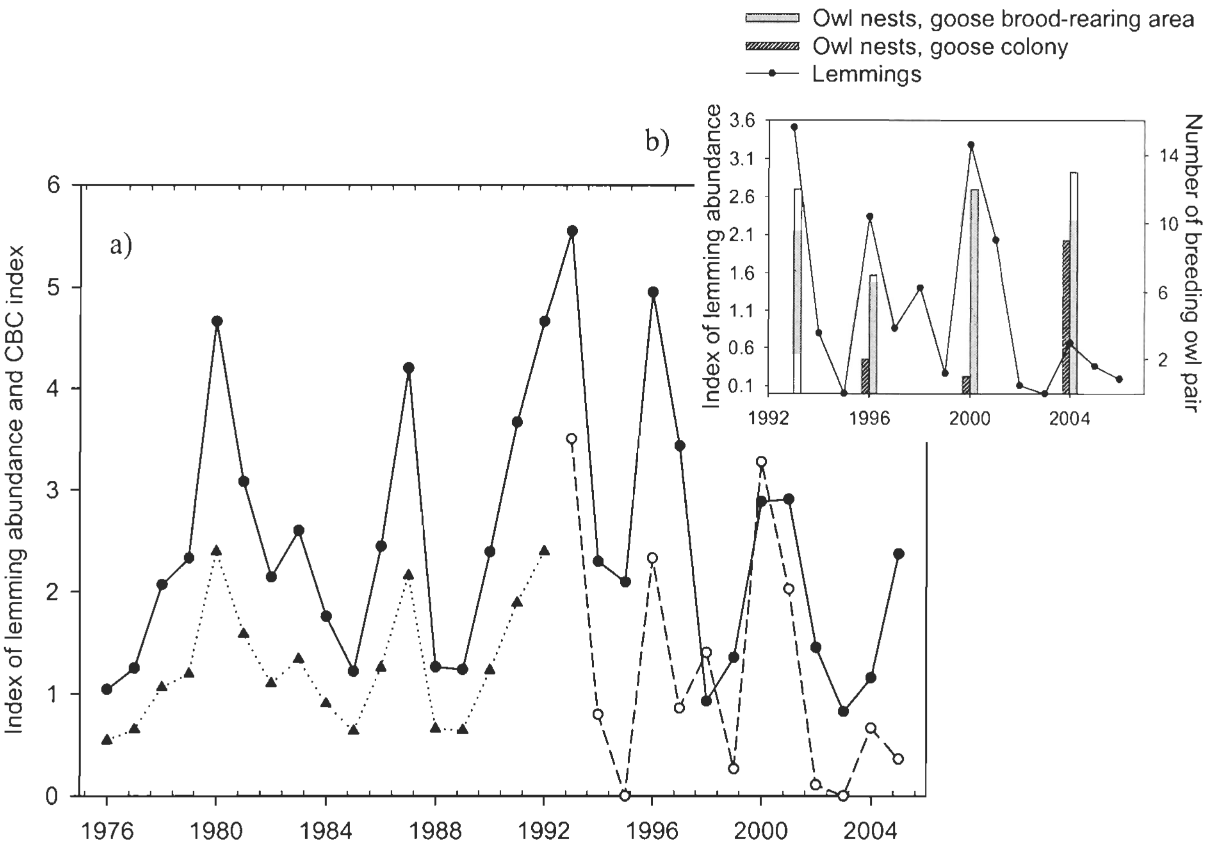
M. Morrissette, J. Bêty and G. Gauthier. **Figure 2.4**

APPENDIXES

APPENDIX 1 Relationships between climatic variables measured at the Bylot Island weather station (Y) and at the Environment Canada weather station of Pond Inlet (X) for the period 1995-2006 according to the different periods of the goose breeding cycle.

Variable	Period	Equation	n	R^2	P
Mean daily temperature	Spring	$Y = 0.80 X + 0.25$	322	0.84	<0.001
	Early summer	$Y = 0.74 X + 0.93$	260	0.64	<0.001
	Mid summer	$Y = 0.50 X + 2.71$	315	0.39	<0.001
	Late summer	$Y= 0.78 X + 0.34$	157	0.68	<0.001
Cumulative precipitations	Early summer	$Y = 0.72 X + 18.37$	12	0.42	<0.001

Note: Overlapping snow depth data from Bylot Island and Pond Inlet were not available. Therefore we used data from Pond Inlet (1976 to 1993) and from Bylot Island (1995 to 2006) to run our analyses.



APPENDIX 2 Relationship between annual lemming and snowy owl abundance. a) Index of annual lemming abundance observed on Bylot Island from 1993 to 2005, (--○--), index of annual snowy owl sightings from the Christmas Bird Count (CBC*100) of Manitoba, Ontario and Québec from 1976 to 2005 (—•—), and estimated lemming abundance from 1976-1992 (···▼···) derived from the predictive regression equation relating lemming abundance and owl counts during the period 1993-2005. b) Index of annual lemming abundance observed on Bylot Island from 1993 to 2006 and number of snowy owl nests recorded on the goose brood-rearing area and main nesting colony. Intensive searches for snowy owl nests in the goose colony was carried out in 2004 only (Gauthier & al., 2004).

APPENDIX 3 Variables, sign of the effect, the number of estimates parameters (k), log likelihood, ΔAICc, Akaike weights and proportion of variation explained by candidate models of annual greater snow goose productivity (% of juveniles in the fall flight between 1976 and 2006; N=30).

Selected models

Variables	k	Log likelihood	Δ AICc	ω_i	R^2
-NAO_sp, -snow, +temp_ms, +NAO_f, +lem, -sp_harv	7	179.85	0.00	0.22	0.69
-NAO_sp, -snow, +temp_ms, +NAO_f, +lem, -sp_harv, -NAO_sp*lem	8	173.77	0.63	0.16	0.72
-NAO_sp, -NAO^2_sp, -snow, +temp_ms, +NAO_f, +lem, -sp_harv	8	173.99	0.85	0.14	0.71
-NAO_sp, -snow, + temp_ms, +NAO_f, +lem, -NAO_sp*lem	7	181.42	1.57	0.10	0.67
-NAO_sp, -snow, + temp_ms, +NAO_f, +lem	6	187.87	2.73	0.06	0.64
-NAO_sp, -snow, + temp_ms, +NAO_f, +lem, -sp_harv, -NAO_ls	8	175.94	2.80	0.05	0.70
-NAO_sp, -snow, +lem, -NAO_sp*lem	5	192.38	2.91	0.05	0.57
-NAO_sp, -snow, + temp_ms, +lem, -sp_harv,	6	183.49	3.63	0.04	0.66
-NAO_sp, -snow, + temp_ms, +NAO_f, +lem, -sp_harv, + temp_ls	8	176.99	3.85	0.03	0.70
-NAO_sp, -snow, + temp_ms, + temp_f, +lem, -sp_harv	7	183.91	4.06	0.03	0.66
-NAO_sp, -snow, +NAO_f, +lem, -sp_harv	6	189.35	4.21	0.03	0.60
-NAO_sp, + temp_ms, +lem, -NAO_sp*lem	5	197.47	4.33	0.03	0.53
-NAO_sp, -snow, +NAO_ms, +NAO_f, +lem, -sp_harv	7	184.21	4.36	0.02	0.61
-NAO_sp, -snow, +temp_ms, +lem, -sp_harv, + -NAO_sp*lem	7	178.06	4.92	0.02	0.67
+temp_sp, -snow, + temp_ms, +NAO_f, +lem, -sp_harv,	7	185.30	5.45	0.01	0.64
-NAO_sp, +lem, -NAO_sp*lem	4	195.49	6.02	0.01	0.51
-NAO_sp, -snow, + temp_ms, +NAO_f, +lem, +sp_harv, -rain	8	180.52	7.38	0.00	0.71
-NAO_sp, -snow, + temp_ms, + temp_ls, +NAO_f, -rain	7	199.16	19.3	0.00	0.48
-NAO_sp, -snow, + temp_ms, + temp_ls, +NAO_f	6	197.87	12.73	0.00	0.47
-NAO_sp, -snow, -snow^2, +temp_ms, +NAO_f, +lem, -sp_harv	8	185.97	12.83	0.00	0.69
-NAO_sp,-NAO^2_sp,-snow,-snow^2,+temp_ms,+NAO_f, +lem, -sp_harv	9	180.01	15.87	0.00	0.71
-NAO_sp, -snow, + temp_ms, +NAO_f, +lem, -sp_harv, -pop	8	200.74	27.60	0.00	0.70
-NAO_sp, -snow, +lem, -sp_harv, -pop	6	216.46	31.32	0.00	0.58
+ temp_sp , -snow, +lem, -sp_harv, -pop	6	218.08	32.94	0.00	0.58
-NAO_sp, -snow, +lem, -pop	5	239.14	33.00	0.00	0.57
Null		229.52	27.84	0.00	

temp_sp = mean temperature in spring, NAO_sp = spring NAO index, snow = spring snow depth, temp_ms = mean temperature in mid-summer, rain = cumulative precipitations, NAO_ms = mid-summer NAO index, temp_ls = mean temperature late summer, NAO_ls = late summer NAO index, temp_f = temperature in fall, NAO_f = fall NAO index, lem = index of lemming abundance, sp_harv = spring conservation harvest, pop = spring population size

CHAPITRE 3 : CONCLUSION DU MÉMOIRE

CONTRIBUTIONS

Notre étude met en relief l'importance relative de facteurs environnementaux (biotiques et abiotiques) qui affectent la productivité annuelle d'un oiseau herbivore clé du Haut Arctique canadien, la Grande Oie des neiges. Nous avons montré que la productivité annuelle, exprimée en termes de pourcentage de juvéniles à l'automne, est grandement influencée par les conditions climatiques et les interactions trophiques indirectes entre les proies (via la prédation). Tel que prédit, les conditions climatiques printanières semblent déterminer le niveau de productivité annuelle maximal de la population de la Grande Oie des neiges. Nos résultats montrent en effet que des températures plus élevées que la moyenne ainsi qu'une faible épaisseur de neige au printemps sont associés à une forte production de jeunes oies. Les conditions printanières semblent principalement avoir un effet sur la productivité en modulant la disponibilité de la nourriture durant la période critique de pré-ponte et de ponte (Bêty & al., 2003; Reed & al., 2004; Dickey & al., 2008). De plus, tel qu'attendu, les cycles de lemmings semblent moduler la proportion de la productivité qui est consommée par les prédateurs au cours de l'été. De fortes abondances de lemmings seraient associées à une réduction de la pression de prédation par le Renard arctique et le Labbe parasite sur les œufs et les jeunes oies (Bêty & al., 2002). La productivité des oies, quoique très variable, n'est toutefois pas cyclique. Il a été montré que chez certaines espèces d'oiseaux de l'Arctique, la productivité pouvait être cyclique et fortement corrélée avec les cycles de lemmings (Summers & Underhill, 1987; Summers & al., 1998). Bien que la pression de prédation soit influencée par les cycles de lemmings, l'absence de cyclicité dans la productivité des oies s'expliquerait par un effet prépondérant des facteurs climatiques. D'une part, les taux de prédation sont inversement reliés à la densité de nids dans les grandes colonies d'oies des neiges (via un effet de dilution; Bêty & al., 2001). D'autre part, le climat printanier détermine en grande partie la taille de la population reproductrice et l'effort de reproduction des individus (Reed & al., 2004; Dickey & al., 2008). Ainsi, les variations dans ces paramètres démographiques clés brouilleraient les effets des fluctuations d'abondance de lemmings et, en conséquence, font en sorte que la productivité globale n'est pas cyclique.

Alors que les conditions climatiques semblent influencer la productivité annuelle davantage à travers des interactions ascendantes (Gauthier & al., 1996; Rustad & al., 2001), les effets indirects des lemmings s'opèrent via des relations descendantes, soit par le biais de la prédation (Gauthier & al., 2004). Selon l'hypothèse d'exploitation des écosystèmes, la faible productivité primaire de la toundra arctique ne peut supporter une abondance de prédateurs suffisante pour que ceux-ci forment un niveau trophique fonctionnel, c'est-à-dire ayant un impact significatif sur les herbivores (Krebs & al., 2003). Nos résultats suggèrent que des relations descendantes peuvent avoir un impact important même dans un écosystème terrestre du Haut-Arctique caractérisé par une faible production primaire. Pour les prédateurs, cela pourrait entre autre résulter d'un apport de nutriments allochtones provenant d'autres écosystèmes durant certaines périodes de l'année (ex.: oiseaux migrateurs et phoques; Giroux, 2006). En augmentant la densité de prédateurs, ces subsides allochtones renforceraient l'influence des relations descendantes dans la toundra de l'île Bylot.

L'indice d'abondance de lemmings utilisé dans cette étude peut être critiqué. L'utilisation de trois différentes sources de données (extrapolation à partir de l'abondance de harfangs des neiges entre 1976 et 1992, du décompte des nids d'hiver en 1993 et de transects de trappage mortel entre 1994 et 2006) peut, en effet, être une source d'erreur ou de biais dans cette étude. En fait, les différentes méthodes de suivi pourraient représenter davantage une différence méthodologique que biologique. Nous sommes confiants que notre indice d'abondance de lemmings représente assez fidèlement l'abondance de lemmings retrouvée sur l'aire de nidification des oies. En effet, lorsque nous utilisons uniquement la base de données de l'île Bylot entre 1993 et 2006 (obtenue essentiellement à partir de trappage), nous obtenons des résultats très similaires quant à l'importance relative des différents facteurs environnementaux influençant la productivité annuelle des oies. Étant donné que la plus longue série temporelle disponible à l'île Bylot demeure courte (n = 13) et que les lemmings ont une grande importance dans la dynamique de l'écosystème arctique, nous considérons que nous avons utilisé le meilleur indice disponible.

Comme pour plusieurs autres espèces d'oies, la population de la Grande Oie des neiges a vu sa population augmenter drastiquement depuis les années soixante (Calvert & al., 2007). Toutefois, contrairement à d'autres études qui ont détecté des effets dépendants de la densité liés à l'augmentation de la taille des populations (Cooch & al., 1989; Owen & Black, 1991; Francis & al., 1992; Williams & al., 1993; Reed & Plante, 1997), notre étude ne fournit aucune évidence d'un effet de la densité sur la productivité des oies. En 1996, lorsque la population comptait environ 670 000 individus, une étude portant sur les milieux humides indiquait que la population à l'île Bylot (principale colonie) avait atteint environ la moitié de la capacité biotique des milieux préférés par les oies (Massé & al., 2001). Cet état est presque idéal pour le maintien à long terme de la population (Reed & al., 1998) et explique possiblement pourquoi aucune relation entre la densité et la productivité n'a été détectée en dépit du fait que la population soit maintenant estimée à plus d'un million d'individus (Menu & al., 2002). De plus, l'augmentation de la taille de la population s'est fait parallèlement à une augmentation de la quantité de nourriture disponible sur les principales haltes migratoires (via les terres agricoles; Gauthier & al., 2005). Ainsi, l'augmentation de la densité ne s'est probablement pas traduite par une diminution de la condition corporelle pré-reproductrice des femelles (Féret & al., 2003). Globalement, nos résultats suggèrent que l'augmentation de la compétition intra-spécifique n'a pas encore eu d'effet négatif mesurable sur le succès reproducteur des oies et la survie des jeunes jusqu'à l'automne. Toutefois, il est possible que notre approche (sans manipulation expérimentale) ne soit pas en mesure de détecter un effet dépendant de la densité. Les effets de la densité, de la disponibilité de la nourriture sur les haltes migratoires et de l'année, par exemple, sont possiblement confondus dans nos modèles. Les approches expérimentales sont effectivement hautement recommandées pour distinguer l'effet de chacun des paramètres, néanmoins de telles approches sont souvent impraticable pour plusieurs espèces et nous devons nous contenter d'études sans manipulation expérimentale.

Par le biais de cette étude, nous avons également montré que l'utilisation des phénomènes climatiques à grande échelle peut être avantageuse lorsque les réponses écologiques doivent être interprétées sur une grande échelle spatiale. En influençant les conditions climatiques locales de l'Arctique, l'Oscillation Nord Atlantique (ONA) s'est effectivement avérée être un bon indicateur des conditions climatiques qui affectent les oies sur l'ensemble de l'aire de reproduction. Lorsque l'on s'intéresse aux espèces présentes sur une grande aire de distribution, l'ONA représenterait donc un indice plus intégrateur du climat que certains paramètres mesurés localement (comme la température de l'air). Globalement, comme le suggérait des études antérieures (Forchhammer & al., 1998; Forchhammer & Post, 2004; Stenseth & Mysterud, 2005), nous appuyons l'intégration des phénomènes climatiques à grande échelle dans l'étude de l'impact du climat sur les espèces animales et végétales, d'autant plus que le réchauffement climatique semble modifier l'amplitude et la fréquence de ces oscillations climatiques (Cassou, 2004).

Finalement, nous aimerions mentionner que cette étude, basée principalement sur des mécanismes de causes à effets documentés localement, permet d'étendre notre compréhension des processus qui modulent la dynamique de la population de la Grande Oie des neiges. La productivité annuelle représente un paramètre important à considérer lorsque l'on s'intéresse à la dynamique de la population puisqu'elle explique une part significative de la variation du taux de croissance de la population. Notre étude amène de ce fait des éléments de réponse supplémentaires sur les processus qui lient les facteurs environnementaux à la structure et à la taille des populations au cours du temps.

PERSPECTIVES D'AVENIR

Dans un contexte de réchauffement global, il est difficile de s'intéresser à la productivité des populations aviaires nicheuses dans l'Arctique sans penser aux conséquences qu'auront les changements climatiques sur l'écosystème terrestre arctique. Le suivi écologique détaillé associé à la population de la Grande Oie des neiges, qui est réalisé depuis près de 20 ans à l'île Bylot, offre une opportunité de mieux comprendre et prévoir la vulnérabilité et le futur des populations et des écosystèmes naturels. Étant relativement simple, le système de l'île Bylot facilite l'étude des relations trophiques indirectes et permet de combiner les effets directs et indirects du climat et des interactions trophiques sur plusieurs niveaux de la chaîne alimentaire. Ainsi, en intégrant les résultats obtenus à partir de divers projets de recherche réalisés à l'île Bylot (du pergélisol aux prédateurs), il sera vraisemblablement possible d'avoir une meilleure compréhension globale de la structure et du fonctionnement de cet écosystème terrestre arctique. Globalement, les données devraient permettre de faire des prédictions plus réalistes des conséquences du réchauffement climatique sur la toundra arctique.

D'autre part, il serait intéressant d'obtenir des informations concernant la reproduction des oies ailleurs dans l'Arctique. Nous pourrions ainsi vérifier quels sont les effets des conditions climatiques locales et des relations trophiques dans des milieux possiblement moins productifs que celui présent à l'île Bylot et dans des colonies de plus faibles tailles. Nous pourrions également évaluer si les données récoltées à l'île Bylot sont bien représentatives des conditions environnementales rencontrées par l'ensemble de la population de la Grande Oie des neiges.

Puisque l'abondance des rongeurs influence considérablement la dynamique du réseau trophique et la reproduction des oiseaux arctiques, il serait pertinent de mieux documenter les effets des variations climatiques hivernales sur les fluctuations d'abondance de lemmings. En effet, la reproduction de ces rongeurs semble être particulièrement influencée par l'épaisseur de neige et les températures prévalant durant cette saison (Hansson & Henttonen, 1988; Ims & Fuglei, 2005). Il serait également pertinent d'obtenir des informations sur la force des relations trophiques entre les prédateurs et les lemmings en hiver. Ces relations ont probablement un impact important sur les abondances de lemmings retrouvées à l'été. Il est évident que les contraintes logistiques hivernales rendent particulièrement difficile ce type d'étude dans l'Arctique, mais notre compréhension du fonctionnement de la toundra nécessitera vraisemblablement ce type de recherche. Espérons que des méthodes comme l'analyse des nids d'hiver de lemmings, le suivi par satellite d'animaux de petites tailles ou l'utilisation des isotopes stables permettront un jour de mieux documenter les interactions survenant durant l'hiver.

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May 23, 2008

Joel Bety
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Rimouski, Québec G5L 3A1

Amendment to Research Permit SIR-2007-1100 for 2008 Field Season

Dear Joel

The terms and conditions of your research permit SIR-2007-1100 apply with the following amendments for the 2008 field season:

1. Erect up to 30 wooden made platforms (30 cm x 30 cm) erected on the top of a 1-2 m post in songbird nesting areas to collect feces of shorebirds and Lapland longspur. Platforms will be erected in June and removed at the end August. Feces will be analyzed to identify prey items through recovery of undigested arthropod body parts

2. Additional members of Research team in 2008 will be:
   - Émilie Chalifour (10340 St-Charles, Montréal, Québec H2C 2L6; 514-381-0563; chalifour.emilie@courrier.uqam.ca)
   - Élise Bolduc (Université du Québec à Rimouski; Tel : 418-723-1986 #1909; FAX : 418-724-1849; elise.bolduc@gmail.com)
   - Émilie D'Astous (26A Rue St-Joseph Est; Rimouski, Qc; 418-723-7551; emiliedastous@hotmail.com)
   - Martin Patenaude-Monette (10475 av. d'Auteuil; Montréal, Qc H3L 2K3; 514-389-1811; Martin.Patenaude-Monette@USherbrooke.ca)
   - Pierre-Yves L'Hérault (466 chemin du Panorama; Rimouski, Qc, G5N 1T7; 418-722-0403; pylherault@hotmail.com) (Firearm licence: 12138028.0001)
   - Inuit assistant (name to be confirmed and provided to park manager before entering the park; orientation required)

   Existing research team members from 2007:
   - Joël Bêty, (Firearm Licence # 10054817.0002)
   - Gilles Gauthier, (Firearm Licence # 11801941.0002)
   - Laura McKinnon, (Firearm Licence # 11412731.0001)
   - Ludovic Jolicoeur, (Firearm Licence # 11789755.0001)
   - François Rousseau,
   - Aurélie Bourbeau-Lemieux,
   - Manon Morrissette, (Firearm Licence # 12029267.0001)

   NOTE: ONLY THOSE WHO PROVIDE THEIR FIREARM LICENCE # TO THE PARK MANAGER PRIOR TO ENTERING FIELD WILL BE AUTHORIZED TO BE IN POSSESSION OF FIREARM.

Please ensure this amendment is attached to your permit documents issued in 2007.