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IMPACT DE LA CHASSE SUR LA DYNAMIQUE D'UNE POPULATION MIGRATRICE

Le cas de la Grande Oie des neiges

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Résumé

En gestion des populations animales, le contrôle d'une population peut être atteint par la modification d'un ou plusieurs paramètres démographiques (survie, reproduction ou mouvements). La population de Grandes oies des neiges (*Chen caerulescens atlantica*), une espèce qui niche en Arctique, est aujourd'hui considérée surabondante suite à la croissance exponentielle de sa population à la fin du 20$^{\text{ème}}$ siècle. En 1999, des mesures spéciales de conservation visant à stabiliser la population via une augmentation du taux de récolte à la chasse ont été instaurées, la plus spectaculaire étant une saison de chasse durant la migration printanière au Québec. Cette thèse a pour objectif d'évaluer les effets de ces mesures sur les processus démographiques sous-jacents suivants : la survie, la reproduction et le recrutement des jeunes en tant que reproducteurs. Nous présentons d'abord un nouveau modèle statistique de survie qui permet de produire des estimés de survie non biaisés en présence d'incertitude sur la perte des marques auxiliaires utilisées pour la détection des individus. Ce modèle utilise toutes les informations provenant des recaptures vivantes, des observations et des reprises à la chasse d'individus marqués de 1993 à 2005. En contrastant deux périodes, avant et à partir de 1999, nous avons montré que la diminution de survie a été la plus marquée chez les adultes durant les migrations automnale et printanière au Québec relativement à la baisse observée l'hiver aux États-Unis. Basé sur des données de la principale colonie, Île Bylot, Nunavut (1995-2007), nous n'avons pas trouvé d'évidence d'un effet reporté de la pression de chasse au Québec durant le printemps sur différents paramètres de reproduction l'été suivant (densité de nid, date et taille de ponte), une fois pris en compte l'effet des conditions climatiques rencontrées durant la migration et à l'arrivée sur le site de nidification. Cependant, le taux de récolte des adultes au printemps après 1998 est apparu comme un facteur important affectant à la baisse le recrutement des jeunes dans la population au cours de la période 1992-2005. En lien avec la stratégie mixte de reproduction des oies qui utilisent à la fois des réserves exogènes et endogènes pour la reproduction, le mécanisme sous-jacent suggéré est un effet reporté du dérangement par la chasse sur l'alimentation au printemps via une diminution des réserves endogènes. Nous démontrons ainsi de façon empirique que si la chasse diminue la survie, elle peut aussi diminuer l'accès à la reproduction. Nous suggérons que la diminution de la productivité de la population qui avait déjà été documentée se ferait principalement via la décision de se reproduire ou non (recrutement et propension à se reproduire) plutôt que par une baisse du succès reproducteur (indépendamment de la décision de se reproduire). Cette population semble aujourd'hui stabilisée, mettant en évidence que ces mesures de conservation ont vraisemblablement porté leurs fruits.

Abstract

In animal population management, the control of a population can be achieved by modifying one or more demographic parameters (survival, reproduction or movements). The population of Greater Snow Geese (*Chen caerulescens atlantica*), a species that nests in the Arctic, is now considered overabundant due to the exponential growth of its population in the late 20th century. In 1999, special conservation measures aimed at stabilizing the population through increased harvest rates by hunting were introduced, the most spectacular being a hunting season during spring migration in Québec. This thesis aims to evaluate the effects of these measures on the following underlying demographic processes: survival, reproduction and recruitment of young adults as breeders. We first present a new statistical model of survival that can produce unbiased estimates of survival in the presence of uncertainty about the loss of auxiliary markers used for the detection of individuals. This model uses all the information from live recaptures, observations and hunt recoveries of individuals marked from 1993 to 2005. By contrasting two periods, before and since 1999, we showed that the decrease in survival was greater for adults during the fall and spring migration in Québec than during wintering in the USA. Based on data from the main colony, Bylot Island, Nunavut (1995-2007), we found no evidence of a carry-over effect of hunting pressure in Québec during the spring on various reproductive parameters the following summer (nest density, clutch size and laying date), once the effect of weather conditions encountered during migration and upon arrival at the nesting site were considered. However, the harvest rate of adults in spring after 1998 emerged as an important factor affecting the decline in the recruitment of young adults during the period 1992-2005. In line with the mixed capital/income breeding strategy of geese, the suggested underlying mechanism is a carry-over effect of disturbance from hunt on foraging during the spring, leading to a decrease in endogenous reserves. We demonstrate empirically that hunting not only decreased survival, but it can also reduce access to reproduction. We suggest that the previously documented decreases in productivity of the population likely occurred via the decision to breed or not (recruitment and propensity to breed) rather than a decrease in reproductive success once the decision to reproduce has occurred. This population appears stable today, highlighting that these conservation measures have been potentially successful.

Avant-Propos

Cette thèse s'articule autour de quatre manuscrits rédigés sous formes d'articles scientifiques, déjà publiés ou destinés à être publiés dans un futur très proche. Une introduction et une conclusion générale viennent apporter la cohésion nécessaire à cette thèse de doctorat en Biologie et souligner la contribution du présent travail au domaine. Ce travail est le fruit de plusieurs années de collaboration avec mes deux directeurs de thèses, Gilles Gauthier (Université Laval, Québec, QC, Canada) et Roger Pradel (Centre d'Écologie Fonctionnelle et Évolutive, Unité Mixte de Recherche du Centre national de la Recherche Scientifique 5175, Montpellier, France). Ceux-ci ont largement prodigué leurs conseils dans la réalisation des quatre différents chapitres dont ils sont co-auteurs. Rémi Choquet (C.E.F.E, U.MR. C.N.R.S. 5175, Montpellier, France), co-auteur de trois chapitres de cette thèse, aura joué un rôle de mentor tout au long de ma thèse et a apporté sans nul doute la plus grande contribution à ce travail, spécialement d'un point de vue de l'approche méthodologique. Je tiens ainsi à remercier vivement ces trois acteurs principaux de ma thèse: Gilles, en particulier pour m'avoir donné la chance de réaliser une thèse qui m'aura fait sortir les pieds de l'eau et découvrir l'Arctique; Roger, pour ton enseignement précieux et me démontrer qu'il est possible de conjuguer excellente science et un style de vie quasi-vacancier; Rémi, pour ta patience pour répondre à mes questions et avoir toujours été disponible. Mes remerciements s'adressent également aux membres qui ont accepté de siéger aux différents comités de thèse tout au long de mon doctorat et dont les commentaires m'auront été grandement profitables, par ordre alphabétique : Daniel Fortin (Université Laval, Québec, QC, Canada), Jean Huot (Université Laval, Québec, QC, Canada), Jean-Pierre Tremblay (Université Laval, Québec, QC, Canada) et Julie Turgeon (Université Laval, Québec, QC, Canada). Je remercie les membres de mon jury de thèse, Julie Turgeon (examinatrice, Université Laval), Jean-Pierre Tremblay (examinateur, Université Laval), Charles Francis (examinateur externe, Service Canadien de la Faune, Centre National de la Recherche Faunique, Ottawa, ON, Canada), Gilles Gauthier et Roger Pradel, qui par leurs commentaires ont contribué à la version finale de cette thèse. Ce travail a également grandement profité de commentaires précieux émanant de discussions informelles avec Joël Bêty, Marie-Christine Cadieux (également co-auteur d'un chapitre), Jean-Dominique Lebreton, Josée Lefèbvre, Laurianne Rouan et Austin Reed qui ont toujours su trouver le temps nécessaire. La dernière personne et non la moins importante qui aura contribué à cette thèse, est Laura McKinnon, par ses nombreux conseils éclairés, ses révisions attentives et détaillées de tous mes manuscrits et le partage de son impressionnante connaissance de l'Arctique.

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Introduction

Dynamique des populations sauvages

L'étude des changements de la distribution des individus dans le temps et dans l'espace constitue le but premier de l'Écologie des populations. L'accent est souvent porté sur l'étude de la variation du nombre d'individus (l'abondance) au cours du temps et de l'espace ou dynamique des populations. La variation de la taille d'une population s'effectue au travers des processus démographiques que sont la reproduction, la mortalité (ou survie) et les mouvements (Williams et al. 2002). Finalement, l'intégration de ces processus démographiques sur une période de temps donnée commande la croissance de la population sur cette même période de temps.

Différents facteurs affectent la croissance d'une population dont la population elle-même. La densité-dépendance se produit quand le taux de croissance *per capita* d'une population dépend de la densité, ou taille, de cette même population (Sinclair and Pech 1996). Cette densité-dépendance s'exprime via l'augmentation des taux de mortalité et d'émigration, et/ou la diminution des taux relatifs à la reproduction et à l'immigration, relativement à l'accroissement de la taille de la population. Parmi les facteurs dépendants de la densité se trouvent la prédation et la compétition intra/inter spécifique. A l'opposé, des facteurs tel le climat affectent la mortalité indépendamment de la taille de la population.

L'équilibre de l'effectif d'une population implique la régulation et la limitation de la population. Les concepts de régulation et de limitation abordent les questions des facteurs et mécanismes (dépendants de la densité ou non) qui stabilisent une population autour d'une taille moyenne donnée (alternance de phase de déclin et de croissance) et de ce qui détermine cette taille moyenne (Krebs 2002). Toutefois, une ambiguïté persiste sur la définition des termes de régulation et de limitation d'une population (pour exemple : Turchin (1999), Murray (1999), Berryman (2004)). Classiquement le processus qui fixe le point d'équilibre de la taille d'une population est désigné par le terme de limitation et les facteurs causaux par facteurs limitants. Cependant cette définition est jugée triviale par Sinclair et Pech (1996). Comme toute cause de mortalité ou d'altération de la reproduction affecte le point d'équilibre de la population, cela veut dire que tout facteur affectant le taux de croissance de la population est un facteur limitant. La régulation correspond au processus par lequel la population montre une tendance à revenir à son point d'équilibre. Celle-ci ne peut avoir lieu sans densité-dépendance. Le climat, cité précédemment, ne peut donc pas réguler une population (Krebs 2002).

Parmi tous les facteurs qui affectent de façon directe ou non la dynamique des populations naturelles, l'Homme occupe une part substantielle et grandissante. La croissance de la population humaine et de ses besoins conduit à l'augmentation de l'agriculture, de l'industrie, du commerce et des loisirs. Une excellente illustration de ce phénomène à grande échelle demeure la surexploitation par la pêche industrielle où près de 90% des grands prédateurs marins ont disparus des océans depuis son apparition (Myers and Worm 2003). Cette suppression des prédateurs naturels ou la création de ressources d'origine anthropique, peut favoriser l'expansion démographique de certaines populations. La surabondance des populations d'ongulés en Amérique du Nord peut en partie être expliquée par cette suppression de grands prédateurs. La régulation par le haut disparue, la surabondance apparaît (Côté et al. 2004).

Dans le contexte de l'apparition de nouvelles ressources alimentaires pendant les périodes traditionnelles de famine, certaines espèces vont pouvoir les utiliser et ainsi échapper à la régulation densité-dépendante liée à cette phase du cycle de vie, diminuant du même coup la mortalité (Nichols 1991, Williams et al. 2002). Cet apport accru de nourriture peut également conduire à une fécondité plus importante (Jefferies et al. 2003). Comprendre l'impact anthropique sur la taille des populations animales revient alors à étudier son effet au niveau des paramètres démographiques. Cette acquisition de connaissance est nécessaire pour une gestion efficace des populations naturelles que ce soit dans une optique de conservation, de contrôle et/ou d'exploitation (Shea and NCEAS Working Group on Population Management 1998).

Gestion des populations naturelles

En gestion des populations animales, l'objectif s'exprime habituellement en termes de taille de population souhaitée. Les actions de gestion visent souvent à modifier les paramètres démographiques dans le but d'apporter les changements désirés sur la taille de la population. Une compréhension de *comment* ces paramètres démographiques varient dans le temps et dans l'espace, en relation aux facteurs environnementaux et aux mesures de gestion, est fondamentale pour une gestion éclairée des populations animales (Williams et al. 2002). Choisir les meilleures actions de gestion n'est pas choses aisée, car il est délicat de prédire même à court terme l'effet d'interventions majeures sur les populations (Walters and Holling 1990). Classiquement, les gestionnaires des populations d'oiseaux exploitées par la chasse (e.g. sauvagine) reconnaissent trois types d'incertitude qui influencent la gestion des récoltes: (1) la variation environnementale (e.g. les conditions environnementales influent sur la reproduction et par conséquence la taille de la population), (2) l'observabilité partielle (e.g. les variables comme la taille de la population et la récolte à la chasse, ne sont pas connues et doivent être estimées), (3) la contrôlabilité partielle (e.g. les variables contrôles comme le taux de récolte ne peuvent pas être changées directement mais seulement via l'instauration de règlements de chasse) (Walters and Hilborn 1978, Williams et al. 1996, Williams et al. 2002).

La chasse comme outil de conservation

Dans le cas où la chasse représente un coût supplémentaire à la survie des individus, celle–ci devient alors un outil fort intéressant pour la gestion des populations. Dans l'optique d'une gestion acceptable des récoltes, il est nécessaire de connaître si la mortalité à la chasse s'additionne à la mortalité naturelle ou non (Nichols 1991). Sous l'hypothèse d'une mortalité à la chasse compensatoire à la mortalité naturelle, l'augmentation du taux de prélèvement par la chasse est compensée par des changements de la densité-dépendance dans les facteurs de mortalité non dus à la chasse. La compensation est complète quand la probabilité de survie ne varie pas en fonction du taux de prélèvement, mais ceci est vrai seulement jusqu'à une valeur seuil du taux de prélèvement. Cette valeur seuil est maximale lorsqu'elle est égale au taux de mortalité naturelle, en l'absence de chasse (Nichols 1991, Williams et al. 2002). Sous l'hypothèse d'une mortalité à la chasse additive à la mortalité naturelle, la mortalité naturelle n'est pas, ou est très peu, affectée par des processus dépendants de la densité. Ainsi l'augmentation du taux de prélèvement s'ajoute au taux de mortalité naturelle. Le taux de survie annuel décroît alors linéairement avec l'augmentation du taux de prélèvement par la chasse (Nichols 1991, Williams et al. 2002). Cependant ces deux hypothèses représentent deux positions extrêmes et la réalité se trouve souvent entre les deux avec une mortalité compensatoire partielle.

Les effets de la chasse peuvent aussi se manifester au travers d'effets indirects et non anticipés comme le dérangement. Par exemple, Madsen (1998) a pu mettre en évidence chez la sauvagine au Danemark, que la chasse était responsable de changements de sites sur les haltes migratoires. La chasse peut ainsi être à l'origine de modification du cycle d'activité diurne et/ou d'augmentation de la distance parcourue pour échapper aux chasseurs, altérant alors l'activité d'alimentation et affectant la condition corporelle. Mais elle peut également altérer la reproduction en brisant des couples (Madsen and Fox 1995).

Les conclusions de l'étude de Madsen (1998) s'appuient sur une expérience d'instauration de zones refuges sans chasse différentes chaque année et s'inscrit dans une démarche de gestion adaptative. L'idée principale d'une gestion adaptative repose sur des actions de gestion (contrôle, exploitation ou conservation de populations naturelles) prises non seulement pour gérer un système mais aussi pour apprendre quels sont les mécanismes qui le gouvernent et ainsi aider à prendre les décisions futures de façon plus éclairée (Shea and NCEAS Working Group on Population Management 1998). La gestion des populations n'est alors plus considérée comme le point final d'un processus scientifique mais est abordée sous l'angle d'une expérience scientifique en soi (McShea et al. 1997). Dans le cas de l'exploitation des populations naturelles, une gestion adaptative des prélèvements consiste non seulement à déterminer la stratégie de récolte optimale (maximisation à long terme) mais également à tenter de comprendre les liens écologiques qui existent entre l'exploitation et les processus biologiques (Walters and Hilborn 1978, Williams et al. 1996, Williams et al. 2002).

Cas des populations surabondantes

Certaines populations naturelles sont considérées comme nuisibles à cause de leur densité importante, de leur taux de croissance rapide ou grandissant et de l'impact qu'elles ont sur leur environnement. Un exemple classique est celui des insectes phytophages comme le criquet migrateur (*Locusta migratoria*) (Thomas 1999). Toutefois, la distinction entre les « bonnes » et les « mauvaises » espèces devient vite difficile quand l'abondance d’une espèce peut varier considérablement dans le temps et l’espace (Garrott et al. 1993). Ainsi, des populations qui ont pu faire l’objet de mesures de protection à leur égard dans le passé peuvent récupérer au point d’être déclarées surabondantes quand elles deviennent la cause de dégradation d’écosystèmes ou de cultures (Garrott et al. 1993). Par conséquent, la notion de surabondance est un jugement de valeur qui n’a de sens que dans un contexte spécifique (McShea et al. 1997). A cette fin, quatre points sont utilisés pour qualifier une population de surabondante : (1) quand les animaux menacent l’homme ou son mode de vie; (2) quand les animaux diminuent la densité d’autres espèces protégées; (3) quand le nombre élevé d’individus dans une population devient un risque pour cette même population; (4) quand leur nombre entraîne une perturbation de l’écosystème (Caughley and Sinclair 1994, McShea et al. 1997, Côté et al. 2004). Dans le troisième point, la notion de densité-dépendance est sous-jacente.

Divers facteurs peuvent être à l’origine de l’allure éruptive d’une population naturelle, que cette surabondance soit généralisée à toute l’espèce ou locale. Les ongulés représentent un modèle privilégié pour le développement de la théorie de la surabondance (McShea et al. 1997, Côté et al. 2004). Sans contrôle, la croissance conduit à une taille de population qui dépasse la capacité de support du milieu et préfigure un déclin de l’effectif de cette population, et mener dans les cas extrêmes à l’extinction. Parmi les facteurs favorables, on trouve la diminution de mortalité via la suppression de prédateur ou de l’effort de chasse (McShea et al. 1997, Riley et al. 2003), l’apparition de nouvelles ressources en habitat et/ou de nourriture, que ce soit d’origine naturelle ou anthropique (sylviculture, agriculture, incendies...), comme dans le cas du Cerf de Virginie (*Odocoileus virginianus*) (Côté et al. 2004). Le confinement peut aussi être source d’augmentation de la densité et création de surabondance (e.g. par isolement sur des îles vraies ou continentales, comme les vallées).

Parmi les conséquences de la surabondance, on peut citer un effet sur la population elle-même via des mécanismes dépendant de la densité ou sur d’autres espèces. Dans le cas de l’irruption d’herbivores, ceci peut se répercuter au niveau de l’activité humaine par le ralentissement des rotations dans les cultures forestières ou l’accélération des successions. L’augmentation de la densité du Cerf de Virginie peut être propice à l’augmentation de transmission de maladies vers d’autres populations ou espèces (comme le caribou) et/ou avoir un effet sur la structure des communautés en modifiant les habitats (Côté et al. 2004). Ce phénomène concerne de plus en plus de populations d'espèces indigènes et introduit la question de la gestion de ces populations (Garrott et al. 1993).

Les populations d'oies

De nombreuses populations d'oies migratrices nichant dans les contrées polaires et hivernant en Europe et/ou en Amérique du Nord présentent globalement une croissance exponentielle depuis ces 40 dernières années. Ces augmentations causent au fil des ans de plus en plus de dommages écologiques et/ou économiques sur leurs sites de nidification et d'hivernage. Il faudra cependant attendre la fin du 20ème siècle pour voir le problème clairement exposé dans la littérature scientifique (Ankney 1996).

Si ces populations d'oies représentent souvent une ressource importante pour la chasse et les activités récréo-touristiques, celles-ci entrent également en conflit avec les intérêts humains comme l'agriculture. Il devient donc important pour les agences de gestion de suivre et comprendre les tendances démographiques de ces populations (Frederiksen et al. 2004). Si les conséquences bénéficient d'une documentation fournie (Giroux and Bédard 1987, Kerbes et al. 1990, Gauthier et al. 1995, Ankney 1996, Batt 1998, Jefferies et al. 2003), ce n'est pas nécessairement le cas des causes. C'est par conséquent sur ces dernières que l'effort a porté récemment afin de mieux comprendre les fluctuations démographiques historiques (Jefferies et al. 2003, Frederiksen et al. 2004, Fox et al. 2005, Gauthier et al. 2005). Parmi les explications fournies, l'intensification de l'agriculture et l'utilisation par les oies de ces aires cultivées sur les sites d'hivernage et de halte migratoire au dépend des aires traditionnelles est à l'heure actuelle mise en avant comme étant le facteur principal. Les populations d'Oie à bec court (*Anser brachyrhynchus*) et d'Oie rieuse du Groenland (*Anser albifrons flavirostris*) ont vu leur mortalité naturelle hivernale diminuer avec l'utilisation des zones agricoles (Fox et al. 2005). Chez les populations de Bernache cravant (*Branta bernicla*), le succès reproducteur est influencé par l'abondance de la nourriture sur les sites d'hivernage et de haltes migratoires au printemps (Ward et al. 2005).

Les oies migratrices sont parmi les principaux herbivores terrestres dans la toundra arctique. L'augmentation importante de l'abondance de l'Oie des neiges (*Chen caerulescens*) en Amérique du Nord engendre une dégradation des écosystèmes côtiers, et notamment des marais salés (Jefferies et al. 2003, 2004) à un niveau tel que les populations deviennent un danger pour l'écosystème arctique et pour elles-mêmes (Ankney 1996). Plusieurs facteurs ont été avancés par Abraham et Jefferies (1997) pour expliquer l'accroissement exponentiel des populations de la Petite Oie des neiges : (1) l'utilisation grandissante des habitats agricoles qui entourent les marais traditionnels comme autre source d'alimentation, durant l'hiver et la migration; (2) la création de refuges migratoires, exempts de chasse, le long des routes de migration; (3) une diminution du taux de récolte par la chasse; (4) les changements climatiques et le réchauffement avéré dans l'Arctique canadien qui rendrait plus favorables les conditions de nidification.

La Grande Oie des neiges

La Grande Oie des neiges (*Chen caerulescens atlantica*) est une sous-espèce migratrice (voir carte, Annexe 1), exploitée, hivernant le long de la côte est américaine et se reproduisant dans l'Est de l'Arctique canadien, au nord du 69$^{\text{ème}}$ parallèle (Batt 1998). Lors des migrations automnale et printanière, les oies s'arrêtent principalement sur les rives du fleuve Saint-Laurent, de Montréal à Rimouski (Maisonneuve et Bédard 1992). Cette population ne semble pas avoir encore atteint la capacité de support du milieu sur les aires de nidification (Massé et al. 2001), mais la tendance de son effectif à la fin du 20$^{\text{ème}}$ siècle laisse présager des conséquences pour son habitat similaires à celles documentées pour la Petite Oie des neiges (Batt 1998).

La population de Grandes Oies des neiges atteignait 25000 individus au milieu des années 1960 (Batt 1998). Mais de 1970 à 1998, la population a été multipliée par 10 pour atteindre 750000 individus en 1998 (Annexe 2), un taux de croissance annuel moyen d'environ 9% (Menu et al. 2002). Durant cette même période, deux périodes de croissance rapide ont été décrites, soit 1970-1974 et 1984-1998, avec une période de stagnation intercalée (Batt 1998, Menu et al. 2002). Au printemps 2005, la population de la Grande Oie des neiges était estimée à près de 815000 individus (Annexe 2). Les causes invoquées pour expliquer la croissance exponentielle des populations de la Grande Oie des neiges sont similaires à celles décrites plus haut pour la Petite Oie des neiges (Gauthier et al. 2005). Une cause majeure est un changement de régime alimentaire, autrefois entièrement basé sur les plantes de marais en hiver et au printemps pour un régime dominé par les plantes fourragères et le maïs.

Les conséquences de cette augmentation de population sur les habitats naturels sont variables. Certaines aires de marais traditionnels au bord du fleuve Saint Laurent montrent un déclin dans la production des plants de scirpe (*Scirpus americanus*) (Batt 1998, Gauthier et al. 2005) dû au broutement par les oies. En Arctique, l'utilisation d'exclos a permis de mettre en évidence que la composition des communautés des milieux humides et la productivité d'*Eriophorum*, la principale plante consommée par les oies en Arctique, ont été altérées par le broutement des oies (Gauthier et al. 2004).

A l'instar de ce qui a été observé chez la Petite Oie des neiges (Cooch and Cooke 1991), Reed et Plante (1997) ont mis en évidence une diminution de la taille et de la condition des jeunes tués à l'automne lors de la chasse sur une période de 19 ans, ce qui pourrait être un indice d'effets dépendant de la densité. Cette diminution de la taille corporelle des oies est consistante avec la diminution des ressources disponibles *per capita* liée à l'augmentation de la taille de la population. Toutefois, Menu et al. (2002) n'ont pas démontré d'effet dépendant de la densité sur la survie ou la reproduction à l'échelle de la population de la Grande Oie des neiges. L'utilisation des terres agricoles au printemps pourrait également contribuer à des oies présentant une meilleure condition corporelle à leur arrivée dans l'Arctique pour la nidification (Gauthier et al. 2005).

Du début des années 1970 à la fin des années 1990, les changements dans les régimes de chasse sont capables d'expliquer en partie la variation du taux de croissance observé dans la dynamique des populations de la Grande Oie des neiges (Menu et al. 2002, Calvert and Gauthier 2005). L'absence de croissance de la population de 1975 à 1984 correspond à la réouverture de la chasse aux États-Unis durant l'hiver. Ainsi, en l'absence d'effets dépendants de la densité, un élément essentiel pour que la mortalité à la chasse soit compensatoire (i.e. que cette mortalité se substitue à la mortalité naturelle ; Calvert et Gauthier (2005)), la chasse peut être employée pour réduire la survie et donc limiter la croissance de la population (Menu et al. 2002). En effet, pour les espèces longévives comme la Grande Oie des neiges qui ont une mortalité naturelle faible, la mortalité à la chasse est largement additive à la mortalité naturelle (Gauthier et al. 2001).

Face à l'impact actuel ou appréhendé de la Grande Oie des neiges sur la végétation naturelle (Gauthier et al. 1995, Gauthier et al. 2004, Gauthier et al. 2005) et les cultures agricoles (Batt 1998), et en l'absence d'une régulation dépendante de la densité significative, les membres du *Arctic Goose Habitat Working Group* ont considéré que cette population devenait surabondante et ils ont recommandé une augmentation du taux de récolte à la chasse afin d'arrêter sa croissance (Batt 1998). En réponse à cette recommandation, les régimes de chasse ont été modifiés à compter de 1999 et diverses mesures spéciales, dont une récolte printanière de conservation dans le sud du Canada et une libéralisation des règlements de chasse durant les saisons régulières d'automne au Québec et d'hiver aux États-Unis, ont été mises en place. L'objectif visé était de stabiliser l'effectif de la population de la Grande Oie des neiges.

Juste après leur mise en place en 1999, certains effets des mesures de gestion spéciales ont pu être montrés ou suggérés. Les mouvements printaniers sur les haltes migratoires ont été affectés par le dérangement suscité par la chasse. Les oies ont expérimenté de nouvelles aires plus à l'ouest des aires traditionnelles où la pression de chasse était moins élevée (Béchet et al. 2003). Féret *et al.* (2003) ont montré une diminution de l'accumulation des réserves endogènes lors de la halte migratoire de printemps durant les premières années où la chasse de printemps était présente. Ceci serait lié à la diminution de l'activité d'alimentation, à une augmentation de la durée de vol, ainsi qu'à une augmentation de l'alimentation dans les habitats de moins bonne qualité dû à la chasse. Les ressources énergétiques acquises sur les aires de haltes migratoires sont essentielles pour la migration et conditionnent le succès reproducteur (Béchet et al. 2003). Basé sur les premières années de récolte printanière, il a été observé une diminution la condition corporelle des femelles durant la ponte ainsi que la taille de ponte et un retard dans la date de ponte moyenne (Mainguy et al. 2002, Bêty et al. 2003). Finalement, la probabilité de reproduction des oies a aussi été réduite durant les premières années de récolte printanière (Reed et al. 2004).

Calvert et Gauthier (2005) ont également mis en évidence que le changement de politique de chasse a entraîné une réduction du taux de survie des adultes sans toutefois modifier celui des jeunes. Leur analyse de mortalité à la chasse sur une base saisonnière a permis de mettre en évidence que parmi toutes les mesures de gestions prises depuis 1999, la récolte printanière a contribué le plus fortement à l'augmentation du taux de mortalité par la chasse, suivie par la chasse hivernale sur la côte est américaine, au moins chez les adultes. Cette mortalité à la chasse s'est donc avérée additive à la mortalité naturelle, en cohérence avec les travaux précédents. D'autres mesures comme la libéralisation à l'automne des méthodes de chasse jusque-là interdites (leurres, appeaux électroniques) auraient eu un effet plus faible. Peut-être est-ce dû à un potentiel de chasse plus élevé aux États-Unis de par sa relative nouveauté comparé au Canada, comme le suggèrent les auteurs.

Bien qu'originale, l'étude de Calvert et Gauthier (2005) est basée sur une analyse utilisant uniquement les récupérations de bagues à la chasse, et par conséquent pourrait souffrir de certaines faiblesses. D'abord, les faible taux de récupération des bagues à la chasse diminue la précision des estimés et la puissance des tests statistiques. L'absence de valeurs précises du taux de retour de bagues par les chasseurs (défini comme la probabilité qu'une oie baguée tuée à la chasse soit rapportée par le chasseur) a peut-être biaisé le calcul des autres paramètres qui en dépendent comme le taux de mortalité. La mise en place depuis 1996 d'un numéro gratuit de téléphone pour rapporter les bagues devrait avoir augmenté le taux de retour mais peut également avoir créé des différences régionales (Calvert et al. 2005). En effet, l'information sur les bagues est en anglais seulement alors que la chasse d'automne et de printemps se situe au Québec, une province majoritairement francophone.

Il est aussi possible que l'effet de ces mesures de gestion pourrait s'atténuer avec le temps. Ainsi, les enquêtes annuelles auprès des chasseurs ont révélé que les taux de récoltes printaniers ainsi que le nombre de chasseurs ayant participé à cette chasse ont fléchi de façon notable depuis 2003 (Reed et Calvert 2007). De plus, on ne peut exclure la possibilité d'une réponse comportementale des individus qui, par apprentissage, pourraient avoir modifié leur comportement pour minimiser leur exposition aux dérangements par les chasseurs (Béchet et al. 2003).

Objectifs de la thèse

Les objectifs de ma thèse sont d'évaluer l'emploi de la chasse comme outil de conservation pour contrôler les effectifs des populations surabondantes. Le cas de la

Grande Oie des neiges et l'instauration des mesures spéciales de conservation depuis 1999 dont la plus extraordinaire est l'introduction d'une nouvelle saison de chasse au Québec chaque printemps, représente une occasion unique pour y parvenir. Afin de mieux comprendre la relation entre les changements de pratiques de chasse et les changements de taille de population, l'objectif premier de cette thèse est de mettre en évidence les effets de ces mesures spéciales de conservation sur les processus démographiques sous-jacents suivants : la survie, la reproduction et le recrutement des jeunes en tant que reproducteurs. Ultimement, et comme pour tout travail scientifique, la distance à la vérité des nouvelles connaissances apportées par mon travail de thèse est tributaire de l'approche méthodologique employée pour produire ces connaissances. Le second objectif consiste par conséquent à appliquer, ou développer au besoin, les approches méthodologiques basées sur les plus récentes avancées théoriques en statistiques afin d'atteindre mon objectif principal.

Organisation de la thèse

La chasse étant employée par les gestionnaires pour diminuer la survie moyenne de la population, escomptant ultimement diminuer la taille de population, il est donc naturel de s'intéresser en premier à la relation entre la probabilité de survie et l'introduction de mesures spéciales de conservations. Les deux premiers chapitres y sont pleinement consacrés.

Le premier chapitre aborde presque exclusivement l'aspect méthodologique. Les modèles de capture-marquage-recapture classiquement utilisés pour estimer la survie sont basés sur des programmes à long terme de capture, marquage et recapture des individus et exploitent seulement une partie de l'information disponible, soit les capture-recaptures vivantes (Lebreton et al. 1992) ou soit les reprises à l'état mort (Brownie 1985). Avec la première approche les estimés de survie produits sont biaisés en présence d'émigration définitive du site d'étude. Dans le second cas la quantité d'information (taux de reprise) est souvent très faible et il en résulte des estimés de survie peu précis. Durant les deux dernières décennies les approches intégrant les deux types d'informations (capture vivantes ou reprises d'individus morts) dans un même modèle ont fait leur apparition. Ceci permet dans une certaine mesure de résoudre les limitations précédentes, particulièrement en présence de reprises à la chasse (Burnham 1993, Lebreton et al. 1999, Conn et al. 2004). Il est apparu très vite qu'une telle approche, jamais mise en œuvre auparavant dans le cas de la Grande Oie des neiges, serait tout à fait souhaitable pour répondre à mon objectif principal. Je décris donc dans ce chapitre un tel modèle de survie intégrant les captures physiques, les reprises mais aussi les observations à distance grâce à la présence de marques auxiliaires (modèle avec mélange d'information). Grâce aux marques auxiliaires l'effort de détection est diminué et il devient possible de collecter assez d'information pour produire des estimés de survie saisonniers (Gauthier et al. 2001). Je démontre de plus dans ce chapitre, à l'aide d'un modèle avec mélange d'information, que la présence d'une marque auxiliaire qui peut être perdue est aussi une source de biais potentielle pour l'estimation de la survie quand l'information sur sa présence est incertaine. Basé sur les plus récents développements théoriques en statistiques, le nouveau modèle présenté permet de gérer ce problème et de produire des estimés de survie non biaisés. D'intérêt général pour toutes les études utilisant des marques auxiliaires, il est illustré avec un jeu de donné comportant les Grandes Oies des neiges marquées adultes.

Dans le second chapitre, l'emphase est portée sur une compréhension aussi fine que possible d'un point de vue biologique de l'impact des mesures spéciales de conservation sur la survie de la Grande Oie des neiges. Calvert et Gauthier (2005) ont réalisé un premier examen de l'effet de ces mesures de conservation. Bien qu'ils aient partitionné la mortalité due seulement à la chasse sur une base saisonnière, l'estimation de la survie (incluant toutes les causes de mortalité, chasse ou non) était sur une base annuelle et basée seulement sur les reprises à la chasse, limitant par la même la précision de leurs estimés. Une évaluation plus complète de l'impact relatif des diverses mesures de conservation mises en place pour cette population exige une analyse plus fine, c'est-à-dire à l'échelle saisonnière. Pour y arriver j'ai appliqué le modèle présenté dans le précédent chapitre à toute la population (tous âges et les deux sexes pour les adultes). J'applique ici ce modèle à un ensemble de données à long terme (13 ans) de marquage sur la Grande Oie des neiges combinant recaptures vivantes, observations et les reprises à la chasse au cours des différentes saisons. En contrastant deux périodes, avant 1999 et à partir de 1999, et en utilisant toutes les informations disponibles, j'étudie l'effet des mesures spéciales de conservation mises en œuvre au cours des différentes saisons (l'automne et le printemps au Québec, l'hiver aux

États-Unis) sur la probabilité de survie saisonnière, avec un niveau de précision jamais atteint auparavant.

Après avoir abordé les effets directs de la chasse sur la survie, le troisième chapitre examine les effets potentiels indirects de la chasse sur la reproduction. Les travaux récents de Morrissette et al. (2010) ont mis en évidence que la productivité des jeunes (exprimé par le ratio jeunes/adultes à l'automne) a été affecté négativement depuis l'introduction de la chasse de printemps au Québec. D'autres études ont également suggéré un impact négatif de la chasse de printemps sur la reproduction au cours des premières années qui suivirent l'implantation des mesures de conservations (Mainguy et al. 2002, Bêty et al. 2003, Reed et al. 2004, Dickey et al. 2008). J'examine pour la première fois la relation entre les changements annuels du taux de récolte adulte au printemps, et les principaux paramètres de reproductions suivant : densité de nid, date de ponte et taille de ponte à la colonie de l'Île Bylot, Nunavut. La Grande Oie des neiges présente une stratégie mixte d'allocation des ressources dans la reproduction qui dépend des réservent accumulées à la fois au printemps durant la migration et aussi des ressources accumulées à l'arrivée sur le site de nidification (Gauthier et al. 2003). Tout comme les études précédentes je pose l'hypothèse que la chasse de printemps affecte négativement la condition corporelle via un effet de dérangement qui se traduit par une diminution d'accumulation des réserves et que cet effet est reporté (*carry-over effect*) sur la reproduction l'été suivant. Adoptant une approche avec inférence multiple j'évalue également l'importance relative de la chasse sur la reproduction lorsque sont aussi considérées les conditions climatiques rencontrée au printemps et à l'arrivée sur le site de nidification.

Dans le quatrième et dernier chapitre il s'agit de comprendre s'il existe une relation entre les changements de taux de récolte au printemps et la probabilité de recruter dans la population des reproducteurs. Les mêmes mécanismes biologiques impliquant un effet reporté de la chasse de printemps sur la condition corporelle due au dérangement sont invoqués. Sous cette hypothèse nous prédisons que la probabilité de recrutement sera diminuée relativement à l'augmentation du taux de récolte. Ici encore, une approche avec inférence multiple est employée et les effets de la chasse sont évalués en présence d'effets confondants comme les conditions climatiques.

L’étude des effets de la chasse sur des paramètres démographiques autres que la survie, abordée dans ces deux derniers chapitres, est une question novatrice encore peu examinée.

Chapitre 1

A capture–recapture model with double-marking, live and dead encounters, and heterogeneity of reporting due to auxiliary mark loss

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Résumé

Les modèles de capture-recapture (CR) assument que les individus marqués demeurent à risque de capture, ce qui peut ne pas être vrai si les individus perdent leur marque ou émigrent définitivement de l'aire d'étude. L'utilisation d'un protocole avec deux marques, une marque principale et une auxiliaire, combinant à la fois les rencontres d'individus vivants et les reprises à large échelle d'individus morts, libère partiellement les modèles de cette contrainte initiale. Cependant, la marque auxiliaire peut être perdue et sa présence ou son absence peuvent ne pas être mentionnées lorsqu'un individu mort est reporté. Nous proposons un nouveau modèle multi-évènement qui gère l'hétérogénéité de détection et l'incertitude sur la présence de la marque auxiliaire. Notre modèle général, basé sur un protocole avec deux marques, utilise l'information issue des captures/recaptures physiques, observations à distance des individus vivants et reprises de la marque principale des individus morts. Nous avons appliqué notre modèle à 13 années de données sur une espèce exploitée, la Grande Oie des neiges (*Chen caerulescens atlantica*). Nous avons ainsi produits des estimés de survie saisonniers pour les adultes des deux sexes. Les estimés de survie différaient entre les modèles où la présence de la marque auxiliaire à la reprise des individus morts était ignorée et les modèles où cette présence était prise en compte. Dans le cadre du nouveau modèle multi-évènement, les estimées de survie ne sont plus biaisés car l'hétérogénéité relative à la présence de la marque auxiliaire est prise en compte dans l'estimation des taux de survie.

Abstract

Capture–recapture (CR) models assume marked individuals remain at risk of capture, which may not be true if individuals lose their mark or emigrate permanently from the study area. Using a double-marking protocol, with a main and auxiliary mark, and both live encounters and dead recoveries at a large geographical scale, partially frees CR models from this assumption. However, the auxiliary mark may fall off and its presence is often not mentioned when dead individuals are reported. We propose a new model to deal with heterogeneity of detection and uncertainty of the presence of an auxiliary mark in a multi-event framework. Our general model, based on a double-marking protocol, uses information from physical captures/recaptures, distant observations and main mark recoveries from dead animals. We applied our model to a 13-year data set of a harvested species, the Greater Snow Goose (*Chen caerulescens atlantica*). We obtained seasonal survival estimates for adults of both sexes. Survival estimates differed between models where the presence of the auxiliary mark upon recovery was ignored versus those where the presence was accounted for. In the multi-event framework, seasonal survival estimates are no longer biased because the heterogeneity due to the presence of an auxiliary mark is accounted for in the estimation of recovery rates.

Introduction

Individual marks or tags are commonly used in natural population studies. Typically, individuals are marked and then further re-observed at discrete intervals of time. The summary of these observations is called capture–recapture data. Capture–recapture models use these data to estimate demographic parameters such as survival (Lebreton et al. 1992, Gauthier et al. 2001), access to reproduction (Pradel and Lebreton 1999, Reed et al. 2003b) or movements (Hestbeck et al. 1991, Lebreton et al. 2003, Henaux et al. 2007a), thereby providing a better understanding of population dynamics. However, the method assumes that all individuals remain at risk of capture which is not true if they emigrate permanently from the study area or lose their mark. In both cases they will appear as dead leading to an underestimation of survival.

In the case of permanent emigration, the information provided by recoveries is often relevant in addition to live encounters (Burnham 1993). Permanent emigration is no longer present if marks are recovered over the entire geographical range of a population, for example via hunters. In this situation, recovery models (e.g. Brownie's model; Brownie (1985)) can provide "real" estimates of survival probabilities. However, because recovery rates are often low, the precision of survival estimates and/or the power to test hypotheses based solely on recoveries is low (Frederiksen et al. 2004, Calvert and Gauthier 2005). The mixture of both live recaptures and dead recoveries in the same model has demonstrated its capabilities to attenuate the previous limitations (Lebreton et al. 1999).

The use of two marks, instead of one, can help to deal with the loss of a mark. For waterfowl, a plastic neck collar is often used in addition to the main mark, typically a metal leg band (Ballou and Martin 1964). Distant observations of these collared individuals are easier and cheaper than physical captures. However, auxiliary marks, such as plastic collars, have a higher loss rate than metal bands (Gauthier et al. 2001), further compounding the problem of biased demographical parameter estimates because the individuals that lose their collar may no longer be observed and may appear as dead. In studies using double-marking, physical recapture events allow the verification of auxiliary mark loss if the probability of main mark loss (e.g. metal leg band) is negligible (Gauthier et al. 2001). Information on probability of auxiliary mark loss can then be used to correct survival estimates *a posteriori* (Kremers 1988, Nichols et al. 1992, Nichols and Hines

1993, Gauthier et al. 2001). More recently, this has been integrated directly in capture–recapture models (Samuel et al. 2001, Alisauskas and Lindberg 2002, Reed et al. 2005, Reynolds et al. 2009).

Among these recent developments, Conn et al. (2004) proposed a multistate model with both mixture of information and auxiliary mark loss (a plastic neck-band) in a harvested waterfowl population, the Lesser Snow Goose (*Chen caerulescens caerulescens*). This model had the advantage of addressing the problems of permanent emigration and mark loss simultaneously. However, to use this model one must know with certainty whether the auxiliary mark is present when an individual is recovered dead. This is a very demanding protocol unlikely to be met in most studies. In the goose study of Conn, Kendall, and Samuel (2004), information on neckband presence came from physical recaptures at banding and a supplementary survey sent to people who reported bands of dead animals. However, the latter information was very costly to obtain in terms of time and amount of work and may not be reliable for all animals reported (Nichols and Hines 1993, Alisauskas and Lindberg 2002, Alisauskas et al. 2006). Thus, uncertainty regarding the presence of the auxiliary mark upon recovery is likely to remain the rule (Calvert and Gauthier 2005). We further suspect that the presence or absence of the auxiliary mark at the death event may contribute to heterogeneity in recovery rates, thereby biasing survival estimates. For many species, higher recovery rates could result from an increased intrinsic value placed on doubly marked individuals or a higher harvesting susceptibility, thus producing underestimated survival probabilities (Alisauskas et al. 2006).

Here we propose a new general mixture of information model dealing with, for the first time, the uncertainty of auxiliary mark presence upon recovery. Our model takes advantage of the multi-event framework, a general approach to account for uncertainties in capture–recapture data (Pradel 2005). Such a model allows one to manage heterogeneity on recovery rates due to the presence of an auxiliary mark and to fully benefit from the additive information gained from distant observations of the auxiliary mark. We illustrate this model using a long-term marking data set on the Greater Snow Goose (*Chen caerulescens atlantica*).

Multi-event model with uncertainty of mark loss

Encounter history

Here we present a general case study based on a double-marking protocol, where the available information includes live physical captures/recaptures, distant observations of auxiliary marks, and main mark recoveries. We assume that the main mark cannot be lost (see Discussion). For a given animal, information is coded into an individual encounter history. For any occasion t, code 1 represents the event "*Captured alive with the main mark only*" (in our study, the main mark is a metal band; see below), code 2 "*Encountered alive (captured or seen) with both marks*", code 3 "*Recovered*" and code 0 "*Not encountered*". Consider a study with K = 6 occasions with physical captures occurring at occasions 1, 3, 5, and distant observations at occasions 2, 4, 6. Recoveries that occur between occasions *t* and *t* + 1 are registered at occasion *t* + 1. An arbitrary encounter history of 221030 would then mean caught and banded with a main mark and an auxiliary mark at the first occasion, observed at a distance at the second occasion, captured without auxiliary mark at the third occasion, not encountered at the fourth occasion and recovered dead between the fourth and the fifth occasions. Because of the information acquired at the third occasion, we know that the auxiliary mark was absent upon recovery. In contrast, the encounter history 222030 (caught and banded with a main mark and an auxiliary mark at occasion 1, observed at occasion 2, captured with the auxiliary mark at occasion 3, recovered at occasion 5) would be uncertain with respect to the presence of the auxiliary mark at 5 because the presence of an auxiliary mark is rarely mentioned when an animal is recovered.

Definitions of states

Before writing probabilities of the two previous encounter histories, we need to specify the notation:

- $\mathrm{C}^{(t-1)}$, probability of retention of the auxiliary mark between occasions $t-1$ and t.
- $\mathrm{S}_{\mathrm{W}}^{(t-1)}$, probability of survival with the main mark only between occasions $t-1$ and t.

- $\mathrm{S}_{\mathrm{Aux}}^{(\mathrm{t}-1)}$, probability of survival with an auxiliary mark and the main mark between occasions *t* − 1 and *t*.
- $p_W^{(t)}$, probability for an individual to be captured in the state "Alive without an auxiliary mark" at capture occasions.
- $p_{Aux}^{(t)}$, probability for an individual to be encountered in the state "Alive with an auxiliary mark" at occasion *t*, where *t* can be a capture or a distant observation occasion.
- $R_W^{(t)}$, probability of recovering an individual that carries only the main mark at occasion *t*.
- $R_{Aux}^{(t)}$, probability of recovering an individual that carries both marks at occasion *t*.

Note that the probability of recovery is defined here as the probability that a newly dead animal will be found and have its band reported, which differs from parameter f (the probability that an animal will be killed, retrieved, and have its band reported) in traditional band recovery models for hunted species (Gauthier and Lebreton 2008). Survival probability is dependent upon the presence or not of the auxiliary mark. We allowed this distinction because auxiliary marks such as neckbands can sometimes increase mortality for some populations (Zicus et al. 1983, Samuel et al. 1990, Alisauskas and Lindberg 2002).

Below we present the probabilities of the two previous encounter histories, with probability of distant observation of animals without auxiliary mark equal to 0 (occasion 4 in these two examples):

$$P(221030) = C^{(1)} \times S_{Aux}^{(1)} \times p_{Aux}^{(2)} \times \left(1 - C^{(2)}\right) \times S_W^{(2)} \times p_W^{(3)} \times S_W^{(3)} \times \left(1 - p_W^{(4)}\right) \times \left(1 - S_W^{(4)}\right) \times R_W^{(5)},$$

$$
\begin{aligned}
P(222030) = {} & C^{(1)} \times S_{Aux}^{(1)} \times p_{Aux}^{(2)} \times C^{(2)} \times S_{Aux}^{(2)} \times p_{Aux}^{(3)} \\
& \times \Bigg[\left[\left(1 - C^{(3)}\right) \times S_{W}^{(3)} \times \left(1 - p_{W}^{(4)}\right) \times \left(1 - S_{W}^{(4)}\right) \times R_{W}^{(5)} \right] \\
& \qquad + \Bigg[C^{(3)} \times S_{Aux}^{(3)} \times \left(1 - p_{Aux}^{(4)}\right) \\
& \qquad \times \Bigg[\left[\left(1 - C^{(4)}\right) \times \left(1 - S_{W}^{(4)}\right) \times R_{W}^{(5)} \right] \\
& \qquad + \left[C^{(4)} \times \left(1 - S_{W}^{(4)}\right) \times R_{W}^{(5)} \right] \Bigg] \Bigg] \Bigg]
\end{aligned}
$$

Multi-event models distinguish between events which are directly observed and coded in the encounter histories, and states which are not observed directly but are of primary interest (for details see Pradel (2005)). Here, when combining the states alive and newly dead, with the retention of the auxiliary mark, we need to define 5 states:

- Alive with the main mark only, noted (A.W)
- Alive with both marks, noted (A.Aux)
- Newly dead, with the main mark only, noted (Nd.W)
- Newly dead, with both marks, noted (Nd.Aux)
- Dead (†)

The transitions between states can be seen as the product of two successive transitions (auxiliary mark retention and survival) (see Figure 1.1). Transitions over the five states from occasions $t - 1$to t are summarized in a transition matrix $\mathbf{\Phi}_{t-1}$ (see Figure 1.2). We assume that individuals are recovered in the season of their death and noted newly dead at the following occasion. After one more interval of time, newly dead individuals enter and remain in the state "*Dead*".

The events "*Captured alive with the main mark only*", "*Encountered alive (captured or seen) with both marks*", and "*Recovered*" are related to the states by the 4 encounter probabilities, $p_W^{(t)}, p_{Aux}^{(t)}, R_W^{(t)}, R_{Aux}^{(t)}$. This is summarized in the event matrix $\mathbf{B_t}$ of the conditional probabilities of the events (in column) given the states (in row) (see Figure 1.2). Using these matrices and following Pradel (2005) and Rouan, Choquet, and Pradel (2009), the probability of any encounter history h, conditional on the first capture at time e, can be written as:

$$P(h) \; = \; (0,1,0,0,0)\left(\prod_{t=e+1}^{K} \Phi_{t-1}D(B_t(.\,,v_t)\right)\mathbf{1}_N$$

if the animal was originally double marked, or

$$P(h) \; = \; (1,0,0,0,0)\left(\prod_{t=e+1}^{K} \Phi_{t-1}D(B_t(.\,,v_t)\right)\mathbf{1}_N$$

if the animal originally received only the main mark. In the above formulas, $D(\theta)$ is the diagonal matrix with diagonal elements equal to the elements of the vector θ, $B_t(.\,,v)$ is the column vector of $\mathbf{B}$ corresponding to event , v and $\mathbf{1}_N$ is the row vector of N ones, where N is the finite set of states. The likelihood L is expressed as the product of probabilities of all the encounter histories:

$$L = \prod_{h} \mathbf{P}(h)^{v_h}$$

where v_h is the number of individuals whose encounter history is h. The parameters are estimated by maximum likelihood.

For the saturated general model (see Figure 1.2), we checked the parameter identifiability issue using the method presented in Rouan, Choquet, and Pradel (2009). All the parameters except those related to the last interval of time are separately identifiable, as in the time-dependent Cormack–Joly–Seber model (Lebreton et al. 1992).

Application: the Greater Snow Goose population

Banding data

All data presented in this paper originated from a long-term marking study of a Greater Snow Goose population started in 1990 by Université Laval and the Canadian Wildlife Service. Marking occurred annually at the breeding colony on Bylot Island, Nunavut, Canada (73°N, 80°W). Several mass banding sessions were conducted at this location during a seven-day period in early August, when adult geese are moulting and thus flightless (see Menu et al. (2001) for details). All individuals considered in the present work were marked as adults of unknown age (≥1 year old). Birds were sexed by cloacal eversion and all birds received an US Fish and Wildlife Service metal band (primary mark). To allow individual identification from a distance (hereafter observations), a random sample of adult females (but no males) also received an alpha-numeric plastic neck collar (see Menu et al. (2000) for details). For the analysis, we limited the data set to adults for the period from summer 1993 to summer 2005, which included 2350 females and 9695 males marked with a metal band only and 7799 females marked with a neck collar and metal band.

Observation/recapture data

Observations of collared females occurred during the summer on Bylot Island in the Arctic (1256 individuals observed at least once) and during the fall and spring migration (5695 individuals seen at least once) along the staging areas of the Saint Lawrence River, Québec, Canada, from fall 1993 to spring 2006 (see Figure 1.3). During the summer, observations occurred mainly during systematic searches in the nesting colony by 2 to 4 people. On the staging areas, 2 to 6 people checked for the presence of collared birds at several sites. The observation periods extended from 30 September to 10 November (40 days) in fall, 1 April to 20 May (50 days) in spring and from 15 June to 20 August (65 days) in summer (for details see Gauthier et al. (2001)). Recaptures occurred during summer banding sessions and 344 females and 566 males with a metal band only and 613 females marked with a collar were recaptured. The presence/absence of a collar was noted on all birds recaptured with a metal band and permitted detection of 125 cases of collar loss.

Recovery data

The Greater Snow Goose is a hunted species and thus all recoveries were reported by hunters to the Bird Banding Office of the Canadian/US Wildlife Service, from which we retrieved the information. In North America, recoveries from waterfowl hunting are reported from all parts of USA and Canada, hence preventing survival estimation to be affected by permanent emigration of marked individuals from the survey sites. In our study, the number of marked individuals reported to the Bird Banding Office was 255 females and 1404 males originally marked with a metal band only and 1526 females originally marked with a collar. In the absence of a specific hunter survey (Conn et al. 2004), it was not possible to know if a collar was still present when previously collared individuals were killed. The traditional hunting season occurs in fall in Québec, Canada, in fall and winter in the USA and in the summer in the Arctic. Since 1999, special conservation measures, including introduction of a spring harvest, have occurred in Québec and USA with the intent to decrease survival and limit population growth (Calvert and Gauthier 2005). We respected the migration cycle by pooling all recoveries from Québec that occurred in fall or spring at the beginning of the next occasion, winter or summer respectively, all recoveries from the USA at the beginning of the spring occasion, and all recoveries from the Arctic at the beginning of the fall occasion (see Figure 1.3). This geographical division of recovery data allowed us to account for potential differences in hunter activities between Canada and the USA (Calvert et al. 2005).

Definition of intervals

At least one kind of encounter of individuals (live or dead) was available in all seasons, thus we could estimate survival on a seasonal basis. To calculate the length of the time interval between each occasion, we used the median date of the period during which information was collected for each season. Hence the length of the time interval between occasions over one year was 2.5 months (summer to fall), 3 months (fall to winter), 3.25 months (winter to spring) and 3.25 months (spring to summer). These unequal intervals of time were used in the software E-Surge to provide estimates of transition probabilities on a monthly scale.

Encounter histories

Individuals could be both seen and caught during the summer, with recaptures occurring at the end of the season. Hence, to separate these two processes, we defined two occasions per summer: Su_{Obs}, which comes first, for the observations and recoveries, and Su_{Cap} for captures/recaptures (see Figure 1.3). As we considered the data from Su_{Cap} 1993 to the *Spring* 2006, the encounter histories had 64 occasions (K = 64). We coded events in individual encounter histories following our general model. For 115 collared females, a collar in poor condition was changed at a recapture occasion. Their encounter histories were censored after this occasion and all information pertaining to the new collar was coded in a new individual encounter history. Even if the age of individuals is not known, the age of the collar is, so this data set preparation allowed us to keep track of the age of the collar without any change in the likelihood computation. We also censored the encounter histories of 25 females and 27 males banded with a metal band only when these individuals were shifted into another program incompatible with the present study.

Structural constraints

Some constraints were applied to the structure of the model to take into account our study protocol. The transition between successive states was a two-step process: first, the auxiliary mark was retained or not (collar retention) and, secondly, the individual survived or not (survival). We fixed the collar retention probability $C^{(t)}$ and survival probability $S^{(t)}$ equal to one between Su_{Obs} and Su_{Cap}. Individuals without collar could only be recaptured at the occasion Su_{Cap} (see Figure 1.3), thus we fixed the probability of capture $p_W^{(t)}$ to zero for all occasions, except Su_{Cap}. For collared females, we fixed the probability of encounter $p_{Aux}^{(t)}$ to be equal to zero for the *Winter* occasions as no observation or capture occurred at these occasions. The recovery probabilities $R_W^{(t)}$ and $R_{Aux}^{(t)}$ were fixed to zero for the Su_{Cap} occasions and all the Su_{Obs} occasions before 1999 (no spring hunting). To simplify nomenclature of fitted models, we gathered all encounter probabilities at observation occasions under the term $p_{\mathrm{Obs}}[t]$ and noted the capture probabilities of all marked individuals $p_{\mathrm{Cap}}[t]$.

Fitted models

We built models by imposing linear constraints on the parameters of the umbrella model as in generalized linear model analysis (Choquet et al. 2009b). In order to evaluate the performance of our model, we fitted two series of models using our multi-event model under mark loss. One series where recovery rates were independent of the presence of the collar mark, $R_W^{(t)} = R_{Aux}^{(t)}$, the other where they differed, $R_W^{(t)} \neq R_{Aux}^{(t)}$. The special conservation measures were introduced between summer 1998 and summer 1999 and all measures were effective after spring 1999. To take into account the effects of special conservation measures on survival, we defined a constant effect from summer 1999 until the end of our study. To render all parameters estimable relative to the data available, we added the following constraints. As previous studies on the same population did not detect any collar effects on survival for the Greater Snow Goose population (Menu et al. 2000, Reed et al. 2005), we constrained the probabilities of survival $S_{W}^{(t-1)}$ and $S_{Aux}^{(t-1)}$ to be equal. A sex effect on survival was also defined and noted '*x*'. Following results from Reed, Gauthier et al. (2005), the probability of retention of collar was kept constant over time as a first approximation (expressed as $C[\cdot]$). Based on our biological knowledge of the system, we fitted a reduced set of models under the umbrella multi-event model $C[\cdot]\ S[x * t]\ p_{Cap}[g * t]\ p_{Obs}[t]\ R[c * t]$. We defined a sex by collar effect on recapture probabilities, called a '*group effect*' and noted '*g*', providing separate estimates for females without collar, females with collar and males, as the probability of detection on Bylot is confounded with reproductive success and temporary emigration (Reed et al. 2005). To limit the complexity of the saturated model relative to the data available and in order to keep parameters estimable, we did not use a sex effect on recovery rates. Recovery rates dependent on the presence of the collar mark are equivalent to a '*collar effect*' noted '*c*'. Similarly, a model with all parameters time-dependent resulted in a model with redundancy in rank estimation. To fit our models we used E-SURGE, the only software dedicated to multi-event models (Choquet et al. 2009b). An illustration of the implementation of a model and its constraints in E-SURGE is provided as supplementary materials online. We adopted the nomenclature of Choquet (2008).

Results

Among all the models fitted (see Table 1.1), the model with the lowest AIC_c, $C[\cdot]\ S[x * (s + m)]\ p_{Cap}[g * t]\ p_{Obs}[t]\ R[c * t]$, was estimated by E-SURGE as being full rank following Rouan, Choquet, and Pradel (2009). This model included, on survival, a linear constant effect of years with special conservation measures (noted '*m*') additive to the seasonal effect (noted '*s*') contrasted by sex (noted '*x*'). Recovery rates were dependent on the presence of the collar (collar-dependent, C.D. model). The equivalent model with recovery rates independent of the presence of an auxiliary mark (collar-independent, C.I. model), C[·] S[x * (s + m)] p_{Cap}[g * t] p_{Obs}[t] R[t], provided a much poorer fit to the data (ΔAIC_c = 31.34 between the C.D. and C.I. models). The constant annual probability of collar retention, C[·], did not differ between the two models with a value of 0.947(S.E. = 0.003) for the C.D. model and 0.952 (S.E. = 0.003) for the C.I. model. Survival estimates, however, differed (Figure 1.4). At the seasonal scale, the difference between the two models is remarkable as the lowest monthly survival probability occurred during the winter–spring period for the C.I. model but in the previous fall–winter period for the C.D. model. For both models, we calculated annual survival probabilities as the product of the monthly survival probabilities by season elevated to the corresponding time interval, for each sex and each period (i.e. with or without conservation measures). The associated standard errors were obtained with the delta method (Powell 2007). Annual survival probabilities were equivalent in both models. For the C.D. model, the annual survival estimates of females decreased from 0.850 (S.E. = 0.005) during the years before special conservation measures to 0.724 (S.E. = 0.005) during the years with measures. For males the decrease was lower, from 0.845 (S.E. = 0.009) to 0.793 (S.E. = 0.012). For the C.I. model, the decrease for females was from 0.844 (S.E. = 0.005) to 0.721 (S.E. = 0.005) and for males from 0.849 (S.E. = 0.008) to 0.799 (S.E. = 0.012).

For capture and observation probabilities, we did not observe any difference between the C.I. and C.D. models. However, some differences appeared for recovery rates, as one would expect (see Figures 1.5 and 1.6). Recovery rates from the summer period did not differ notably and were very low in both models. For the fall season in Québec, there was only a small difference in recovery rates between birds with and without a collar, and when the presence of the collar was ignored, in the C.I. model, recovery rates were estimated slightly higher than in the C.D. model. In contrast, during the winter in the USA, we observed a large difference in recovery rates between females with and without collars. Under such circumstances, ignoring the presence of the collar resulted in recovery rates similar to those of females without collar in the C.D. model, but much lower than those of females with collar. Finally, recovery rates since the introduction of the spring harvest in 1999, were similar between the two models.

Discussion

Applying our new general model and using live and dead encounters across a large geographical scale allowed us to account for permanent emigration and to deal with auxiliary mark loss in the presence of uncertainty. We estimated seasonal monthly survival probabilities for both sexes using data from an adult Greater Snow Goose population. We fitted our multi-event models with the now standard and accessible E-SURGE software, which was specifically designed to handle state uncertainty (Choquet et al. 2009b).

Our multi-event model can be seen as an extension of the multistate model presented by Conn, Kendall, and Samuel (2004), which did not consider uncertainty in mark presence upon recovery. An important assumption of mark loss models is that the probability to lose the main mark is negligible. This assumption is generally considered to be satisfied in double-marked bird studies (Conn et al. 2004), where the main mark is a metal leg band, regardless of the auxiliary mark used to allow for distant observations. As emphasized by Nichols and Hines (1993), physical recaptures are essential to control for auxiliary mark presence. In practice, detection of individuals at physical recaptures (conditional that the bird is alive and in the study area) would not be influenced by auxiliary marks. On the contrary, for recoveries, report of the mark or the probability to be killed for harvested populations can be influenced by the presence of an auxiliary mark (Samuel et al. 1990, Alisauskas et al. 2006). In the absence of physical recaptures or if physical recaptures are marginal, it is no longer possible to estimate an auxiliary mark retention rate. In this case, the only solution to account for the influence of an auxiliary mark on recovery rate is by conducting a survey for persons who reported the metal band number, in order to know if the auxiliary mark was present or not, as in Conn et al. (2004). In order to decrease uncertainty and complexity in CR models, it would be useful to always ask for the presence of any mark when a recovered marked individual has been reported.

Free of the constraint imposed by the uncertainty regarding mark presence during recovery events, our model can be applied to a large range of studies using double-marking protocols because it allows one to fully account for heterogeneity of detection associated with the presence of an auxiliary mark. By comparing models with collar-dependent (C.D. model) or with collar-independent recovery rates (C.I. model) we demonstrated, in our example that the heterogeneity of detection is non-negligible. The C.I. models consistently exhibited higher AICc values than the C.D. models. In the best C.D. model, at least for one season (winter), recovery rates of females with collar were considerably higher than for those without a collar. A look at the parameters of interest, i.e. survival probabilities, shows that this heterogeneity of detection could have serious consequences depending on the scale considered. At the annual scale, the models showed no differences in estimated survival values but at the seasonal scale, the models differed on the part of the annual cycle where the monthly survival is the lowest (see Crespin et al. (2008) for a similar effect of detection heterogeneity on seasonal population growth rates). The biological implications of these differences are not negligible for the understanding of the population dynamics of the species or in management decisions for example (see Chapter 2). Seasonal recovery rates in both the C.D. and the C.I. models showed important temporal variation over the course of the study. For the C.D. model, it was difficult to predict these patterns and the intensity of the effect of the auxiliary marks a priori, as is likely to be the case in many studies.

The Greater Snow Goose data also illustrate the benefit of using both mixture of information and auxiliary marks. We are now able to provide precise survival estimates on a full seasonal scale for both sexes rather than over 3 seasons for collared females only (Gauthier et al. 2001) or for both sexes on an annual temporal scale only (Calvert et al. 2005). As expected and demonstrated at an annual scale in Calvert and Gauthier (2005), seasonal survival estimates decreased during the period with conservation measures relative to the period without conservation measures.

We kept the collar retention constant over time and independent of the age of the marker on the basis of a previous study (Reed et al. 2005). However, this constraint can be relaxed to test such effects in a more thorough analysis of the data and for other biological models. In long-term studies, it is frequent to use more than one type of auxiliary mark as the manufacturing of the marks may change or because the population is marked by more than one team. In this case, one could expect a difference in probability of detection and in retention rate of the auxiliary marks. In our model we only defined state as a function of the presence or absence of an auxiliary mark but it can be easily extended to studies with several auxiliary marks by defining more groups and/or more states.

Application of our model in a biological context implies the use of a model selection procedure. This procedure is sensitive to lack of adjustment of the umbrella models. Goodness-of-fit (GOF) tests are commonly used to detect, interpret and solve this problem (Pradel et al. 2005b). At present, no genuine GOF tests are available for multi-event models. However, we are currently exploring different methods to estimate an overdispersion coefficient, because its value will influence the model selection procedure. The application of our multi-event model and model selection is greatly simplified by the availability of the software E-SURGE with advantageous tools to deal with issues of parameter redundancy and identifiability in time-dependent CR models (Choquet et al. 2009b, Rouan et al. 2009).

Table 1.1: Table of fitted models. The dagger indicates the presence of redundancy and bold type emphasizes models presented in the paper. Abbreviations: C = probability of retention of the collar, S = probability of survival, p_{Cap} = probability of capture, p_{Obs} = probability of observation, R = recovery, x = sex effect, s = seasonal effect, m = conservation measures, g = group effect (sex.collar), t = time, c = collar effect, (.) = constant effect.

Model					**Number of parameters**	**AIC_c**	**ΔAIC_c**
C[·]	**$S[x * (s + m)]$**	**$p_{Cap}[g * t]$**	**$p_{Obs}[t]$**	**$R[c * t]$**	**177**	**699.6**	**0.0**
C[·]	$S[x * s * m]$	$p_{Cap}[g * t]$	$p_{Obs}[t]$	$R[c * t]$	183	704.1	4.5
C[·]	$S[s + m]$	$p_{Cap}[g * t]$	$p_{Obs}[t]$	$R[c * t]$	172	717.2	17.6
C[·]	$S[s * m]$	$p_{Cap}[g * t]$	$p_{Obs}[t]$	$R[c * t]$	$173^{\dagger}$	717.5	17.9
C[·]	**$S[x * (s + m)]$**	**$p_{Cap}[g * t]$**	**$p_{Obs}[t]$**	**$R[t]$**	**131**	**730.9**	**31.3**
C[·]	$S[x * s * m]$	$p_{Cap}[g * t]$	$p_{Obs}[t]$	$R[t]$	137	732.0	32.4
C[·]	$S[s * m]$	$p_{Cap}[g * t]$	$p_{Obs}[t]$	$R[t]$	127	822.5	122.9
C[·]	$S[s + m]$	$p_{Cap}[g * t]$	$p_{Obs}[t]$	$R[t]$	126	822.5	122.9
C[·]	$S[s * m]$	$p_{Cap}[g * t]$	$p_{Obs}[t]$	$R[c * t]$	175	1034.7	335.1
C[·]	$S[s]$	$p_{Cap}[g * t]$	$p_{Obs}[t]$	$R[c * t]$	170	1050.0	350.4
C[·]	$S[s * m]$	$p_{Cap}[g * t]$	$p_{Obs}[t]$	$R[t]$	129	1058.0	358.4
C[·]	$S[s]$	$p_{Cap}[g * t]$	$p_{Obs}[t]$	$R[t]$	124	1138.0	438.4

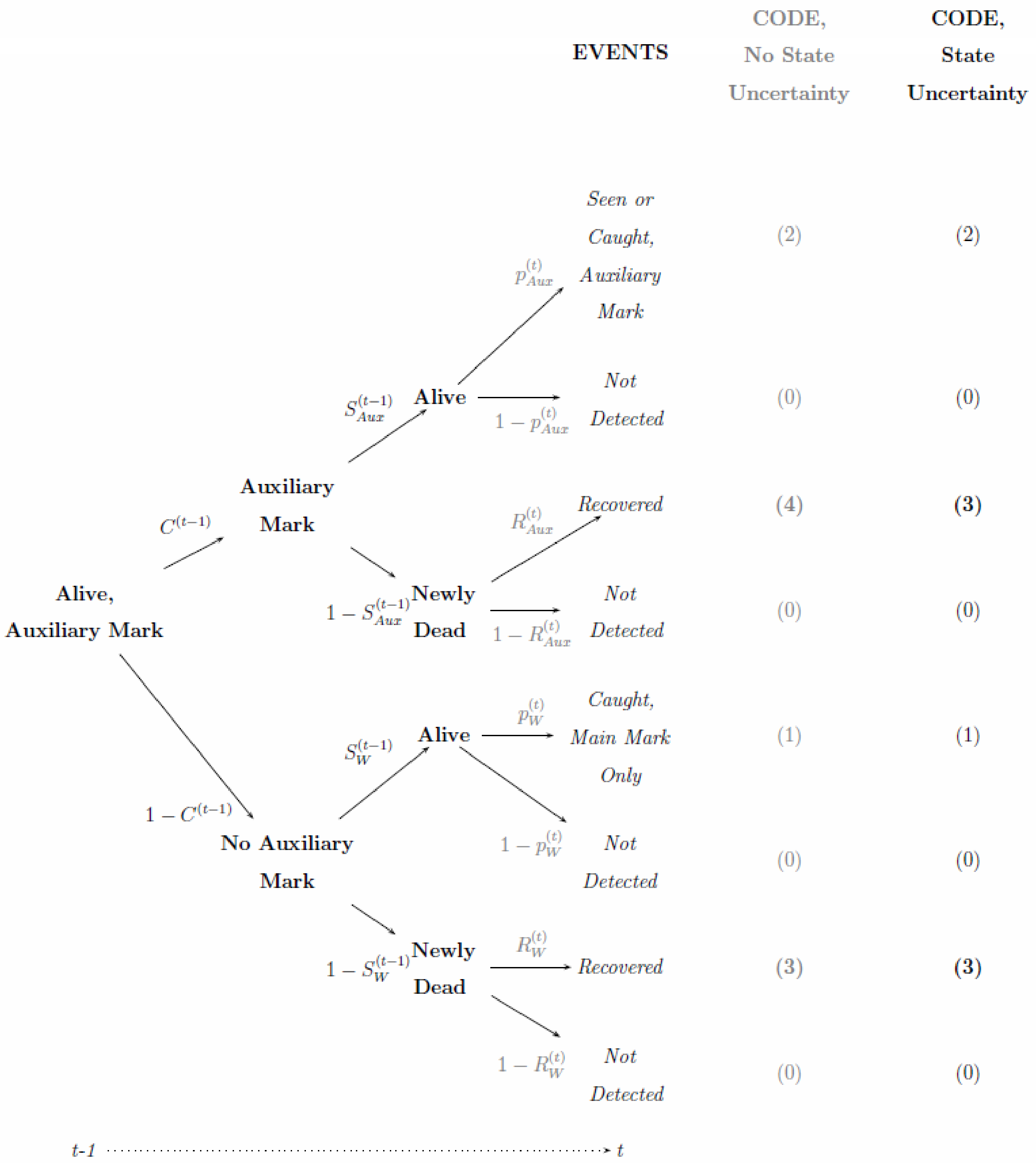
EVENTS
CODE, No State Uncertainty
CODE, State Uncertainty
Alive, Auxiliary Mark
$C^{(t-1)}$
Auxiliary Mark
$S_{Aux}^{(t-1)}$
Alive
$p_{Aux}^{(t)}$
Seen or Caught, Auxiliary Mark
(2)
(2)
$1 - p_{Aux}^{(t)}$
Not Detected
(0)
(0)
$1 - S_{Aux}^{(t-1)}$
Newly Dead
$R_{Aux}^{(t)}$
Recovered
(4)
(3)
$1 - R_{Aux}^{(t)}$
Not Detected
(0)
(0)
$1 - C^{(t-1)}$
No Auxiliary Mark
$S_W^{(t-1)}$
Alive
$p_W^{(t)}$
Caught, Main Mark Only
(1)
(1)
$1 - p_W^{(t)}$
Not Detected
(0)
(0)
$1 - S_W^{(t-1)}$
Newly Dead
$R_W^{(t)}$
Recovered
(3)
(3)
$1 - R_W^{(t)}$
Not Detected
(0)
(0)
t-1
t

Figure 1.1: Tree diagram of fate from the state "*Alive with both marks, main and auxiliary*" between occasion $t-1$ and occasion t. The state occupied at occasion t is the result of the progression of an individual alive with an auxiliary mark at occasion $t-1$ across a 2-step transition. The first step is the retention of the auxiliary mark, with a probability C, and the second step is the survival, with a probability S. Associated events are noted in italics and encounter probabilities are noted in grey. We added the corresponding coding in encounter histories with and without state uncertainty. In the multi-event framework, the event coded in the encounter history can be linked to more than one state and highlights the state uncertainty. The situation with no state uncertainty is the particular case of a multistate model. This multistate model is a simpler model than the one presented by Conn et al. (2004) in a multistate framework. Note that in the multi-event framework we can estimate different recovery probabilities according to the presence or absence of the auxiliary mark. Abbreviations: Aux = with an auxiliary mark, W = without an auxiliary mark.

- Transition matrix: $\mathbf{\Phi_t} = (\mathbf{\Phi_{ij}})_\mathbf{t}, t \in \{1, \ldots, K-1\}$

$$\mathbf{\Phi_t} \quad = \quad \left(\begin{array}{c|ccccc} & A \cdot W & A \cdot Aux & Nd \cdot W & Nd \cdot Aux & \dagger \\ \hline A \cdot W & S_W^{(t)} & 0 & 1 - S_W^{(t)} & 0 & 0 \\ A \cdot Aux & \left(1 - C^{(t)}\right) \cdot S_W^{(t)} & C^{(t)} \cdot S_{Aux}^{(t)} & \left(1 - C^{(t)}\right) \cdot \left(1 - S_W^{(t)}\right) & C^{(t)} \cdot \left(1 - S_{Aux}^{(t)}\right) & 0 \\ Nd \cdot W & 0 & 0 & 0 & 0 & 1 \\ Nd \cdot Aux & 0 & 0 & 0 & 0 & 1 \\ \dagger & 0 & 0 & 0 & 0 & 1 \end{array} \right)_t \quad ,$$

- Encounter matrix: $\mathbf{B_t}$, $t \in \{2, \ldots, K\}$

$$\mathbf{B_t} \quad = \quad \left(\begin{array}{c|cccc} & \begin{array}{c} \textit{Not} \\ \textit{Detected} \end{array} & \begin{array}{c} \textit{Captured,} \\ \textit{Main Mark Only} \end{array} & \begin{array}{c} \textit{Encountered,} \\ \textit{Auxiliary Mark} \end{array} & \textit{Recovered} \\ \hline A \cdot W & 1 - p_W^{(t_{Cap})} & p_W^{(t)} & 0 & 0 \\ A \cdot Aux & 1 - p_{Aux}^{(t_d)} & 0 & p_{Aux}^{(t)} & 0 \\ Nd \cdot W & 1 - R_W^{(t)} & 0 & 0 & R_W^{(t)} \\ Nd \cdot Aux & 1 - R_{Aux}^{(t)} & 0 & 0 & R_{Aux}^{(t)} \\ \dagger & 1 & 0 & 0 & 0 \end{array} \right)_t \quad .$$

Figure 1.2: Multi-event model of mixture of information integrating auxiliary mark loss with uncertainty. Transition and encounter matrices are presented. We defined: $C^{(t)}$ as the auxiliary mark retention probability between two successive occasions, $t-1$ and t; $S_W^{(t)}$ and $S_{Aux}^{(t)}$ as the survival probability between two successive occasions, $t-1$ and t, for individuals without or with an auxiliary mark respectively; $p_W^{(t)}$ as the capture probability for individuals with a main mark only at occasion t; $p_{Aux}^{(t)}$ as the alive encounter probabilities at occasion t for individuals with auxiliary mark, where occasion t can be a capture or a distant observation occasion; $R_W^{(t)}$ and $R_{Aux}^{(t)}$ as the recovery rates between two successive occasions for individuals without or with an auxiliary mark. Abbreviations: A = alive, Aux = with an auxiliary mark, Nd = newly dead, W = without an auxiliary mark, † = dead.

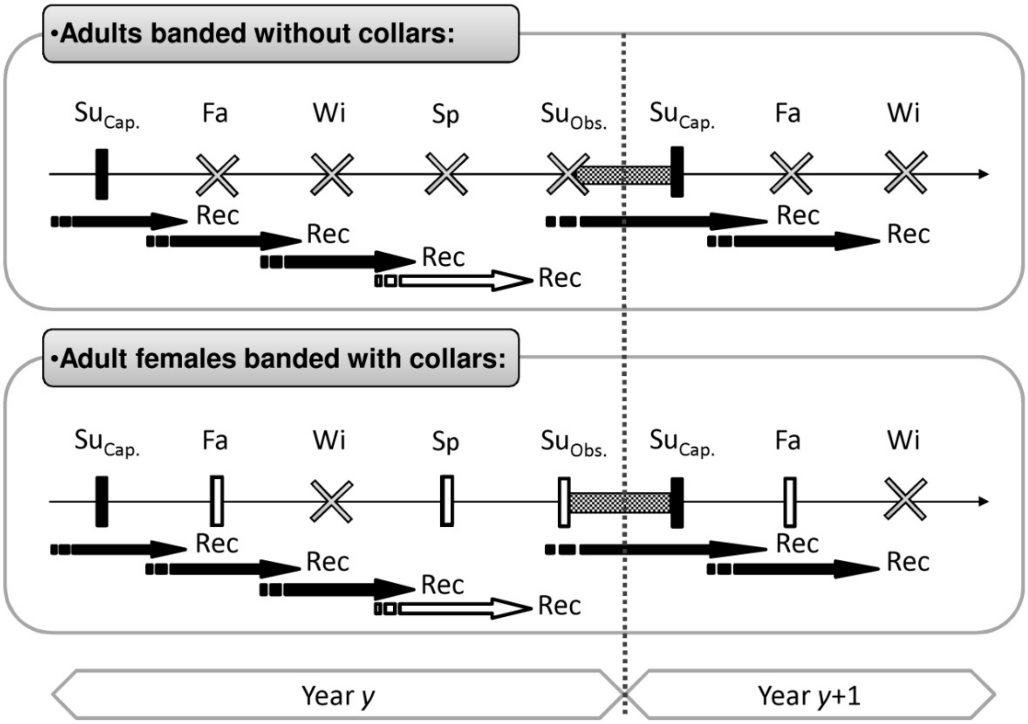

Figure 1.3: Definitions of occasions and events for the Greater Snow Goose population over time. Solid black bars represent recaptures, open bars represent observations, solid black arrows represent recoveries from harvest pooled over the migration cycle on a geographical basis, open arrows represent recoveries from conservation harvest since 1999. Pooled recoveries were coded at the beginning of the next occasion following the considered migration stage. A cross indicates the absence of information. The stippled interval of time indicates that during this period survival and auxiliary mark retention are equal to one. Abbreviations: Su_{Cap} = summer capture occasion, Fa = fall, Wi = winter, Sp = spring, Su_{Obs} = summer observation occasion, Rec = recoveries.

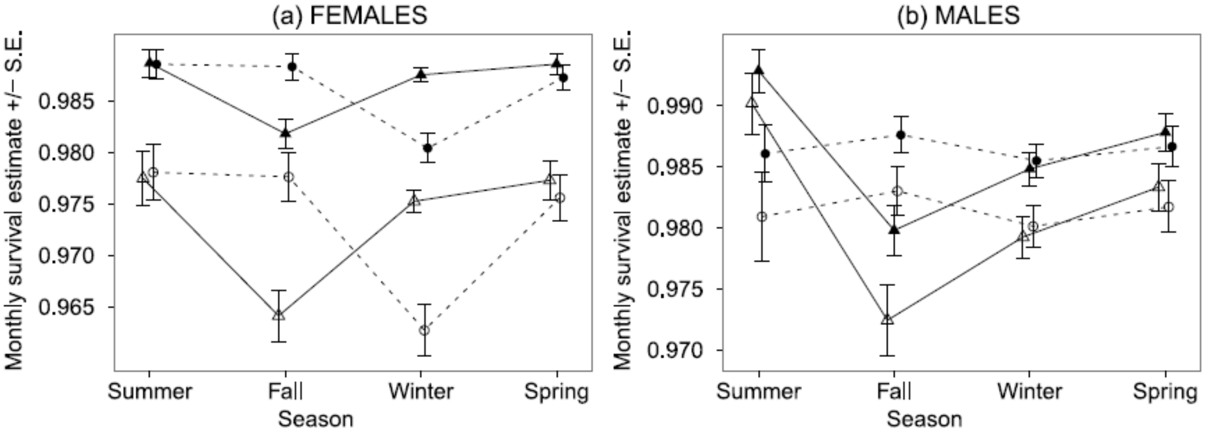

Figure 1.4: Seasonal survival probabilities for females and males in the multi-event framework for the models C[·] S[x * (s +m)] p_{Cap}[g * t] p_{Obs}[t] R[c * t] and C[·] S[x * (s +m)] p_{Cap}[g* t] p_{Obs}[t] R[t]. The two models differ in collar dependency in the estimation of recovery rates. The seasons indicated refer to the season at the beginning of the interval of time considered. (Solid black symbols: period without special conservation measures; open symbols: period with special conservation measures; circles: collar-independent recovery rates; triangles: collar-dependent recovery rates).

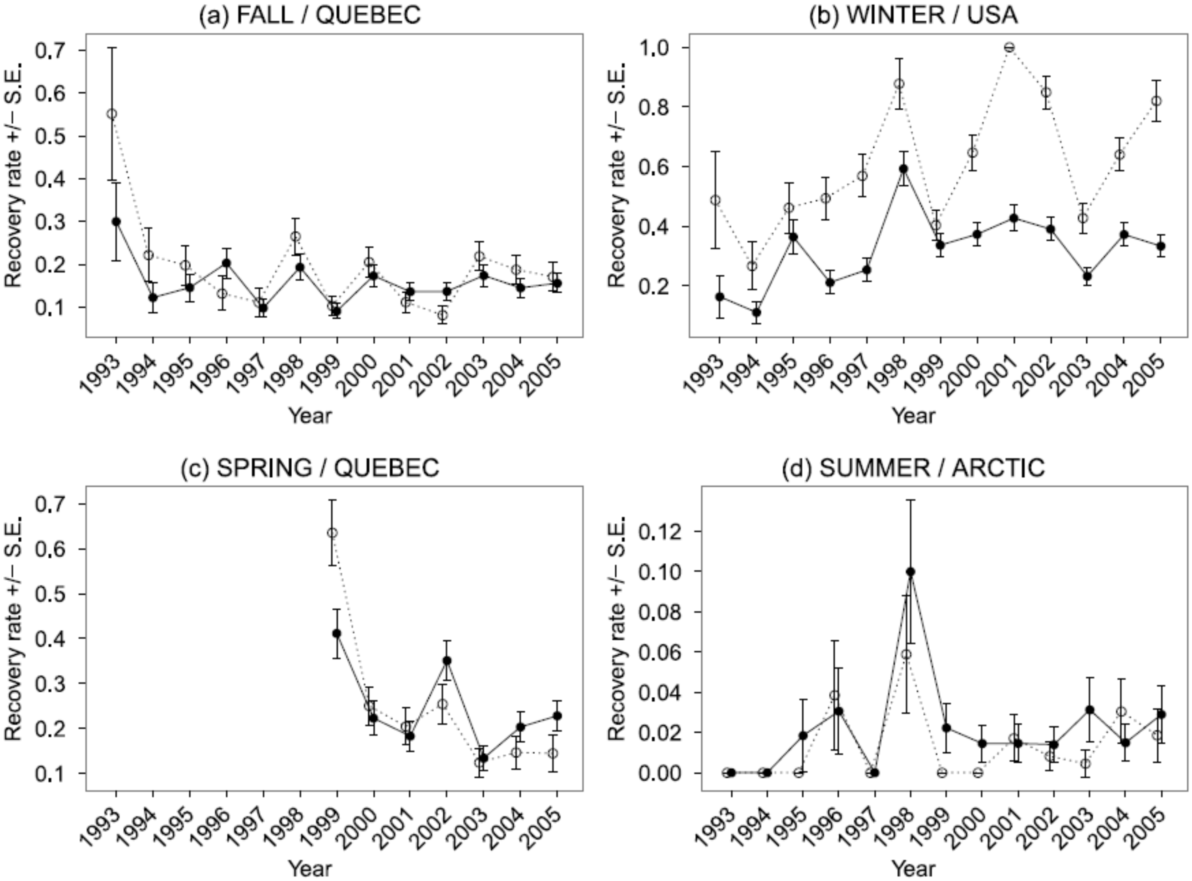

Figure 1.5: Seasonal recovery rates for the model $\mathrm{C}[\cdot]\ \mathrm{S}[x * (s + m)]\ \mathrm{p}_{\mathrm{Cap}}[g * t]\ \mathrm{p}_{\mathrm{Obs}}[t]\ \mathrm{R}[c * t]$ contrasted for the presence of the collar in the multi-event framework. Seasons indicated refer to the season in which recoveries were actually reported. The year indicated for winter corresponds to the year at the beginning of the season. (Solid black circles: individuals without collar; open circles: collared females).

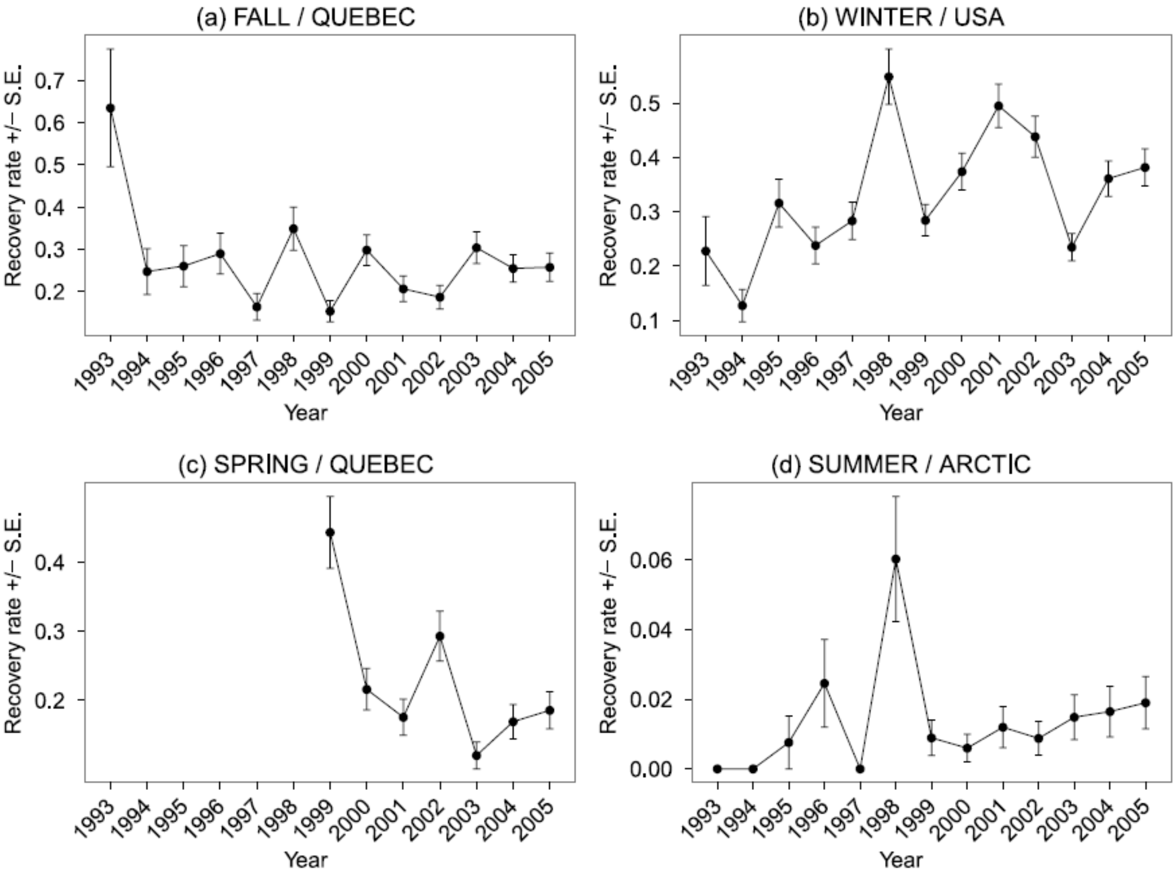

Figure 1.6: Seasonal recovery rates in the multi-event framework for the model C[·] S[$x * (s + m)$] $p_{Cap}[g * t]$ $p_{Obs}[t\ ]$ R[t]. No collar effect was integrated in the recovery rates estimation. The year indicated for winter corresponds to the year at the beginning of the season.

Appendix: implementation in E-SURGE

Our best model C[·] S[x * (s + m)] p_{Cap} [g * t] p_{Obs} [t] R[c * t] is used to illustrate (1) how to define the structure of our general model in E-SURGE (v1.4.6) and (2) how study-specific constraints can be applied, based on the example of the Greater Snow Goose population.

- Initial settings
  - The data set we used had 5 occasions per year (Figure 3) for a total of 64 occasions (from the first capture summer 1993 to the last observation, spring 2006). In the data file (*.inp) the 64 first columns represent the occasions and the last two columns represent for a given encounter history, respectively, the number of females with and without collar (group 1) and the males (group 2) having the considered encounter history. Once the data set is launched in E-Surge, the "Data Status" window of E-SURGE and its elements have to be checked and modified if necessary. We give below what final values would appear for our example:
    - Number of occasions: 64
    - Number of states: 5
    - Number of events: 4
    - Number of groups: 2
    - Number of age classes: 1
  - Different options have to be set in the main menu.
    - In the 'Models' menu, in 'If any factorization', we have to check 'transition & encounter' only (no state uncertainty at initial capture).
    - In the 'Setting' menu, in 'Link function': check 'Generalized Logit'.
    - In the 'Setting' menu, in 'Unequal time interval: Set', we launch a

        text file (*.txt) with the repetition of the five following values: 2.5, 3, 3.25, 3.25, 1, until we get 63 intervals defined (64 occasions minus 1).

        - We define also transitions concerned by length of time intervals, auxiliary mark retention (step 1) and survival (step 2).
        - In the ‘Setting’ menu, in ‘Unequal time interval: # of steps’: ‘1 2’.

    - In the ‘Advanced Numerical Option’ window:
        - We select the ‘Analytical gradient for the model rank’.
        - We modify the optimization parameter setting as follows:

          Tolerance to parameters change: 0.00000001

          Tolerance on gradient: 0.00000001

- Defining the general model with the Gepat tool

  The general model presented in this paper can be applied to different studies using a double-marking protocol (Figure 1.2) and using any timescale (e.g. seasonal or annual). Matrices would stay the same and one can just copy and paste the following file in a text editor, save the file with a *.pat extension and launch it in E-SURGE. To proceed, from the Gepat module and in the ‘Input–Output for patterns’ menu, we use ‘Load file with patterns’.

```
%%%% VERSION 2.0 %%%%%%
3

%%%% Initial state %%%%%%
1
1 4 IS
P * - -

%%%% Transition %%%%%%
2
5 5 C
* - - - -
* c - - -
- - - - *
- - - - *

5 5 S
s - * - -
- s - * -
- - - - *
- - - - *
- - - - *

%%%% Event %%%%%%
1
5 4 E
* b - -
* - b -
* - - b
* - - b
* - - -
```

- Defining study-specific constraints using the Gemaco tool:

  All estimates which are fixed to 1 are defined by a shortcut starting with the string ‘one’, and all parameters fixed to 0 are defined by the keyword ‘others’. Refer to the user’s manual of E-SURGE for the general notation used in the software.

  - for ‘Initial State’: `i`
  - for ‘Transition’,

    Step 1, auxiliary mark retention:

    `oneC+f(2).g(1).[cstC]+others`

    where:

    ∗ oneC = [f(2).t(5:5:64)]

    ∗ cstC = [t(1:5:64)&t(2:5:64)&t(3:5:64)&t(4:5:64)]

    Step 2, survival:

    `oneS+f(1:2).g(1,2).[Season+Cons]+others`

    where:

    ∗ oneS = [f(1:2).t(5:5:64)]

    ∗ Season = [t(1:5:64)+t(2:5:64)+t(3:5:64)+t(4:5:64)]

    to define the 4 seasons

    ∗ Cons = [t(1:5:64)&t(2:5:64)&t(3:5:64)&t(4:5:64)].t(31:64)

    to define the period of conservation measures

- for ’Event’:

  `oneE+a(2).[f(1:2).to(2).g(1,2).cap.t+f(2).g(1).to(3).[cap+obs].t +f(3,4).g(1:2).to(4).[rec.t]]+others`

  where:

  ∗ `oneE = a(1).to(2:3)`

  ∗ `cap = t(6:5:64)`

  to define the capture occasions

  ∗ `obs = [t(2:5:64)&t(4:5:64)&t(5:5:64)]`

  to define the observation occasions

  ∗ `rec = [t(2:5:64)&t(3:5:64)&t(4:5:64)&t(30:5:64)]`

  to define the recovery occasions

- Fixing parameters values in the IVFV interface
  - for ‘Initial State’,

    Beta #1 = 0.5

  - for ‘Transition’,

    Step 1, auxiliary mark retention:

    Beta #1 = 1 (the first one)

Beta #3 = 0 (the last one)

Step 2, survival:

Beta #4 = 1 (the first one)

Beta #14 = 0 (the last one)

- for ’Event’,

  Beta #1 = 1 (the first one) Beta #168 = 0 (the last one)

Chapitre 2

Changes in seasonal survival probability according to age and sex, in relation to conservation harvest of an overabundant migratory species.

C. Juillet, R. Choquet, G. Gauthier and R. Pradel

Résumé

Pour les espèces migratrices, une compréhension fine de l’effet de mesures de conservation sur la survie peut seulement être apportée sur une base saisonnière. La chasse est souvent utilisée comme outil de gestion pour contrôler la taille de population d’une espèce surabondante, via une baisse de survie. Avec pour objectif de contrôler la taille de la population de la Grande Oie des neiges (*Chen caerulescens atlantica*), une espèce surabondante nichant en Arctique, des mesures spéciales de conservations ont été introduites depuis 1999. La mesure la plus spectaculaire a été l’introduction d’une nouvelle saison de chasse au printemps au Québec lors des haltes migratoires en plus de la libéralisation des règlements de chasse lors des saisons régulières à l’automne au Québec, Canada, et l’hiver aux États-Unis. En utilisant les plus récentes avancées dans le domaine des modèles de capture-marquage-recapture et basé sur un programme de baguage de 1993 à 2005, nous avons examiné les effets de ces mesures spéciales de conservation sur la survie saisonnière et ce pour tous les âges et les deux sexes de la population. Ceci a été rendu possible en intégrant les captures, observations à distance d’individus vivant et les reprises d’individus morts. La probabilité de survie des adultes a diminué après la mise en œuvre des mesures de conservation en 1999 durant les trois saisons de chasse, en automne et au printemps au Québec et l'hiver aux États-Unis, mais pas de manière identique pour toutes les saisons. Les changements de probabilité de survie ont été de moindre ampleur l'hiver durant la chasse aux États-Unis. Aucune diminution de la survie n’a été documentée pour la partie nordique du cycle qui englobe la migration dans l'Arctique et la saison de reproduction estivale. En revanche, il semble y avoir peu d'effet des mesures de conservation sur la survie des juvéniles durant leurs premiers automne et hiver et, de façon surprenante, la survie mensuelle au cours de la seconde partie de la migration printanière a eu tendance à augmenter au cours des années des mesures de conservation. Si une baisse supplémentaire de la probabilité de survie est nécessaire pour réduire encore davantage cette population, notre analyse indique que les gestionnaires devraient cibler l'hiver aux États-Unis parce que c'est durant cette période que la survie mensuelle a le moins changé depuis l'introduction de mesures spéciales de conservation en 1999.

Abstract

For migratory species, a fine understanding of the effect of conservation measures on survival can only be provided at a seasonal scale. As a management tool, hunt is often used to control the population size of overabundant species, via a decrease in survival. In order to control the population size of the Greater Snow Goose (*Chen caerulescens atlantica*), an overabundant arctic-nesting species, special conservation measures have been introduced since 1999. The most spectacular action was a spring hunting season implemented on the migratory staging area in Québec in addition to a liberalisation of regulations during the regular hunting seasons during fall in Québec and winter in USA. Using the most recent advances in capture-mark-recapture models and based on a long term banding program (1993-2005), we examined the effects of the special conservation measures on survival of all sex/age classes on a seasonal basis by integrating recoveries, resightings and recaptures of marked individuals. Survival probabilities of adults decreased during all three hunting seasons after the implementation of conservation measures in 1999: fall and spring in Québec, Canada and winter in USA, though not equally in all seasons. Changes in monthly survival were of a lower magnitude during winter in relation to hunt in the USA. No apparent decrease in monthly survival was documented for the northern part of the cycle which primarily encompasses the summer breeding season and portion of the fall migration occurring in the Arctic. In contrast, there appeared to be little effect of the conservation measures on survival of juveniles during their first fall and winter and, surprisingly, monthly survival during the second part of the spring migration tended to increase during the years with conservation measures. If an additional decrease in survival is required to reduce further this population, our analysis suggests that managers should target the winter in the USA because it is during this period that monthly survival changed the least since the introduction of the special conservation measures in 1999.

Introduction

Conservation measures such as increased hunting pressure or culling can be implemented to curb the population growth of overabundant species (Ankney 1996, Brown et al. 2000). For migratory species, these measures are often applied mainly or exclusively during one part of the annual cycle. Consequently, their effects are difficult to anticipate, especially if different measures are applied in different seasons. Only a year-round analysis of demographic parameters can help to evaluate how successful such measures are (Martin et al. 2007, Bolger et al. 2008). Indeed, the estimation of vital rates such as survival on a seasonal basis can allow wildlife managers to determine specific seasons in which conservation measures have the greatest impact while still evaluating the overall effects over the full annual cycle. This approach nonetheless requires the collection of a considerable amount of information across large spatial scales, which, thanks to co-operative international banding programs (Møller and Fiedler 2010), is becoming more and more common. However, the statistical treatment of these large, heterogeneous datasets remains a significant challenge.

In North America, several migratory goose populations like the Greater Snow Goose (*Chen caerulscens atlantica*) are now considered overabundant because the exponential growth of their populations, linked with changes in agricultural practice during the second half of the 20th century (Gauthier et al. 2005), now threaten their natural habitats. Consequently, managers decided to introduce special measures to stop further growth (Batt 1998). In long-lived species such as geese, hunting mortality is mainly additive to natural mortality (Gauthier et al. 2001) and thus harvest can be an effective tool to manipulate the growth rate of a population, especially because this latter is highly sensitive to changes in adult survival. In 1999, exceptional conservation measures, which involved a radical change in harvest strategy at the scale of the entire population, were implemented. Bag-limits and hunting season length were increased and hunting practices were liberalized during the fall in Québec, Canada and during winter in the Atlantic Flyway, USA. The most spectacular action, however, was the introduction of a special spring conservation harvest (spring hunt) in Québec, Canada, beginning in 1999. Because these special conservation measures remained in effect for several years, they are equivalent to a quasi-experiment (Williams et al. 2002) with the period before 1999 acting as the control and the period from 1999 onwards as the treatment.

Calvert and Gauthier (2005) made a first assessment of the impact of these special conservation measures on survival rate in this population. Although they partitioned mortality from hunting on a seasonal basis, they assessed survival (for all sources of mortality) solely on an annual basis and they only used dead recoveries, which limited the precision of their estimates. Moreover, Calvert and Gauthier (2005) found an increase in hunting mortality in both adults and young of the year but found a decrease in annual survival only in the adults after 1998. A more complete assessment of the relative impact of the various conservation measures introduced for this population on the targeted demographic trait, survival, requires a finer analysis at a seasonal scale and for the entire population (all age and sex classes). In this study, we used a recently developed multievent Capture-Mark-Recapture (CMR) model based on both live and dead encounters and accounting for potential biases related to the use of auxiliary markers for detection of individuals (Juillet et al. 2010). We previously showed that this model was suitable to examine this question, using a subset of the data used in this paper (adults only) as an illustrative example (Juillet et al. 2010). Here we apply this model to a long-term (13 years) marking dataset on the Greater Snow Goose combining live recaptures, resightings and dead recoveries occurring in all seasons. Using all available information, we investigate the effect of special conservation measures implemented during various seasons (fall and spring in Québec, winter in the USA) on the seasonal survival probability with a level of precision never reached before.

Methods

Banding data

All information presented in this study originated from a long-term marking study started in 1990 by Université Laval and the Canadian Wildlife Service. Marking occurred annually at the breeding colony on Bylot Island, Nunavut, Canada (73°N, 80°W). Several mass banding sessions were conducted at this location during a seven-day period in early August, when adult geese are moulting and thus flightless (see Menu et al. 2001 for details). Individuals were marked as adults of unknown age (≥1 year old) or flightless juveniles (a few weeks after hatching). Birds were sexed by cloacal eversion and all birds received an US Fish and Wildlife Service metal band (primary mark). To allow individual identification from a distance (hereafter observations), a random sample of adult females (but no males) also received an alpha-numeric plastic neck collar (Menu et al. 2000). Due to computing resource limitations (see below), we limited the analysis to birds banded during the period from summer 1993 to summer 2005, which included 2350 female adults, 9695 male adults, 10958 female juveniles and 10831 male juveniles marked with a metal band only and 7799 female adults marked with a neck collar and metal band.

Observation/recapture data

Observations of collared females occurred during the summer on Bylot Island in the Arctic (1256 individuals observed at least once) and during the fall and spring migration (5695 individuals seen at least once) along the staging areas of the Saint Lawrence River, Québec, Canada, from fall 1993 to spring 2006 (see Figure 1.3, Chapter 1). During the summer, observations occurred mainly during systematic searches in the nesting colony by 2 to 4 people. On the staging areas, 2 to 6 people checked for the presence of collared birds at several sites. The observation periods extended roughly from 30 September to 10 November (40 days) in fall, 1 April to 20 May (50 days) in spring and from 15 June to 20 August (65 days) in summer (for details see Gauthier et al. 2001). Hargrove and Borland (1994) showed that using extended observation periods induces only a very small bias on survival if both mortality and capture probabilities do not exceed 50%. Recaptures occurred during summer banding sessions. A total of 344 female adults, 566 male adults, 364 female banded as juvenile and 39 males banded as juvenile, all with a metal band only, were recaptured, along with 613 adult females marked with a collar. The presence/absence of a collar was noted on all birds recaptured with a metal band and permitted detection of 125 cases of collar loss.

Recovery data

The Greater Snow Goose is a hunted species. All available recoveries in Canada and the USA come from reporting by hunters to the Bird Banding Office of the Canadian/US Wildlife Services, from which we retrieved the information. Because recoveries come from the whole of North America, survival estimation is not affected by permanent emigration of marked individuals from the survey sites. In the absence of a specific hunter survey (Conn et al. 2004), it was not possible to know if a collar was still present when previously collared individuals were killed as this information is not in the record. The traditional hunting season occurs in fall in Québec, Canada, in fall and winter in the USA and in the summer in the Arctic. The new spring hunt introduced in 1999 occurred in Québec only from 1 April to 31 May. We respected the migration cycle by pooling all recoveries from Québec that occurred in fall or spring at the beginning of the next occasion, winter or summer respectively, all recoveries from the USA that occurred in fall or winter at the beginning of the spring occasion, and the small number of recoveries from the Arctic during the summer at the beginning of the fall occasion (Juillet et al. 2010). In this way, a bird that is killed in fall in Québec, i.e. that died during the fall migration, is ascribed to the interval from the fall to the winter occasion while a bird that is killed in fall in the States, i.e. that died after achieving its fall migration, is ascribed to the interval from the winter to the spring occasion. This geographical division of recovery data allowed us to account for potential differences in hunter activities between Canada and the USA (Calvert, Gauthier, and Reed 2005). In our study, 255 females and 1404 males originally marked as adult with a metal band only and 1526 females originally marked with both a metal band and a collar were reported to the Bird Banding Office. For individuals banded as juveniles, 1166 females and 1134 males were reported.

Definition of time intervals

At least one kind of encounter of individuals (live or dead) was available in all seasons, allowing the estimation of survival on a seasonal basis. A difficulty comes from the fact that the observations during a season span a great length of time while the models treat each season as punctual. We calculated an average length for the time interval between each pair of occasions based on the median date of the period during which information was collected for each season. The length of the time interval was 2.5 months from summer to fall, 3 months from fall to winter, 3.25 months from winter to spring, and 3.25 months from spring to summer. These unequal intervals of time, introduced in the software E-SURGE (Choquet et al. 2009b), yielded seasonal transition probabilities estimated on a monthly scale.

Modelling strategy

Modelling the effects of the special conservation measures on survival of all sex/age classes on a seasonal basis required the integration of recoveries, resightings and recaptures, and resulted in a very large model in terms of number of parameters. The general structure of the model is identical to the one described in Juillet et al. (2010) and only differs by the addition of individuals banded as juveniles. Due to computer power limitations (a model took 4 to 7 days to run on a workstation equipped with an Intel© Xeon© E5506 CPU cadenced at 2.13Ghz and with 4Ghz of memory), we fitted only three carefully chosen models to the data covering the period from summer 1993 to spring 2006 (64 occasions). However, the fit of a same model was repeated several times until the convergence was confirmed. To define a common general structure for all three models, we relied on the results of a previous analysis of the same population (Chapter 4; Juillet et al. 2010).

The structure of the live and dead encounter probabilities was kept as flexible as possible to account for potential heterogeneity of detection between different segments of the population. Summer capture probability (noted 'p_{Cap}') was fully time dependent (noted 't') and different at 2, 3 and >4 years of age to account for the progressive recruitment and thus presence on the breeding ground with age (Chapter 4). Due to their high dispersal from the natal colony, the capture probability of males banded as juvenile, was modeled separately, with full time dependence but no age effect. Because an effect of the collar on female breeding propensity has been previously detected (Reed et al. 2005), the time-dependent capture probability of collared females was kept different from that of non-collared individuals (collar effect noted 'c'). Because recruitment and dispersal are both linked to fidelity of individuals to the capture site, we grouped them under the notation 'fidelity' effects. The probability of a distant live encounter of collared females (noted 'p_{Obs}') was made fully time dependent, i.e. estimated separately for each year and each season (Summer on Bylot Island, Fall and Spring in Québec).

Recovery probability (noted 'R') was also fully time dependent and differed between collared and non-collared individuals (Juillet et al. 2010). Note that the recovery probability here is the probability that a newly dead animal will be found by a hunter and have its band reported, which differs from the parameter 'f' (the probability that an animal will be killed by a hunter, retrieved, and have its band reported) of traditional band recovery models for hunted species (Gauthier and Lebreton 2008). For the sake of simplicity, we did not define an age effect on recovery probability, a point that will be addressed in the discussion.

Our model included a collar retention probability (noted ‘C’) which was kept constant (noted ‘.’). Survival probability (noted ‘S’) was made age-dependent with two age classes: first year after hatching (juvenile) *vs* subsequent years (adult) (notation ‘2a’). Because we expected the difference in survival between juveniles and adults to be most important during the first months following hatch (Menu et al. 2005), the age effect was in interaction with seasons. Due to an absence of long distance observations of juveniles in Québec in the fall following hatching (juveniles are not equipped with collars), we estimated the first survival from Summer to Winter, thus considering only 3 seasons for juveniles. The resulting model was considered as the basis for our 3 models:

Base: C[.] S[2a*seasons] p_{Cap}[t*(c+fidelity)] p_{Obs}[t] R[c*t]

To investigate the effects of the special conservation measures on survival we defined two periods, a period prior to spring 1999 when the special conservation measures were absent and a period from spring 1999 onward when they were present (this effect was noted ‘Cons’). We also added a sex effect on adult survival to consider the possibility that the measures could have differentially affected each sex. When considering all potential interactions between the sex, the effect of special conservation measures and the common structure, or base, defined a priori, we judged that 2 models would be sufficient to assess the effects of these measures in addition to the previously defined base model (Figure 2.1A). The first model has a sex effect on adults (noted ‘Sex|a1+’) in interaction (‘I’) with the seasonal age model (noted ‘Base’) and the ‘Cons’ effect (Base + Cons. + (Sex|a1+) + I(Base, Sex|a1+) + I(Sex|a1+, Cons.); Figure 2.1B). In the second model we dropped all sex effects (Base + Cons + I(Base, Cons.); figure 2.1C). The models were fitted in the software E-SURGE v1.7 (Choquet et al. 2009b, Juillet et al. 2010) and the evidence of the effects were verified using a model selection approach based on Akaike’s information criterion (QAICc) corrected for overdispersion and small sample size (Burnham and Anderson 2002).

Goodness of fit tests

The CMR model selection is sensitive to a lack of adjustment to the data of the umbrella model. At present, no genuine goodness-of-fit (GOF) tests are available for multi-event models (Pradel et al. 2005b, Choquet et al. 2009a). Due to the long computing time required for one model, an omnibus approach like bootstrapping is unfeasible. The program U-CARE (version 2.3) can be used to calculate GOF tests for a mixture of live and dead encounters because it allows the inclusion of observable absorbing states (i.e. state newly-dead; Choquet et al. (2009a)). The GOF tests, which are based on contingency tables, are applied to the fully time-dependent multistate model (Pradel et al. 2003) but do not account for state uncertainty. Since multistate is a particular case of the more general multievent models, applying these GOF tests on our dataset was actually a conservative approach because using state uncertainty presumably accounted for some of the lack of fit detected with those tests (Crespin et al. 2008, Juillet et al. 2010). Because our model is on a seasonal basis, we applied a series of independent GOF tests on subsets of data according to the kind of information used (captures, resightings or recoveries), the presence of collar, the age and the sex of individuals (Gauthier et al. 2001).

Results

Goodness of fit tests

The GOF tests combining summer recapture data from Bylot Island and annual recoveries were not significant when sex, age at banding and presence of collar were considered, indicating an adequate fit (Table 2.4, Supplemental Materials). For adult females marked with a collar, complementary GOF tests were conducted on an annual basis from a subset of data considering resightings only from the same season/area over the study period and combining recoveries pooled over one year (Tables 2.5 and 2.6, Sup. Mat.). Overall, the GOF tests for the three subsets of data (Summer to Summer, Fall to Fall, Spring to Spring) were significant. When looking at the subcomponents of the GOF tests, we detected positive trap dependence (trap-happiness) on the stopover site in Québec, during southward and northward migration and on the breeding ground. On the breeding ground, transience, or permanent emigration of collared females following initial capture, was also detected. It is in theory possible to incorporate most of these effects in the model structure; however, in practice, due to the complexity of the base model and limitation in computing power, this was not feasible. We thus opted for the use of a coefficient of overdispersion (c-hat). We chose to apply the maximum value among all the complementary tests conducted (2.945) to the model selection process. This procedure leads to wider confidence intervals and to a preference for reduced models with fewer parameters and is thus a conservative approach.

Seasonal survival

We found that the model with conservation measures, but without the sex effect was the preferred one (Table 2.1).

In this model, monthly survival was affected by the special conservation measures but this effect varied according to season and age. Survival was lower during the first year of life (juveniles, Figure 2.2, *vs* adults, Figure 2.3). At a finer scale, juvenile survival was lower during the first fall migration to USA and early winter (Summer-Winter) than during late winter and the first part of the return northward migration (Winter-Spring; Figure 2.2). This trend remained the same without or with special conservation measures although survival was slightly lower during the latter period (before 1999: monthly increase from 0.917, S.E. = 0.017 to 0.979, S.E. = 0.005 for Winter-Spring; afterward: from 0.912, SE =0.011 for Summer-Winter to 0.959, S.E. = 0.006 for Winter-Spring). Surprisingly, divergent results were found during the last portion of the northward migration, starting from the Québec stopover area (Spring-Summer). Survival remained high (0.967, S.E. = 0.008) during years with special conservation measures but had been much lower (0.893, S.E. = 0.034) previously. However, confidence intervals are very large during this latter period.

For adults, monthly survival decreased during the period of special conservation measures in all seasons but the first stage of the southward migration, from the arctic breeding grounds to the Québec stopover area (Summer-Fall) where survival was estimated close to the upper boundary (Figure 2.3). After the special conservation measures were introduced, adult monthly survival declined mainly between the fall stopover period in Québec and early winter in the USA (Fall-Winter; from 0.973, S.E. = 0.004, to 0.955, S.E. = 0.004) and between the spring stopover period in Québec and the arctic breeding grounds

(Spring-Summer; from 0.995, S.E. = 0.004, to 0.977, S.E. = 0.003). For both of these periods, the absolute decline in monthly survival was approximately 2%, whereas on the US wintering grounds the decline was lower (Winter-Spring, close to 1%; from 0.990, S.E. = 0.001, to 0.978, S.E. = 0.003). The absence of a sex effect in our preferred model indicates that survival patterns were similar in both sexes.

The seasonal pattern in monthly survival probability changed slightly between the period without and with the special conservation measures (Figure 2.3). During the first period, the riskiest parts of the annual cycle were the end of the fall migration, which included the stopover segment in Québec, and the wintering period in the USA (Winter-Spring), with very low mortality occurring during the fall and spring migrations between Québec and the Arctic and the summer breeding period (Spring to Summer and Summer to Fall). During the period with special conservation measures, the riskiest part of annual migration was clearly during the southward migration from Québec to USA (Fall-Winter) whereas the spring migration to the Arctic (Spring-Summer), which included the stopover in Québec, became as risky as the wintering period in the USA (Winter-Spring).

Live encounter probability

Capture probabilities at the breeding colony of females banded as juveniles was very low at two years of age (mean = 0.005, range: 0-0.018) but increased at 3 years (0.026, range: 0-0.054) and 4 years of age when it was constrained equal to that of individuals banded as adults (0.035, range: 0.013-0.069, Figure 2.4, Sup. Mat.). All capture probabilities estimated at 0 at 2 or 3 years of age occurred during the period with conservation measures, possibly because the spring harvest reduced the probability of recruitment of females into the breeding population (see Chapter 4). Capture probability of males banded as juveniles remained extremely low across years (mean = 0.003, range: 0-0.008). For collared females, live encounter probabilities from resightings were highest and similar during the fall and spring stopover period in Québec (Figure 2.5, Sup. Mat.; Fall, mean = 0.360, range: 0.203-0.468; Spring, 0.357, range: 0.156-0.496). Capture probabilities of collared females in late summer (mean = 0.034, range: 0.006-0.055) were lower than probabilities of resightings during the same period (mean = 0.089, range: 0.016-0.284) but were less variable over time. Based on detection of collar loss during these physical captures in summer, we were able to estimate a monthly collar retention probability of 0.993 (SE = 0.001).

Dead recovery probability from hunt

Recovery probability of collared females was globally higher than that of individuals banded with a metal band only, with the highest difference occurring on the wintering ground (collared females, mean = 0.683, range: 0.321-1; with metal band only, mean = 0.318, range: 0.178-0.705). When compared among seasons (Figure 2.6, Sup. Mat.), recovery probabilities were the lowest in Québec during the fall (collared females, mean = 0.14, range: 0.062-0.367; metal band only, mean = 0.102, range: 0.043-0.215) followed by the spring from 1999 onwards (collared females, mean = 0.202, range: 0.120-0.330; metal band only, mean = 0.154, range: 0.094-0.252) and winter (the three seasons where almost all the hunting mortality occurs). Recovery probability was intermediate in the Arctic (collared females, mean = 0.296, range: 0-1; metal band only, mean = 0.222, range: 0-0.602) but confidence intervals were very large with parameters estimated at both boundaries in several years because few individuals were killed by native hunters during the summer.

Discussion

Using the most recent advances in CMR models, and taking advantage of both live and dead encounters while accounting for potential biases related to the use of auxiliary markers (Juillet et al. 2010), our analysis provides a reliable assessment of the seasonal effect of conservation measures on all age and sex classes of the Greater Snow Goose population. On a seasonal basis, we showed that monthly survival probabilities of adults decreased during all three hunting seasons (fall, winter and spring) after the implementation of conservation measures in 1999, though not equally in all seasons. No apparent decrease in survival was documented for the northern part of the annual cycle which primarily encompasses the portion of the migration occurring in the Arctic and the summer breeding season, a period during which no conservation measures were in effect. In contrast to adults, there appeared to be little effect of the conservation measures on juvenile survival during their first fall and winter and, surprisingly, survival during the second part of the spring migration increased during the years with conservation measures.

Effects of conservation measures on adult seasonal survival

In long lived species, adult survival is the life history trait with the largest contribution to the population growth rate (Saether and Bakke 2000). As such, when populations become overabundant, conservation measures directed at reducing adult survival will often be the most effective (Gauthier and Brault 1998). Faced with a burgeoning population of Greater Snow Geese, wildlife managers decided to liberalize hunting regulations and to introduce a new spring hunt in an attempt to stabilise the Greater Snow Goose population. Our results indicate that this management strategy was successful as adult survival decreased during the 3 hunting seasons that were targeted, resulting in a decrease of annual survival probability of 15% (from 0.876 to 0.747). We did not find evidence for a differential survival cost between sexes across the seasons and in relation to the increase of hunting pressure. It is worth noting that a previous analysis of a subset of the present dataset demonstrated an interaction between sex and the special conservation measures as males had a higher annual survival in the presence of conservation measures than females (Juillet et. al 2010). Since the previous analysis included only adults banded as adults (2+ years old) whereas the present one included all individuals, i.e. those banded initially as adults and those banded initially as goslings (0-1 years old), the present dataset most likely has an age distribution skewed more towards young adults, which could explain this discrepancy. Moreover, Juillet et al. (2010) did not correct for overdispersion in the data, which may have affected their model selection.

In a previous analysis, Calvert & Gauthier (2005) showed that mean annual adult survival declined by 13% (from 0.830 to 0.725) when comparing the periods 1990-1998 and 1999-2002 (Calvert and Gauthier 2005). Using hunting band recovery data Calvert and Gauthier (2005) further showed that this decrease in survival was due to a genuine increase in hunting mortality following introduction of the special conservation measures, which was also confirmed by the increase in the number of killed geese observed in the annual CWS and USFWS hunter survey (Calvert et al. 2007). The present analyses allowed an extension of the work of Calvert and Gauthier (2005) since we determined how these management actions affected survival on a seasonal basis. Calvert and Gauthier (2005) suggested that the strongest impact of the special measures on the population occurred in winter in the USA and secondarily during the spring in Québec based on their estimation of seasonal kill rates. Our analysis only partly supports their conclusions because we found that the largest decline in seasonal survival of adults occurred early during the spring migration and, secondarily, late during the fall migration, both in Québec, but little during the winter in the USA. It thus appears that the spring hunt in Québec is the single action that had the strongest impact on the survival rate of the population over the period 1999-2005.

Special conservation measures during the fall in Québec included an increase in bag limits, allowing stalking, a 10-day extension of the hunting season, the use of electronics calls and, under special conditions, baiting (Reed and Calvert 2007). In contrast, the only measures implemented in the USA were an increase in bag limit and an extension of the hunting season, which could explain why the decline in survival was more important during the Fall-Winter season than the Winter-Spring season. Hunting mortality is considered additive to natural mortality if an increase in harvest is associated with a concomitant decrease in survival, otherwise a compensatory process is concluded (Williams et al. 2002). Under the premise that hunting mortality is additive to natural mortality (Francis et al. 1992, Gauthier et al. 2001), and assuming a stable seasonal distribution of kill rates since 1999, our results combined with those of Calvert and Gauthier (2005) (increase in mortality from hunt) suggest that the degree to which hunting mortality is additive versus compensatory could vary by season. This could explain why the decrease in monthly survival from USA to Québec at the end of winter (Winter-Spring) is less than the decrease during Fall-Winter and Spring-Summer. An alternative explanation is that Calvert and Gauthier (2005) assumed a reporting rate identical between Canada and USA in order to estimate the kill rate, which may be inappropriate. If reporting rate is higher in the USA than in Québec (Zimmerman et al. 2009), then their winter kill rate would have been overestimated.

Effects of conservation measures on juvenile seasonal survival

The seasonal pattern of decrease in adult survival associated with special conservation measures was not detected during the first year after fledging when, surprisingly, an increase in seasonal survival from spring to summer occurred. On an annual basis, the survival probability tended to increase from 0.401 before 1999 to 0.470 during the period of special conservation measures. A lack of relationship between annual juvenile survival and harvest rate has already been documented on the same population using recovery models (Calvert and Gauthier 2005) and on another North American goose species, the Ross's goose (*Chen rossii*) (Alisauskas et al. 2006). Increased harvest of Ross's geese from the 1989 hunting season (˜8,000 birds) to the 2001 season (90,000 birds) was related to a decrease in adult survival, but was unrelated to juvenile survival (Alisauskas et al. 2006). Annual survival during the first year of life is approximately half that of adult annual survival (1+ year old) in the absence of special measures, allowing more room for compensatory processes between natural and hunting mortality to occur in juveniles. Another form of compensatory process could be that a high hunting pressure during fall and winter results in non-detectable changes in survival probability at the end of the period if survival of the remaining juveniles is higher due to an artificial selection (via hunting) against more vulnerable juveniles early on. However, we must recognize that a serious limitation of our analysis is that we were unable to apply an age effect on the recovery probability conditional upon death of the individual. This simplification may introduce some biases as previous studies showed that juveniles are more vulnerable to hunt than adults, especially during the first months of life (Calvert and Gauthier 2005, Calvert et al. 2005), which would affect the first year recovery rates. However, considering that Summer-Fall and Fall-Winter are combined into one season for juveniles in our analysis (Summer-Winter), and that natural mortality of juveniles occurs mostly on the initial part of their first migration between the Arctic and Québec (Summer-Fall) (Menu et al. 2005), it is possible that by the end of the winter difference in recovery probability conditional upon death are attenuated.

Research and management implications

Due to the complexity of building a survival model with all age and sex classes on a seasonal basis, we are currently limited by computing power, which forced us to fit a limited number of models. The problem of complex population models is not new and has been well discussed by Levins (1966) when he presented the trade-offs between generality, realism and precision in theoretical population modeling. Our approach was at the mid-point between theoretical and statistical modelling in that we had to define a priori an important part of the structure of our models without any empirical model selection. The distance between our findings and reality will essentially depend upon the assumptions made on our base model, and thus on our previous biological understanding of the system. By contrasting seasonal survival probability between two periods, before and during the special conservation measures, and accounting for as much heterogeneity of detection as possible (e.g. tag loss, recruitment or dispersal), our goal was to conserve realism and generality while addressing our hypothesis of primary interest. By proceeding in this manner, we were able to provide new insights into our understanding of the effect of the special conservation measures on seasonal variation in survival probability for different components of the population. We defined most of our encounter parameters as fully time dependent, but these components of the model could benefit from further refinement or simplification through inclusion of more biological information in future applications of this model.

When different management actions are applied at various stages of the annual cycle of a species, estimation of survival probability on an annual basis does not allow us to distinguish which action had the strongest effect. Here, we clearly demonstrate the benefits of working at the level of the entire population and integrating all available information in order to produce survival probabilities at the same geographical or temporal scales at which management strategies are applied. Even if a loss of precision may occur in terms of modelling, the richness of the qualitative information can still bring new insights when evaluating management strategies. Based on the current analysis, we conclude that adult survival decreased the most due to management actions implemented in Québec during both the fall and spring migrations and less so via changes taking place in the USA over the period 1999-2005. The population trends of Greater Snow Geese show that the population has stabilised during this period despite some annual fluctuations (Reed and Calvert 2007). However, if an additional decrease in survival is required to reduce further this population, our analysis suggests that managers should target the winter in the USA because it is during this period that survival changed the least since the introduction of the special conservation measures in 1999. The introduction in 2009 of a new Conservation Order in the Atlantic Flyway of the USA for this population, which includes an extension of the hunting season beyond the original 110 days and the use of new hunting techniques such as electronic call, may well achieve this goal.

Table 2.1 : Fit of the models to our data based on Akaike's information criterion corrected for overdispersion (c-hat = 2.945) and small sample size (ΔQAICc). Abbr.: a = age, Cons. = conservation measures, I = interaction, Rank = number of identifiable parameters.

Model	Rank	Deviance	ΔQAICc
Base + Cons. + I(Base, Cons.)	202	158174.657	0.000
Base + Cons. + I(Base, Cons.) + (Sex|a1+) + I(Base, Sex|a1+) + I(Sex|a1+,Cons.)	210	158156.297	9.866
Base	195	158586.254	125.678

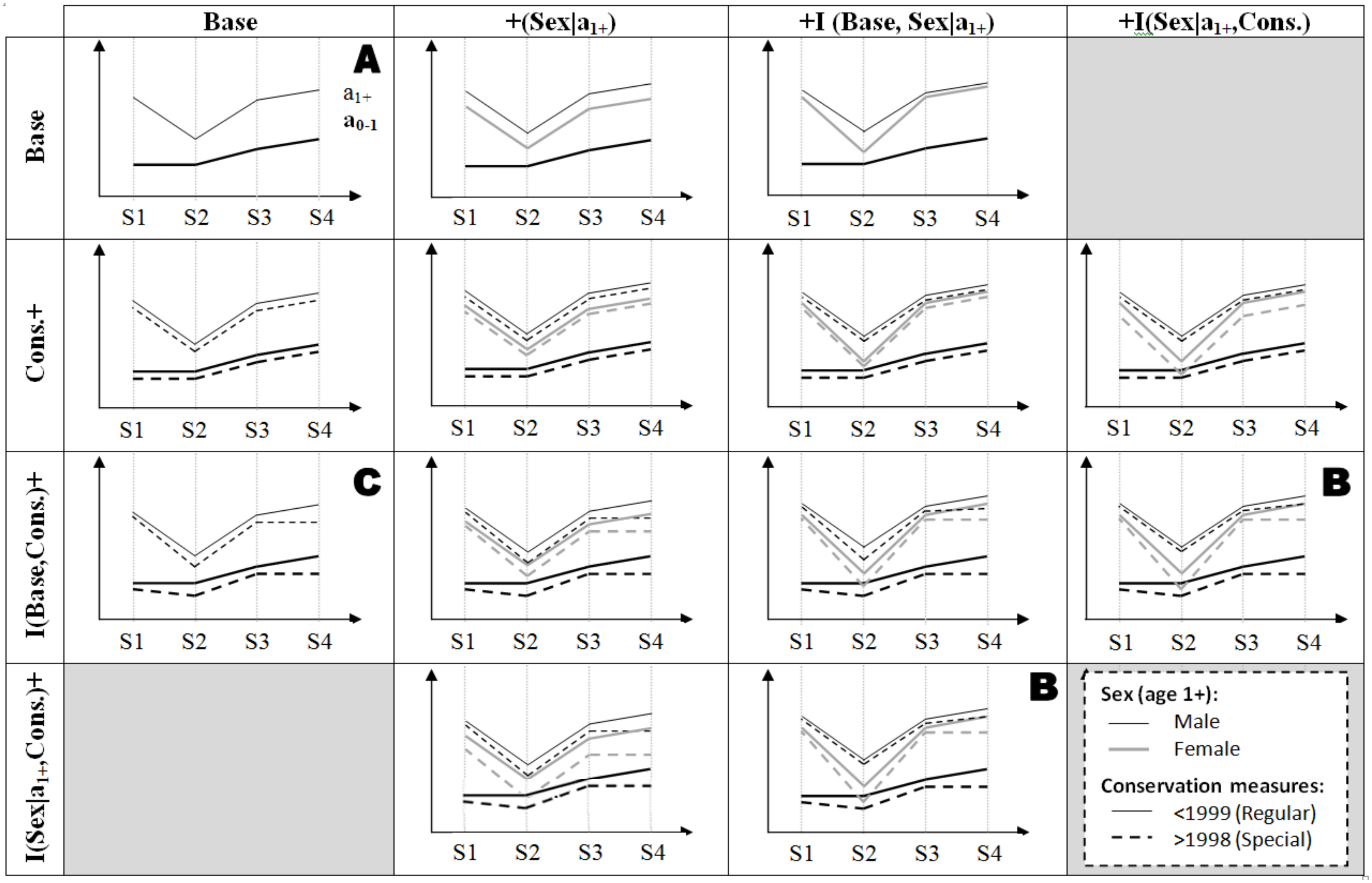
Base
+(Sex|a_{1+})
+I (Base, Sex|a_{1+})
+I(Sex|a_{1+},Cons.)
Base
Cons.+
I(Base,Cons.)+
I(Sex|a_{1+},Cons.)+
A
B
C
B
a_{1+}
a_{0-1}
S1
S2
S3
S4
Sex (age 1+):
Male
Female
Conservation measures:
<1999 (Regular)
>1998 (Special)

Figure 2.1: Hypothetical illustration of sex (in age 1+ only) and conservation measures factors in modeling of survival probability (y axis) by season (x axis) and by age (0-1, 1+). Abbr.: a = age, Cons. = conservation measures, I = interaction; A, B, C = fitted models.

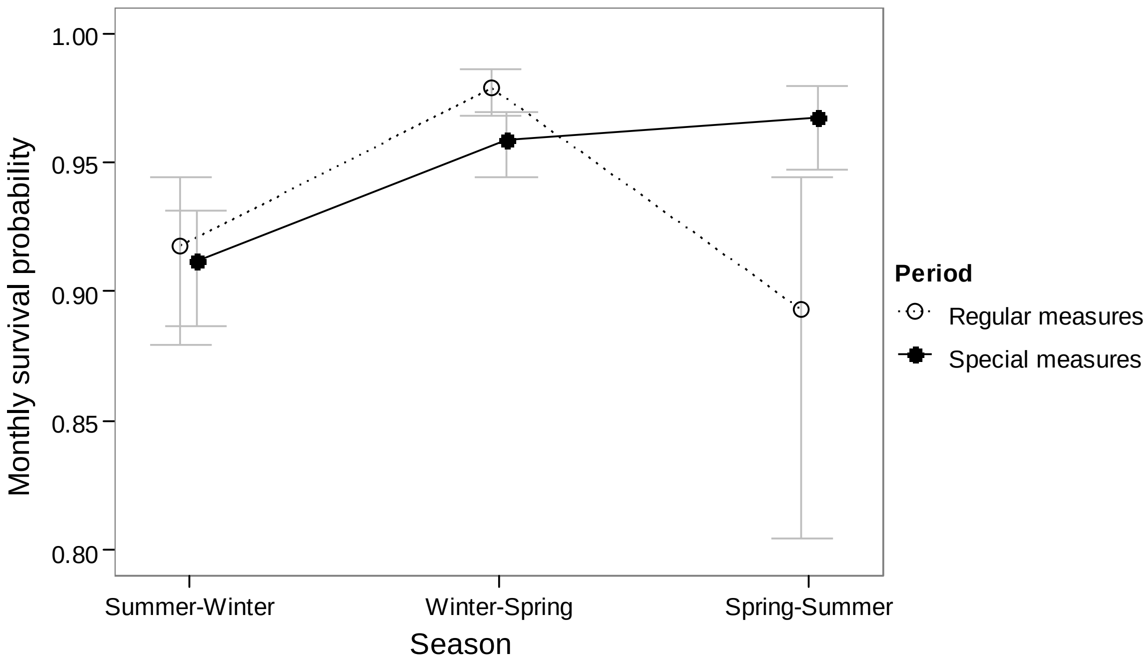

Figure 2.2: Monthly seasonal survival probability during year of hatching (0-1 year old) with 95% confidence intervals, contrasted for years with special conservation measures (elevated harvest, from spring 1999 to spring 2005) and years preceding these measures (regular harvest, 1993-1998).

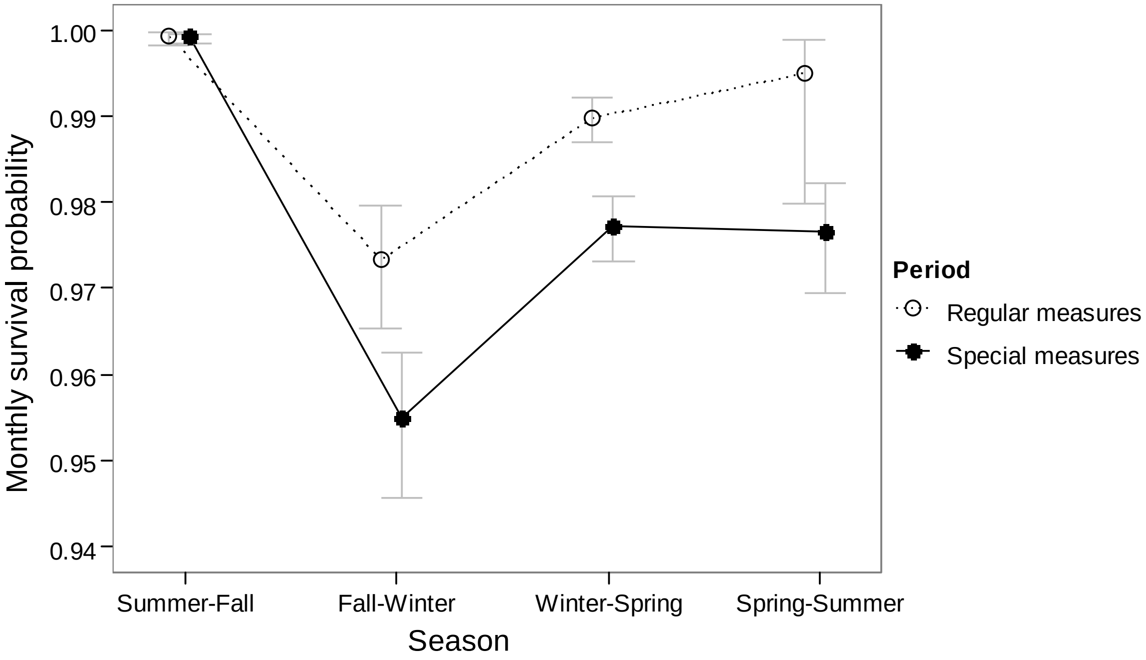

Figure 2.3: Monthly seasonal survival probability for individuals of one year old and more with 95% confidence intervals, contrasted for years with special conservation measures (elevated harvest, from spring 1999 to spring 2005) and years preceding these measures (regular harvest, 1993-1998).

Supplemental materials

Table 2.2: Global goodness-of-fit tests on contingency tables based on annual summer adult recapture data from 1993 to 2005 on Bylot Island, NU, Canada and annual recoveries pooled until the next summer and reported at this occasion. Information related to males banded as juveniles is not presented due to sparse data from recaptures.

Group	*Overall test*	
Females, banded juvenile, no collar	χ^2	37.05
	p-value	0.09
	df	27
	c-hat	1.37
Females, banded adult, no collar	χ^2	28.65
	p-value	0.94
	df	42
	c-hat	0.68
Females, banded adult, collar	χ^2	27.09
	p-value	1.00
	df	56
	c-hat	0.48
Males, banded adult, no collar	χ^2	50.23
	p-value	0.69
	df	56
	c-hat	0.90

Table 2.3: Global goodness of fit tests on contingency tables for female individuals banded adult with a collar, based on annual observation data from 1993 to 2005 and annual recoveries pooled between two occasions.

Subset of data	*Overall test*	
Summer, Bylot Island (NU), initial capture and observations	χ^2	473.75
	p-value	<0.01
	df	196
	c-hat	2.42
Summer, Bylot Island (NU), observations only	χ^2	112.69
	p-value	0.05
	df	89
	c-hat	1.27
Fall, Québec, observations only	χ^2	544.78
	p-value	<0.01
	df	185
	c-hat	2.95
Spring, Québec, observations only	χ^2	290.89
	p-value	<0.01
	df	161
	c-hat	1.81

Table 2.4: Detailed goodness-of-fit tests on contingency tables for female individuals banded adults with a collar, based on annual observation data from 1993 to 2005 and annual recoveries pooled between two occasions. The 3G.SR component is associated to the detection of transience and the M.ITEC component is associated to the detection of immediate trap-dependence. The two remaining components are used in the computation of the overall test in the previous table.

Subset of data		**Goodness of fit test components**			
		3G.SR	**3G.SM**	**M.ITEC**	**M.LTEC**
Summer, Bylot Island (NU), initial capture and observations	χ^2	54.37	133.46	111.40	174.54
	p-value	<0.01	<0.01	<0.01	<0.01
	df	12	57	33	94
	c-hat	4.53	2.34	3.38	1.86
Summer, Bylot Island (NU), observations only	χ^2	10.24	19.44	50.19	32.83
	p-value	0.42	0.85	<0.01	0.20
	df	10	27	25	27
	c-hat	1.02	0.72	2.00	1.22
Fall, Québec, observations only	χ^2	36.89	87.91	277.59	142.40
	p-value	<0.01	0.13	<0.01	<0.01
	df	12	74	32	67
	c-hat	3.07	1.19	8.68	2.13
Spring, Québec, observations only	χ^2	13.87	71.91	110.17	94.94
	p-value	0.24	0.23	<0.01	<0.01
	df	11	64	29	57
	c-hat	1.26	1.12	3.80	1.67

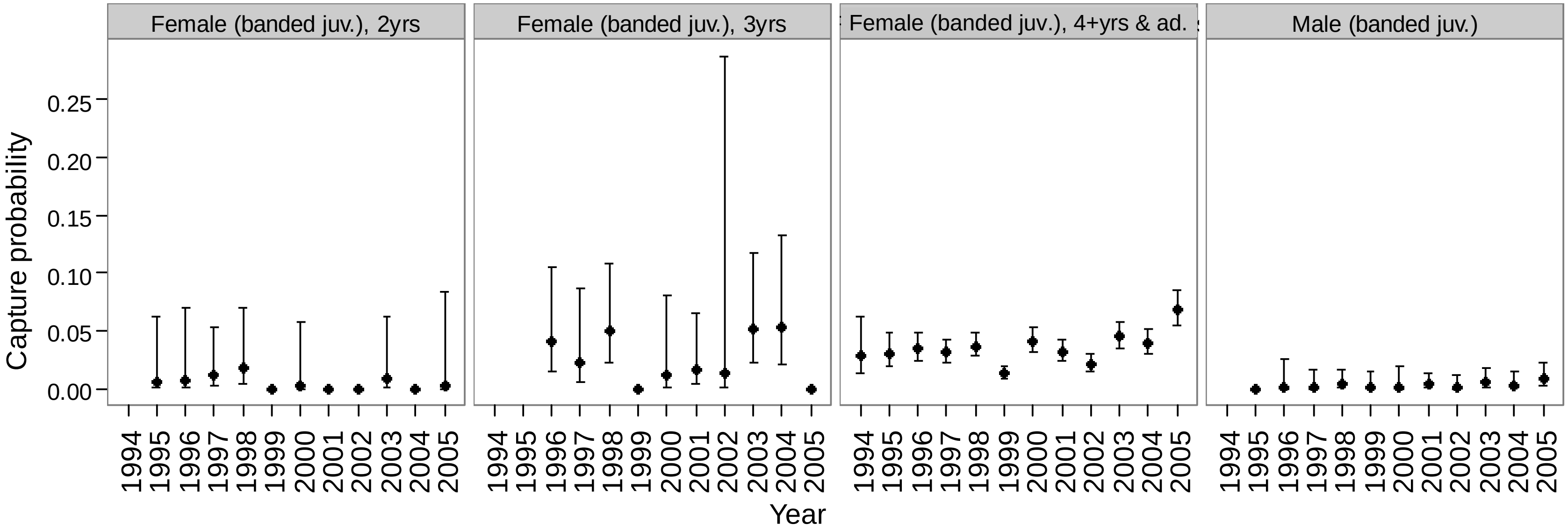

Figure 2.4: Capture probabilities (with 95% CI) at the breeding colony on Bylot Island, NU, of non-collared individuals depending on the sex and the age from the preferred model in Table 2 (ad. = adults, juv. = juvenile).

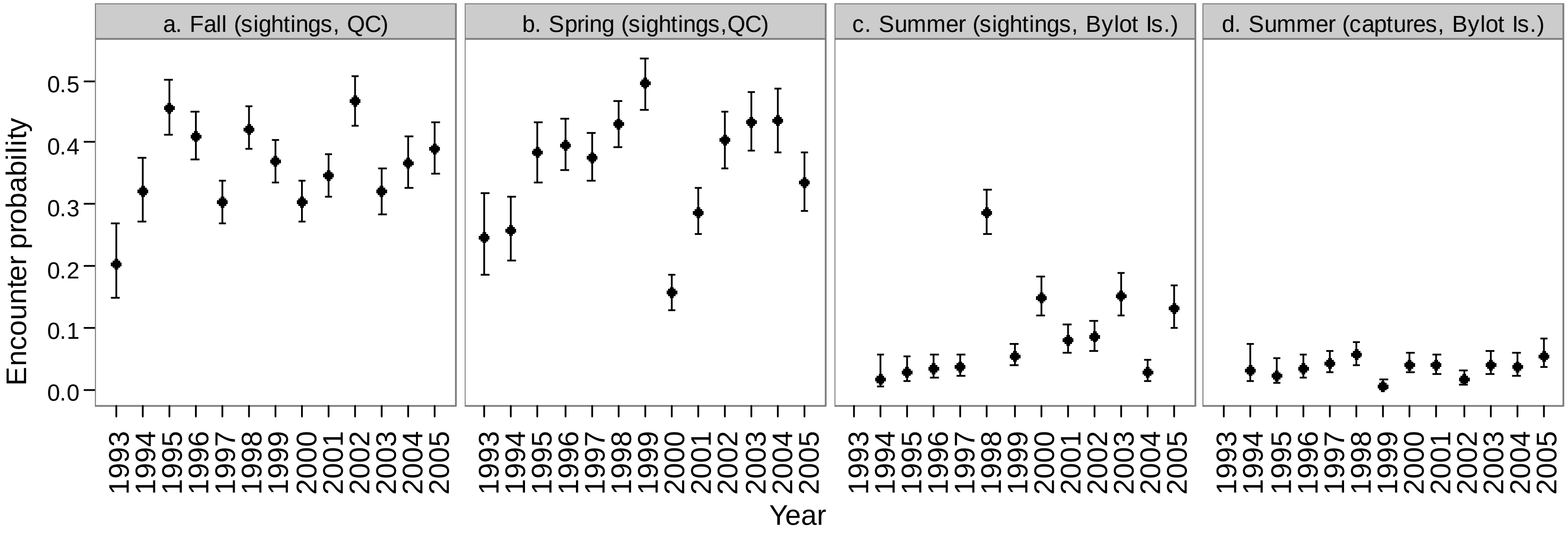

Figure 2.5: Encounter probabilities (capture or resightings, with 95% CI) of adult collared females depending on the season. Abbr.: QC = Québec.

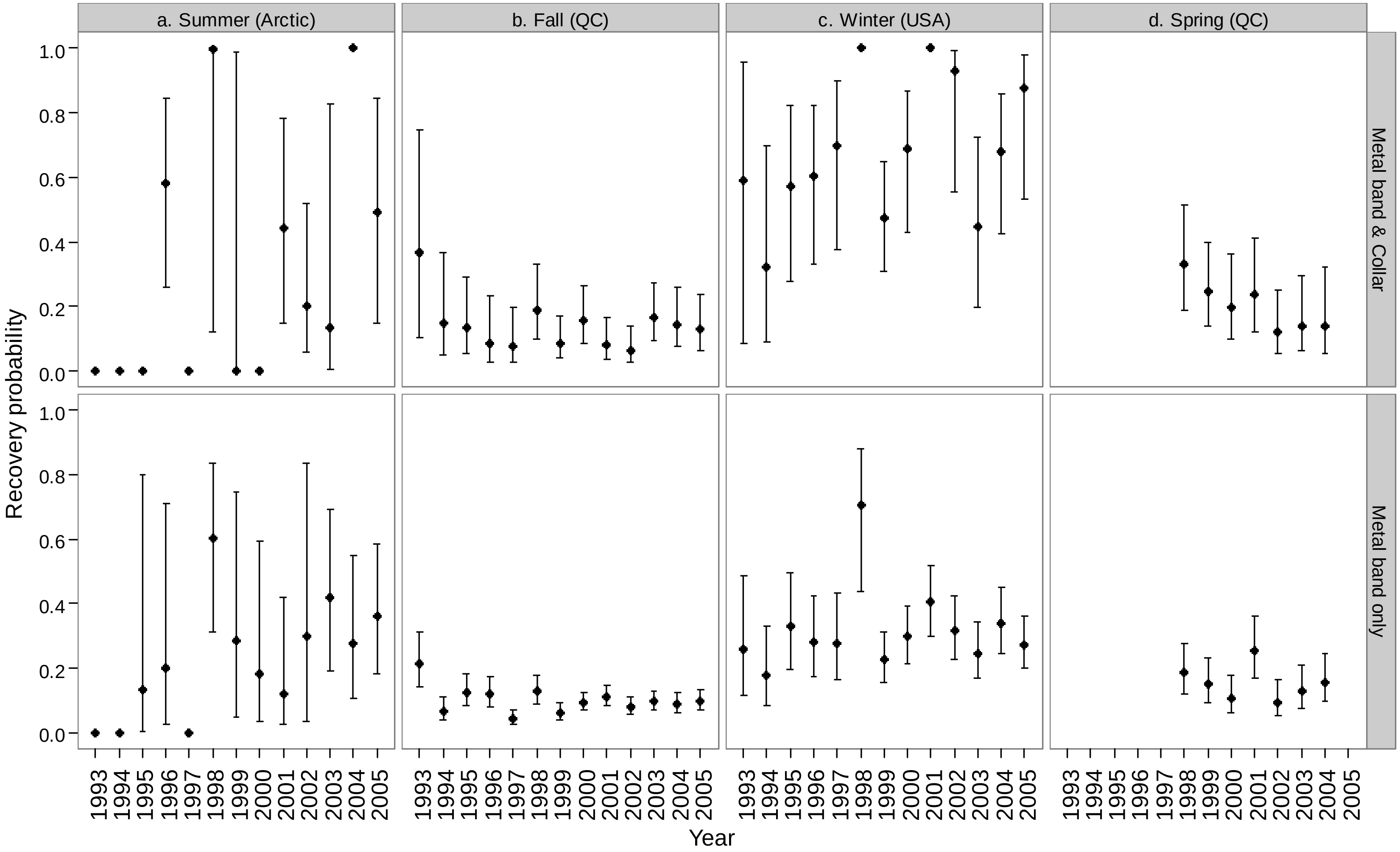

Figure 2.6: Recovery probabilities (with 95% CI) dependent upon the presence/absence of auxiliary marker (plastic collar), in addition to the metal band and the season/geographic region. Abbr.: QC = Québec.

Chapitre 3

Carry-over effects of a spring hunt on the summer reproduction of a long-distance migrant

C. Juillet, G. Gauthier, Marie-Christine Cadieux and R. Pradel

Résumé

Les effets potentiels des mesures de gestion pour rétablir ou contrôler la taille de la population des espèces migratrices doivent prendre en compte leur cycle migratoire. En raison de sa croissance exponentielle au cours de la seconde moitié du 20$^{\text{ème}}$ siècle, la Grande Oie des neiges (*Chen caerulescens atlantica*) est une espèce maintenant considérée comme surabondante, et une chasse de printemps a été mise en place durant la halte migratoire au Québec depuis 1999 afin de contrôler sa taille de population. Nous examinons les effets reportés (*carry-over effects*) de la chasse de printemps sur trois paramètres de la reproduction (la densité des nids, la date de ponte et la taille des couvées) de cette espèce nichant dans l'Arctique, tout en contrôlant pour les conditions climatiques durant la migration printanière et à l'arrivée sur le site de reproduction. Nous avons posé l'hypothèse que les effets de report, suggérés par des études précédentes menées au cours des premières années de la chasse de printemps, pourraient être transitoires en raison de la diminution observée du taux de récolte de printemps au fil du temps. Nous avons utilisé un ensemble de données à long terme (1995 à 2007) de suivi annuel de la nidification des oies sur l'île Bylot (Nunavut, Canada; 73 ° N, 80 ° W). Nos résultats ne fournissent pas de réelle évidence d'un effet reporté de la chasse de printemps sur la date et taille de de ponte pour la période 1999-2007, excepté un faible support pour la densité de nid. Au lieu de cela, un indice synthétique des conditions climatiques sur le site de reproduction a été suffisant pour expliquer la variation annuelle de la densité des nids et de la date de ponte. La densité des nids a augmenté et la date de ponte a été avancée lorsque la température de l'air était plus chaude que la moyenne au cours de la période du 20 mai au 19 juin et que la couverture neigeuse au début juin était inférieure à la moyenne. Nous n'avons pas été en mesure de détecter un facteur expliquant la taille de la couvée après avoir contrôlé pour la date de ponte individuelle. En conclusion, les effets reportés des mesures spéciales de conservation sur les paramètres de reproduction pour la colonie de Bylot n'ont pas été détectés, et s'ils existent (faible évidence pour la densité de nid), ils sont marginaux par rapport à l'ampleur des effets climatiques à l'arrivée sur le lieu de reproduction.

Abstract

The potential effects of management actions to re-establish or to control the population size of migratory species have to consider their migratory cycles. Because of its exponential growth during the second half of the 20th century, the Greater Snow Goose (*Chen caerulescens atlantica*) population is now considered overabundant, and a spring hunt has been implemented on its stopover sites in Québec since 1999 to control its size. We studied the carry-over effects of the spring hunt on three reproductive parameters (nest density, laying date and clutch size) of this arctic-nesting species while controlling for climatic conditions experienced during spring migration and upon arrival on the breeding ground. We hypothesized that carry-over effects suggested by previous studies conducted during the early years of spring hunt could be transient due to a decrease in spring harvest rate over time. To proceed, we used a long-term dataset (1995 to 2007) from the annual monitoring of nesting activity of geese on Bylot Island (Nunavut, Canada; 73°N, 80°W). Our results provide no evidence for a carry-over effect of the spring hunt on laying date and clutch size and at least a weak evidence on nest density over the period 1999-2007. Instead, a synthetic climatic index of conditions on the breeding ground was sufficient to explain annual variation in nest density and laying date. Nest density increased and laying date was advanced when air temperature was warmer than average during the period May 20 to June 19 and snow cover lower in early June. Clutch size was not affected by spring hunt or our climatic index after controlling for individual laying date. In conclusion, at the level of the breeding population of this arctic colony, carry-over effects of the special conservation measures on several reproductive parameters have not been detected, and if present (little evidence for nest density), they are marginal in comparison with the magnitude of climatic effects at arrival on the breeding ground.

Introduction

Conservation measures aimed toward the recovery of declining populations, or the control of overabundant population, are directed to act on at least one of three basic demographic processes: survival, reproduction or movement. The application of conservation measures to migratory species is often limited in time and space, for instance to a particular period of the annual cycle. Therefore, one challenge in planning and evaluating conservation actions for migratory species is to account for confounding effects occurring throughout their entire annual cycle, and not only at one stage of the migratory cycle (Martin et al. 2007, Bolger et al. 2008). A prominent example of a large scale management problem involves several Arctic-nesting goose populations which have exhibited exponential growth during the second half of the 20th century and become overabundant by the end of the last century (Ankney 1996). A major cause of these population explosions is that the intensification of agriculture ('Green revolution') in temperate regions provided new food resources on the wintering grounds and stopover sites during migration (Jefferies et al. 2004, Gauthier et al. 2005), which improved vital rates. For instance, winter mortality of Greenlandic Pink-footed geese (*Anser brachyrhynchus*) and White-fronted geese (*Anser albifrons*) has decreased (Fox et al. 2005) and reproductive success of Brant geese (*Branta bernicla*) improved due to greater food abundance during winter and spring (Ward et al. 2005). Overabundant populations may also conflict with human activity, e.g. by negatively impacting crops, or with other species, e.g. by altering or destroying natural habitats.

Several North American Snow Goose (*Chen caerulescens*) populations are now so abundant that in some areas they have become a threat to their arctic habitat and to themselves (Jefferies et al. 2004). In an attempt to control the Greater Snow Goose (*C. caerulescens atlantica*) population, that was considered overabundant (Batt 1998), a special conservation harvest (hunt) was implemented in 1999 on the spring staging grounds in Québec, Canada. This hunt was additional to the traditional hunt occurring each fall in Québec and winter in the USA (Calvert and Gauthier 2005). The spring hunt was the most spectacular action among a series of changes in hunting regulations implemented in 1999 to increase the sports harvest (e.g. increase in bag limit, use of electronic calls etc.). As hunting mortality is additive to natural mortality in Greater Snow Geese (Gauthier et al.

2001), these conservation measures targeted the survival component of the population. As expected, a decrease in survival occurred following the implementation of the special conservation measures (Calvert and Gauthier 2005, Juillet et al. 2010). However, hunt may also have unexpected carry over effects on other demographic parameters such as reproduction.

The spring hunt was a considerable source of disturbance for geese, modifying their distribution and movements during staging (Béchet et al. 2003, Béchet et al. 2004a), and resulted in a reduction of their spring body condition in the first few years after the introduction of the hunt (Féret et al. 2003). Greater Snow Geese have a mixed capital/income strategy for egg production, meaning that egg nutrients come from both food ingested on the breeding ground and body reserves acquired prior to arrival on the breeding grounds (Gauthier et al. 2003). Consequently, conditions experienced during migratory stages prior to breeding can have an impact on reproduction via a carry-over effect (Laaksonen et al. 2006, Norris and Taylor 2006, Inger et al. 2010). Some evidence of carry-over effects such as reduced breeding propensity of geese and delayed laying were indeed detected during the first few years following the introduction of the spring hunt (Mainguy et al. 2002, Bêty et al. 2003, Reed et al. 2004). However, since the introduction of the hunt in 1999, spring harvest rates have been decreasing steadily (Canadian Wildlife Service, CWS, unpublished data). Therefore, it is possible that the carry over effects of the spring hunt on reproduction have decreased over time. However, when evaluating these effects one also has to consider climatic factors, which may have a considerable impact on the reproductive success of arctic-nesting geese, either directly on the breeding ground (Madsen et al. 2007, Dickey et al. 2008, Morrissette et al. 2010), or through a carry-over effect for climatic conditions experienced during the spring migration (Davies and Cooke 1983). This is especially relevant considering that Greater Snow Geese have experienced a warming trend both during spring staging in Québec and on their arctic breeding ground (Gauthier et al. 2005).

To investigate potential carry-over effects of the special conservation measures, we examined the relationship between hunting pressure (spring adult harvest rate) and reproductive parameters (nest density, laying date and clutch size). We used a multiple inference framework (Anderson 2008), allowing us to account for alternative effects such as weather conditions experienced during the spring migration at stopover sites and upon arrival to the breeding grounds. In light of the decline in spring harvest rate that has occurred since the implementation of the special conservation measures, we predicted that the carry over effects of spring hunt on reproduction suggested by previous studies, may have decreased in the following years.

Material and methods

Study species

The Greater Snow Goose is a monogamous, migratory species wintering on the Eastern coast of the U.S.A. and breeding in the Canadian High Arctic. During migration, the population uses the Saint Lawrence River Valley in Québec, Canada, as a major stopover area during 6 to 8 weeks in spring (from late March to late May) before continuing on to the arctic breeding grounds, 3000 km further north, where they arrive in late May/early June. Most of the body reserves (fat and protein) required for migration and reproduction is accumulated during spring staging in Québec (Gauthier et al. 1992, Gauthier et al. 2003).

Nesting data

Nesting data came from a long-term study initiated in 1994 at the main breeding colony of Snow Geese on Bylot Island, Nunavut, Canada. Annual nest monitoring involved a combination of the two following sampling schemes: 1) one long term ~100ha plot located in the center of the colony and 2) 6 to 27 random 1ha plots scattered throughout the colony from 1999 onward (new plots were selected every year). Reed et al. (2005) did not find any differences in the nesting parameters between these two sampling methods. Some females marked with neck bands were excluded from this study because neck bands can affect the breeding propensity (Reed et al. 2005).

Laying date, *id est* when the first egg is laid, was estimated following 3 methods dependent upon the stage of a nest at discovery and information collected at revisits during the laying, incubation and/or hatching stage (Lepage et al. 1999). Clutch size was defined as the total number of eggs laid (maximum number of eggs found in the nest after incubation had started). All nests with more than 6 eggs or less than 2 eggs, indicative respectively of brood parasitism or partial predation before discovery, were excluded from the analyses (Lepage et al. 1999). The local habitat, wet or dry, was noted for almost all nests since 1995. As factors such as snow cover and predation risk may vary by habitat in our study site and affect reproduction or sampling (Lecomte et al. 2008a, Lecomte et al. 2008b), we controlled for the potentially confounding effect of habitat (mesic or wet) in the analyses. As such, only data from 1995 onwards were used in our study. The total number of nests monitored annually ranged from 107 to 451, of which 52 to 141 nests came from the random plots after 1998. Finally, nest density was calculated by counting all nests initiated in a 30 ha plot located within the 100 ha long term nest monitoring patch each year.

Explanatory variables

Harvest rate

We computed adult harvest rate by dividing the estimated number of adults killed in Québec during the spring hunt (CWS, unpublished data) by the population size estimated in early May of the previous year. Population size was determined by an aerial photographic survey conducted by the CWS (Béchet et al. 2004b). The population size of the previous year was preferred to that of the actual year because it did not include juveniles, which, by definition, are not part of the breeding segment of the population until age 2 (Chapter 4).

Climatic indices

We retrieved data on mean daily air temperature (minima, maxima and mean) and mean daily precipitation for 3 cities (Saint Guillaume, Québec City, and Mont-Joli) along the Saint Lawrence River for the period of 1 April to 19 May, the staging period of geese in southern Québec (National Climate Data and Information Archive, Environment Canada website, http://www.climate.weatheroffice.ec.gc.ca). We also retrieved data on the number of days with snow on the ground for Saint Guillaume and Mont-Joli (data was not available for Québec City).

On the breeding grounds, we collected climatic data from Pond inlet, NU and from an automated weather station located in the Qarlikturvik valley, Bylot Island, NU located at 30 and 67 km respectively from the main breeding colony. We computed mean daily air temperature, and mean daily precipitation from Pond Inlet, NU and mean daily air temperature in the Qarlikturvik valley for the period of 20 May to 19 June, the period of goose arrival and nest initiation. The percentage of snow cover in the Qarlikturvik valley on 5 June, which was visually estimated every year, was also considered.

The North Atlantic Oscillation (NAO) Index, a large-scale climatic phenomenon, is increasingly used as an explanatory climatic variable in wildlife ecological studies in the northern hemisphere (Descamps et al. 2010). This is based upon the assumption that variation in local climatic conditions (temperature and precipitation) is associated with variation in the NAO index (Stenseth and Mysterud 2005). We defined two regional climatic variables by computing the mean NAO index over the 2 time periods defined above.

Because these variables are not fully independent, principal component analyses were conducted on all climatic variables separately for both spring migration, and the breeding stage. Each synthetic variable (or axis) retained from a given PCA represents a group of correlated variables (Grosbois et al. 2008). To facilitate biological interpretation, a 'varimax' rotation of principal axes was executed when necessary (Jolliffe 2002) using the 'FACTOR' procedure in SAS (version 9.1).

Statistical analyses

We defined *a priori* a list of linear models to be fitted to each of the reproductive parameters: laying date, clutch size and density (Figure 3.1). Each model included one or more fixed effects based on a set of retained explanatory variables. To limit the number of covariates and models, the set of explanatory variables common to all analyses (Figure 3.5, Sup. Mat.) contained two climatic indices (the first axes from each PCA, i.e. the most informative), one describing the condition experienced during the spring migration at stopover sites (Climatic Index Stopover Site, CI_SS, Figure 3.6, Sup. Mat.) and one describing the conditions at arrival on the breeding ground (Climatic Index Breeding Ground, CI_BG, Figure 3.7, Sup. Mat.), in addition to the adult spring harvest rates (Harvest Rate Stopover Site, HR_SS). To prevent spurious model selection, the association between all the a priori retained variables was tested using Pearson's correlation coefficient. As no pairs of explanatory variables showed a significant coefficient rho (Table 3.3, Sup. Mat.), all variables were retained in the analyses. Harvest rate was multiplied by

100 in order to prevent a convergence problem due to differences in scale between explanatory variables in the same model. We purposely limited the number of effects in the common fixed structure to 5, and the incorporation of interaction terms to the second order. As recommended by Burnham and Anderson (2002), we used the second order of the Akaike's Information Criterion (AICc) for small sample size to select the best model among the set of a priori defined models. In the present study the number of clusters (sample size) used in the computation of AICc was the number of years, $n = 13$. The 'AICcmodavg' package (Mazerolle 2009) in R was used to sort all fitted models by the difference in AIC_c (ΔAIC_c) relative to the best fitted model. Both laying date and clutch size analyses were based on the measures of many nests each year hence the use of a linear mixed model where year is treated as a random effect because we were not particularly interested in the years of the study but rather considered them to be a random sample of all possible years. The random year effect actually accounts for what differences remain between years once the environmental conditions measured by CI_BG, CI_SS and HR_SS have been taken into account. This year effect is attainable separately from the residuals in the laying date and clutch size analyses because of the replications provided by the different nests within each year. On the other hand, it is confounded with the residual term in the analysis of density because we have just one measure of density per year. This is why, in this latter analysis, we employed a multiple regression approach.

Laying date

Prior to fitting the linear-mixed models containing the *a priori* defined fixed component structures we first determined a common random component structure while including all fixed effects (most complex structure of the fixed component determined a priori) as recommended by Zuur et al. (2009). For a nest *i* and a year *j*, the following equation describes the relationship between the vector of laying dates (Date) to the vectors of environmental conditions (CI_BG, CI_SS, HR_SS and Habitat):

$$\begin{aligned}\mathrm{Date}_{ij} &= \alpha + \beta_1 \mathrm{CI\_BG}_j + \beta_2 \mathrm{CI\_SS}_j + \beta_3\, \mathrm{HR\_SS}_j + \beta_4 \mathrm{Habitat}_{ij} \\ &+ \beta_5 \mathrm{CI\_BG}_j {*} \mathrm{CI\_SS}_j + \beta_6 \mathrm{CI\_BG}_j {*} \mathrm{HR\_SS}_j + a_j + b_j \mathrm{Habitat}_{ij} + \varepsilon_{ij}\end{aligned} \qquad \text{(Equation 1)}$$

Where the parameters estimated in the fixed component are $\boldsymbol{\alpha}$, the fixed intercept or the mean laying date in the wet habitat over the study period given for mean climatic conditions (covariate centred on the mean) and in the absence of spring hunt (a value of zero for the explanatory variable), and β_{k}, the fixed slopes corresponding to the k^{th} explanatory covariates (X) or interaction terms included. The term $\beta_k X_j$ represents the mean population response to the environmental covariate X for a given year *j*, while $\beta_k X_j X'_j$ represents the mean population response to the interaction between the covariates X and X' a given year *j*. The random component of the model was provided by year defined as a random effect a_j, which represents a random deviation from the intercept according to a given year *j* in an average environment and in the absence of spring hunt with, $a_j \sim N(0,\sigma^2_a)$. The year ∗ habitat term, b_jHabitat$_{ij}$, allows us to define a random effect accounting for habitat (dry or wet) as source of heterogeneity of variance for a year *j* with $b_j \sim N(0,\sigma^2_b)$. Because in the equation presented above habitat is also defined as a fixed effect, the term b_jHabitat $_{ij}$ accounts for heterogeneity in slopes and the resulting model is a mixed model with random intercept and random slopes (Zuur et al. 2007). Finally ε_{ij} is an error term encompassing the nest and the year accounting for the residual error not explained by the model with $\varepsilon_{ij} \sim N(0,\sigma^2)$. We used the package 'nlme' to fit the different models in R (Pinheiro et al. 2009). To determine the best variance structure (to meet the assumption of homogeneity of residual variance) we fit a new model derived from the Equation 1 where the year ∗ habitat term, b_jHabitat $_{ij}$, was dropped. We compared these two models via likelihood ratio tests. Because we were interested here by the random component, these two models were fitted using the restricted maximum likelihood (REML) method, which is not influenced by the fixed component structure unlike the maximum likelihood (ML) method (Pinheiro and Bates 2000, Zuur et al. 2007, Zuur et al. 2009).

Once the selection of a random structure was completed, we retained the preferred model and fitted a series of models presenting all the different fixed structures defined *a priori*. The same series of fixed structures were fitted once with habitat as a fixed effect and once without habitat as a fixed effect, the random component structure (determining the variance structure in relation to the sampling design) remaining unchanged. This time, the estimation of deviance was based on the maximum likelihood (ML) (Zuur et al. 2007, Zuur et al. 2009) and the model selection to determine the most parsimonious structure of the fixed component fitting the best our data was based on AICc. When the best model fitting our data was determined, we validated this model graphically, checking for problems of dispersion in residuals by plotting residuals against fitted values. We also controlled for problems of autocorrelation of residuals graphically (function 'acf' from the 'stats' package in R, R Development Core Team (2009)) and fitted different autoregressive models for residuals to select the most appropriate (Zuur et al. 2009). All validation methods were completed after refitting the model using the REML method (the estimation of parameters being less sensitive to outliers than with the ML method).

Clutch size

As clutch size is known to be strongly related to laying date (Bêty et al. 2003), we accounted for this effect. We centred all our individual laying dates on a value of 12.7 (June), the mean and intercept of the best model from our analyses on laying date (see Results). The same modeling and validation strategy for the random and fixed components described in the laying date analyses was applied to the clutch size analyses. The resulting equation describing the relationship between the clutch size (Clutch) of a nest *i* during a year *j* and the different explanatory variables (CI_BG, CI_SS, HR_SS and laying date for a given nest (Date)) is:

$$\begin{aligned}\text{Clutch}_{ij} = \alpha + \beta_1\text{CI\_BG}_j + \beta_2\text{CI\_SS}_j + \beta_3\,\text{HR\_SS}_j + \beta_4\text{Date}_{ij} \\ + \beta_5\text{CI\_BG}_j{*}\text{CI\_SS}_j + \beta_6\text{CI\_BG}_j{*}\text{HR\_SS}_j + a_j + b_j\text{Date}_{ij} + \varepsilon_{ij}\end{aligned} \qquad \text{(Equation 2)}$$

The terms of this equation are identical to the terms described in the previous equation defined for laying date analyses. The only difference being that in the random effect of habitat in interaction with year, habitat is replaced here by the laying date for a given nest *i* in the year *j*. The year ∗ laying date term, $b_j\text{Date}_{ij}$, allows us to define a random effect accounting for heterogeneity in slopes with $b_j \sim N(0,\sigma^2_b)$ and the resulting model is a mixed model with random intercept and random slopes (Zuur et al. 2007). We determined the best random component structure by fitting a version of this model (Equation 2) and another one where the $b_j\text{Date}_{ij}$ term was dropped. We compared these two models, fitted using the REML method, with a LRT test. We then fitted the fixed structure components defined a priori in the presence of the previously selected random component structure. As in the laying date analyses, the same series of fixed structures were fitted once with laying date as fixed effect and once without. Note than in presence of habitat as a fixed effect we had to limit the number of interaction terms to one in the fixed component structure due to the high number of parameters relative to the number of years. For the clutch size analyses we also repeated these two series with or without habitat as a fixed effect while dropping the term $\beta_1 CI\_BG_j$ because we could not exclude the possibility that climatic conditions at arrival was only affecting the laying date and hence not useful in explaining the remaining non explained variation in clutch size. The model selection on the fixed component was conducted using the AICc from models fitted with the maximum likelihood method (Zuur et al. 2007, Zuur et al. 2009). Finally the validation of the best model was completed as in the laying date analyses.

Nest density

Because only one value of nest density was available per year, we fitted a series of multiple regression models including all the fixed structure defined a priori.The presence of a nonlinear relationship with covariates was controlled by conducting preliminary model selection using AICc over a range of generalised additive models. The general structure of the models describing the nest density (Density) in relation to the different explanatory variables (X) for a year *j* is provided by:

$$Density_j = \alpha + \beta_k X_{jk} + \varepsilon_j$$

(Equation 3)

Where α is the intercept, β_k are the slopes corresponding to the k^{th} fixed effects and ε_j is the error term with $\varepsilon_j \sim N(0,\sigma^2)$. The model selection was conducted using AICc and the best model validated graphically.

Results

Climatic indices

At the stopover sites in Québec, air temperature at the 3 stations loaded highly and negatively on the first axis of the PCA, followed by a positive contribution of precipitation at the same 3 stations (Figure 3.6, Sup. Mat.). A positive value on this first axis (corresponding to CI_SS), indicated a colder year with higher than average precipitation over the period 1995-2007.

On the breeding grounds the air temperature from Pond Inlet and Bylot Island were highly positively loaded, whereas percent of snow cover on June 5 and the NAO index were negatively loaded on the first axis of the PCA (Figure 3.7, Sup. Mat.). A positive value on this first axis (corresponding to CI_BG), indicated a warmer than average year associated with a low snow cover on 5 June and a low NAO index value over the period 1995 to 2007.

Laying Date

Models including a random effect of habitat in interaction with year provided the best fit to the laying date data (for all pairs of models compared, Likelihood Ratio Test: d.f.= 2, $\chi^2 > 59$, $p<0.0001$), therefore all subsequent models testing fixed effects included this random component. The only fixed effect retained during model selection was the climatic index on the breeding ground, CI_BG. The weight of ΔAICc, which can be interpreted as the weight of evidence in favour of a given model being the best one among a set of models, was of 97% for our best model (Table 3.1). The next best model included an effect of harvest rate but this model was rejected (ΔAICc = 8.15). We detected a slightly significant dependence of residuals between years and we corrected for this using an Auto-Regressive Moving Average (ARMA) model with 3 parameters for the residuals. This correction did not change the results of our model selection, but did influence slightly the estimates. The intercept from our best model was 12.69 (S.E. = 0.49) representing a mean laying date of 13 June. The effect of our climatic index CI_BG on laying date was negative ($\beta = -2.36$, S.E. = 0.51). Hence the laying date in the colony was delayed during years with colder temperatures and higher snow cover, and was advanced during years with warmer temperatures and lower snow cover over the period 20 May to 19 June (Figure 3.2).

Clutch Size

Models including a random intercept and random slope for the laying date provided the best fit to the clutch size data (for all pairs of models compared, Likelihood Ratio Test: d.f. = 2, $\chi^2 > 12$, $p<0.002$), therefore all subsequent models testing fixed effects included this random component. The only fixed effect retained during model selection was laying date (ΔAICc of 3.03 compared to the next best model, Table 3.1).With a weight of ΔAICc of 80%, this model was almost 4.5 times more likely than the second top model including a climatic effect on the breeding ground (Table 3.1). No problems in residual dispersion or autocorrelation were detected. In our best model, the intercept indicated a mean clutch size of 3.72 (S.E. = 0.10) with clutch size decreasing with later laying dates ($\beta = -0.14$, S.E. = 0.01).

Nest density

In the best model, nest density was explained by the climatic index on the breeding ground only (Table 3.2). The third best ranked model included our variable of interest, the spring harvest rate in Québec in addition to the climatic index, but received less support (ΔAICc=2.78). The ratio of the weights of ΔAICc between these 2 models indicated that the model with climate only (Intercept = 354.95, S.E. = 53.43; $\beta_{CI\_BG} = 134.26$, S.E. = 55.62) was 4 times more likely than when the spring hunt was also considered (Intercept = 279.92, S.E. = 84.95; $\beta_{CI\_BG} = 159.60$, S.E. = 59.37, $\beta_{HR\_SS} = 27.59$, S.E. = 24.56). Nest density in the colony was higher during years with warmer temperatures than average over the period 20 May to 19 June and lower snow cover on 5 June from 1995 to 2007 (Figure 3.4).

Discussion

Contrary to previous studies on this population, we found little evidence for a negative carry-over effect of the special conservation measures on only one of the reproductive parameters studied, the nest density (as there was no relationship between harvest rate and laying date or clutch size). Laying date and nest density were both positively associated with warmer than average temperatures and lower than average snow cover upon arrival to the breeding ground. These results support those of Dickey et al. (2008) who also noted that air temperature and snow cover affected laying date and nest density in the same manner. However, we did not detect a carry-over effect of climatic factors encountered during spring staging on those reproductive parameters. Annual variation in clutch size was best explained by laying date alone indicating that the number of eggs laid is mostly determined by the phenology of the reproduction, as previously reported (Bêty et al. 2003, Dickey et al. 2008). Despite the fact that previous studies have suggested an impact of the spring hunt on reproduction in this population (Mainguy et al. 2002, Bêty et al. 2003, Dickey et al. 2008, Morrissette et al. 2010), our analyses did not reveal any such effects except perhaps for a slight evidence of carry-over effects on nest density.

Assessing the relative importance of environmental factors such as climatic conditions on life history traits is difficult and can be dependent upon the methodological approach used (Grosbois et al. 2008). In the case of the Greater Snow Goose, the special conservation measure of interest was the spring hunt introduced in Québec since 1999. In previous studies, the effect of the spring hunt on reproduction was evaluated by coding hunt as a dummy variable taking a null value before 1999 and a value of 1 afterwards. Although dummy covariates can be relevant in the context of a well controlled experimental design, caution should be exercised when using dummy covariates in field studies. For this population, special conservation measures were introduced in an attempt to regulate an increasing goose population thus, contrasting the 2 periods, before and after 1999, could imply contrasting for low and high population size. Furthermore any other covariate with a temporal trend (e.g. increase of temperature in the Arctic) could also be confounded with a dummy covariate which contrasts 2 successive periods of time. In contrast, we used the actual spring adult harvest rate in Québec as a covariate in order to better represent the temporal variation in hunting pressure using a multiple inference approach. Though effects of spring hunt on reproductive prarameters have been previously detected, we predicted that these effect could have waned over time because harvest rate, initially high, decreased in subsequent years. In contrast, we failed to detect any relationship between harvest rate and the reproductive parameters studied indicating that there could be no detectable carry-over effects of the special conservation measures on reproduction. A possible change in the behaviour or distribution of birds in spring in response to hunting disturbance (something that may not be well accounted for when using spring harvest rate as an index of hunting distrurbance) may explain why, over a longer time period, we failed to detect any effect of the special conservation measures on several reproductive parameters. We attempted *a posteriori* this possibility by replacing harvest rate by a categorical covariate defining 3 time periods to allow for non-linear relationship: years without spring hunt, the early years of the hunt (until 2002) and later years. In all cases (laying date, clutch size and nest density), these models were a poorer fit compared to the models with harvest rate.

A negative effect of the spring hunt on productivity of the Greater Snow Goose (*id est* the ratio juveniles/adults) in fall was nonetheless reported by Morrissette et al. (2010) over the period 1999-2007, though this effect was weak compared to the impact of climatic conditions on the breeding ground. Annual productivity is dependent upon several components, including breeding propensity, summer reproductive success conditional on breeding, and the survival of juveniles during the initial fall migration. Reed et al. (2004) provided evidence for a negative effect of spring hunt on breeding propensity during the first 3 years. In another study with a larger number of spring-hunt years, a negative effect of spring hunt on age at first reproduction was also detected (Chapter 4). In our study, nesting density, a surrogate of breeding propensity, was the only breeding parameter for which there was some uncertainty for a possible negative effect of the spring hunt. We therefore suggest that the reduction in productivity reported by Morrissette et al. (2010) may have been primarily driven by the decision to breed or not (i.e. recruitment probability and, possibly, breeding propensity). However, when females do commit themselves to reproduce, other breeding parameters (laying date and clutch size) appear to be little affected by carry over effects of the spring hunt. In our study, we did not consider other breeding parameters such as nesting success because this component is primarily driven by local predation pressure (Lecomte et al. 2008a) and there was no previous evidence of any carry over effects on such parameters.

Detecting the effects of environmental covariates on time series data often requires long term surveys. This is complicated by the fact that some factors, such as climatic conditions on the breeding ground, may have considerably more impact on reproductive parameter than our covariate of primary interest. It is always possible that we require more years of data with greater variation in harvest rate to detect the impact of these special conservation measures. One alternative to detect these effects is to use a finer scale and investigate the effect of covariates at the individual level instead of the population level. If we could use trajectories of individuals nesting in the colony over time, the degrees of freedom would be based on the number of trajectories instead of the number of years, thereby increasing considerably the power of the analysis. Nonetheless, our primary interest here was to assess the relative importance of special conservation measures and our results indicate that early reproductive parameters such as laying date and nest density are primarily determined by the climatic conditions met after departure from the spring staging areas and upon arrival to Bylot Island. Higher than average snow cover, colder than average temperatures and positive NAO values will likely delay laying date by delaying access to suitable nesting habitat and food (Gauthier 1993, Choiniere and Gauthier 1995, Crick and Sparks 1999, Both and Visser 2001, Sanz 2002).

Investigating potential carry over effects of the special conservation measures on snow goose reproduction was of primary interest in the context of adaptive management. The unprecedented decision of implementing a new hunt during the pre-breeding season, and preliminary assessment upon implementation indicated of a carry-over effect on most reproductive parameters via decreased body condition during migration. Based on a longer time series from 1999 to 2007 we were not able to detect evidence of an effect of special conservation measures on some of these reproductive parameters even in presence of a quantitative index of hunting pressure, the harvest rate. These results are a reminder that even if the impact of an effect is expected to be important, the effect needs to be assessed over a minimum amount of time in order to sufficiently separate this effect from potential confounding factors such as climate or other possible changes over time.

Table 3.1: Results of model selection on fixed components for laying date and clutch size. Only top models are presented ($\Delta AIC_c \leq 10$). Abbreviations: CI = Climatic Index, HR = Harvest Rate, BG = Breeding Ground, SS = Stopover Sites).

Fixed component											
Laying Date	Habitat	CI_BG	CI_SS	HR_SS	CI_SS × CI_BG	CI_BG x HR_SS	CI_SS × HR_SS	Rank (K)	ΔAIC_c	Weight (ΔAIC_c)	Cumulative weight
Laying date											
		X						6	0.00	0.97	0.97
		X		X				7	8.15	0.02	0.99
		X	X					7	9.53	0.01	0.99
	X	X						7	10.28	0.01	1.00
Clutch size											
X								6	0.00	0.80	0.80
X		X						7	3.03	0.18	0.98
X			X					7	8.97	0.01	0.99
X				X				7	10.07	0.01	0.99
X	X							7	10.22	0.00	1.00

Table 3.2: Results of model selection on fixed component for nest density. Only top models are presented (ΔAIC_c <10). Abbreviations: CI = Climatic Index, HR= Harvest Rate, BG=Breeding Ground, SS=Stopover Sites.

Fixed component									
Intercept	CI_BG	CI_SS	HR_SS	CI_SS × CI_BG	HR_SS × CI_BG	Rank (K)	ΔAIC_c	Weight (ΔAIC_c)	Cumulative weight
X	X					3	0.00	0.51	0.51
X						2	2.06	0.18	0.69
X	X		X			4	2.78	0.13	0.82
X	X	X				4	3.68	0.08	0.90
X			X			3	5.48	0.03	0.93
X		X				3	5.52	0.03	0.96
X	X	X	X			5	6.97	0.02	0.97
X	X		X		X	5	7.78	0.01	0.98
X	X	X		X		5	8.52	0.01	0.99
X		X	X			4	9.80	0.00	1.00

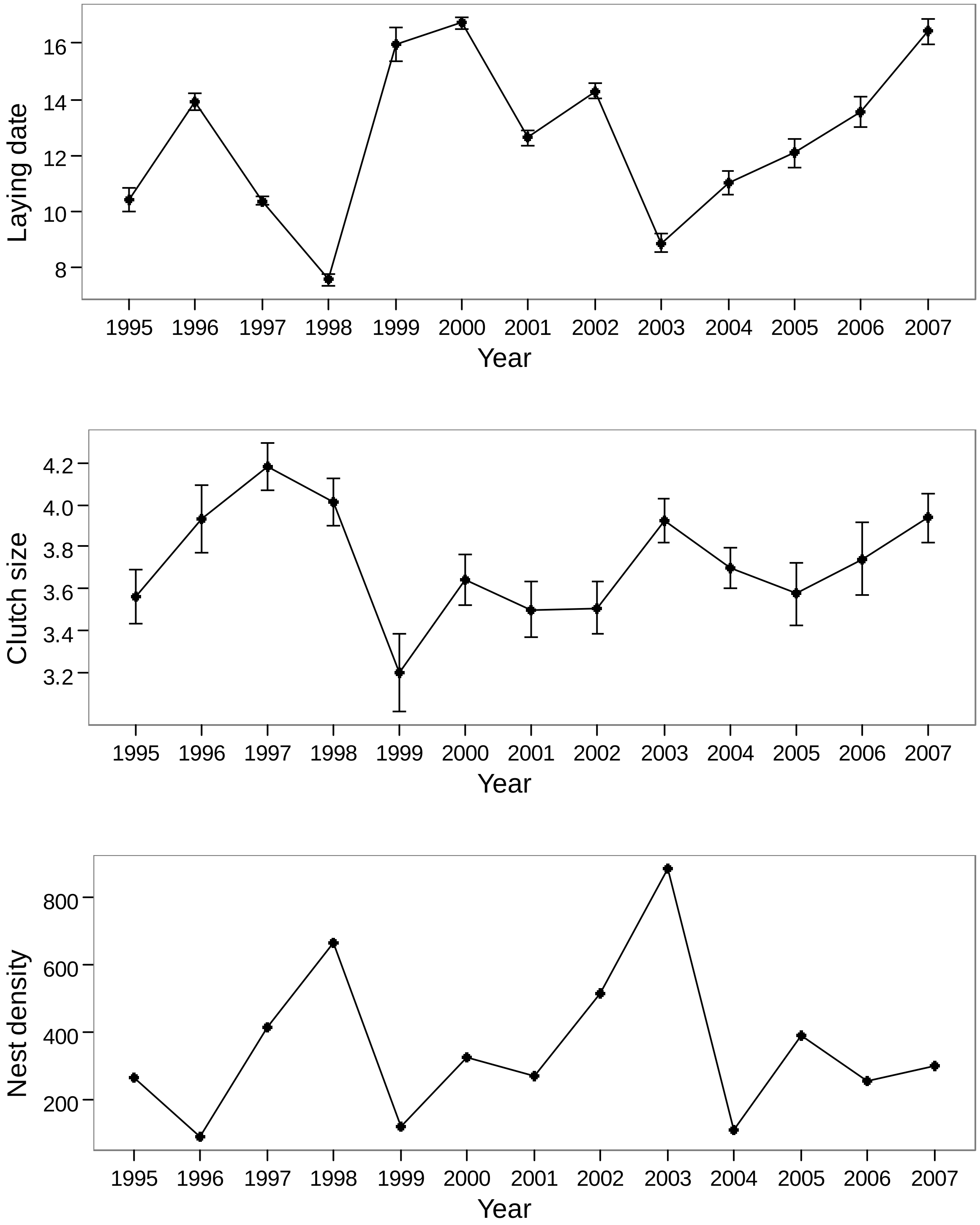

Figure 3.1: Time series of the three reproductive parameters of interest (for laying date and clutch size: mean ± confidence interval 95%). Laying date is given as the n^{th} day of June; Nest density is the number of nests/km².

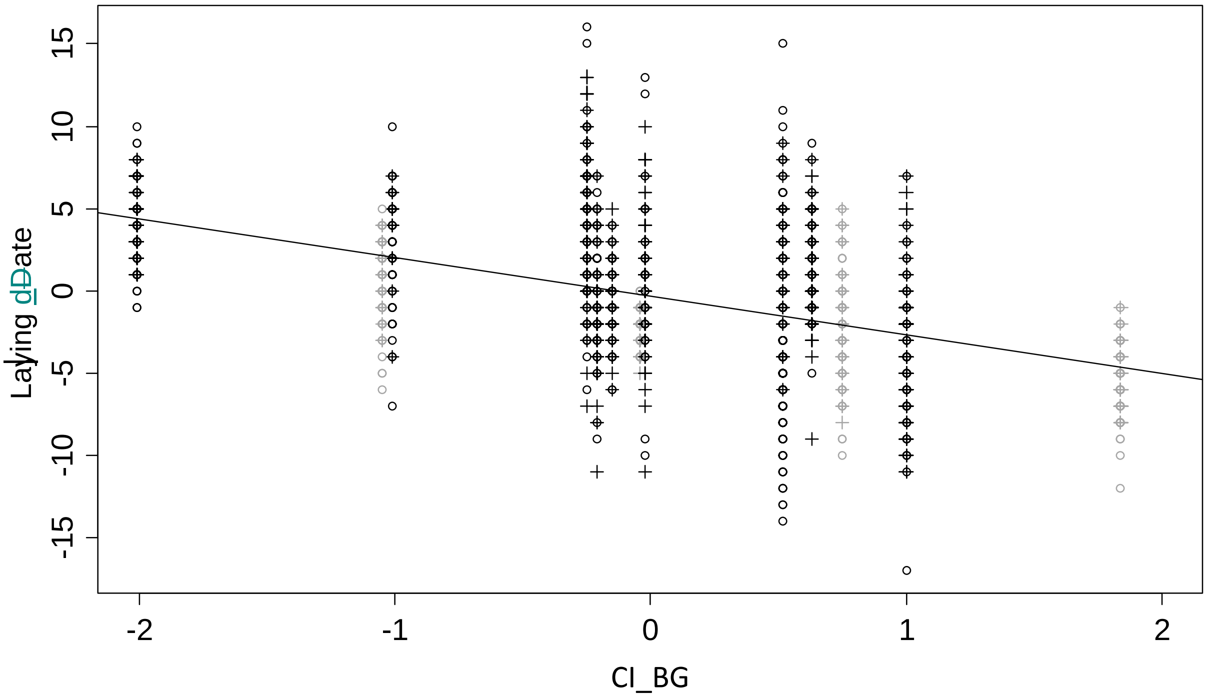

Figure 3.2: Relationship between laying date and the climatic index retained to describe the conditions experienced at arrival on the breeding ground (CI_BG) for the Greater Snow Goose population nesting on Bylot Island, NU, from 1995 to 2007 (in gray the years without special conservation measures). A positive value of CI_BG indicates a warmer daily mean temperature during the period May 20 to June 19 with a lower snow cover on June 5 than the mean over the years 1995-2007. We centred the laying date on the mean laying date observed over the period 1995-2007 (13 June). Legend: open circle = wet habitat, cross = dry habitat.

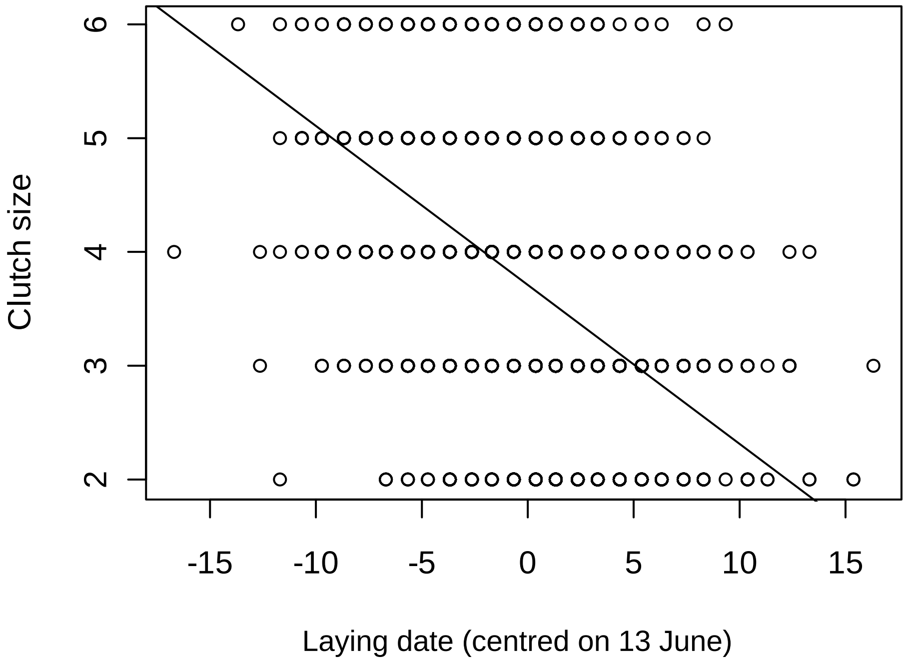

Figure 3.3: Relationship between clutch size and laying date for the Greater Snow Goose population nesting on Bylot Island, NU, from 1995 to 2007.

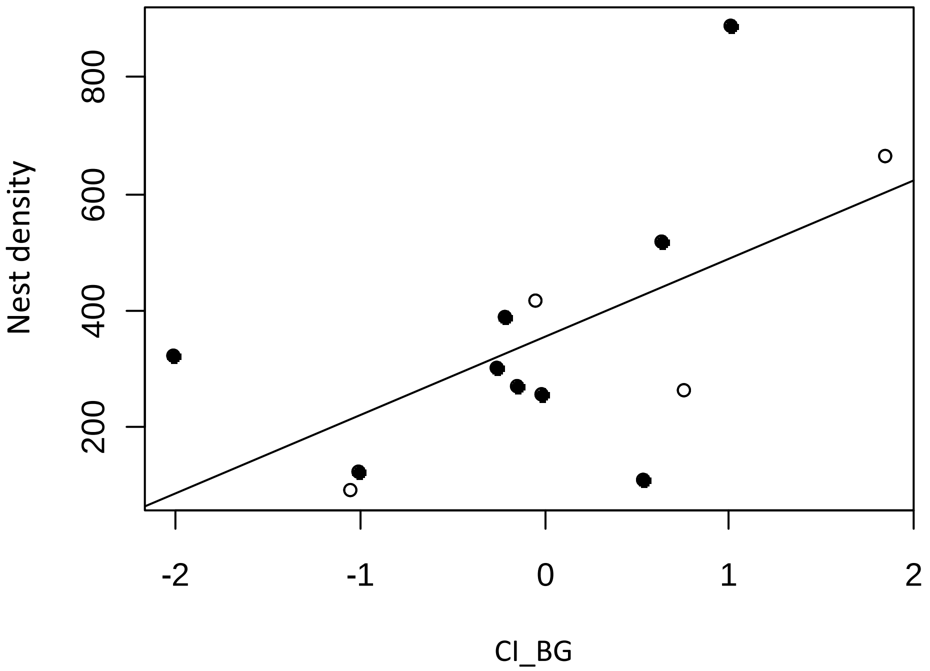

Figure 3.4: Relationship between nest density (nests/km²) and the climatic index retained to describe the conditions experienced at arrival on the breeding ground (CIBG) for the Greater Snow Goose population nesting on Bylot Island, NU, from 1995 to 2007. A positive value of CI_BG indicates a warmer daily mean temperature during the period 20 May to 19 June with a lower snow cover on 5 June than the mean over the years 1995-2007. Black dots indicate the years with spring hunt and white dots indicate the years without.

Supplemental materials

Table 3.3: Table of Pearson's correlation coefficients (rho) for environmental explanatory variables available for analyses. Climatic indices were obtained from Principal Component Analyses (Figures 3.6 and 3.7, Sup. Mat.). The p-value is indicated in parentheses (H0: rho = 0, α = 0.05). The P.ATI.SS and AT.SCI.BG indices correspond to the climatic indices on the stopover sites (CI_SS) and on the breeding ground (CI_BG) retained for the analyses.

	P.ATI.SS	**SCI.SS**	**NAO.SCI.SS**	**AT.SCI.BG**	**PI.BG**	**HR.SS**
P.ATI.SS Precipitation and Air Temperature Index, Stopover Sites	1.00	- -	- -	- -	- -	- -
SCI.SS Snow Cover Index, Stopover Sites	0.00 -	1.00	- -	- -	- -	- -
NAO.SCI.SS NAO and Snow Cover Index, Stopover Sites	0.00 -	0.00 -	1.00	- -	- -	- -
AT.SCI.BG Air Temperature and Snow Cover (June 5) Index, Breeding Ground	-0.20 (0.523)	0.39 (0.191)	-0.11 (0.720)	1.00	- -	- -
PI.BG Precipitation Index, Breeding Ground	0.09 (0.765)	-0.04 (0.905)	0.29 (0.333)	0.00 -	1.00	- -
HR.SS Harvest Rate, Stopover Sites	-0.12 (0.701)	-0.26 (0.392)	0.53 (0.061)	-0.38 (0.202)	0.44 (0.133)	1.00

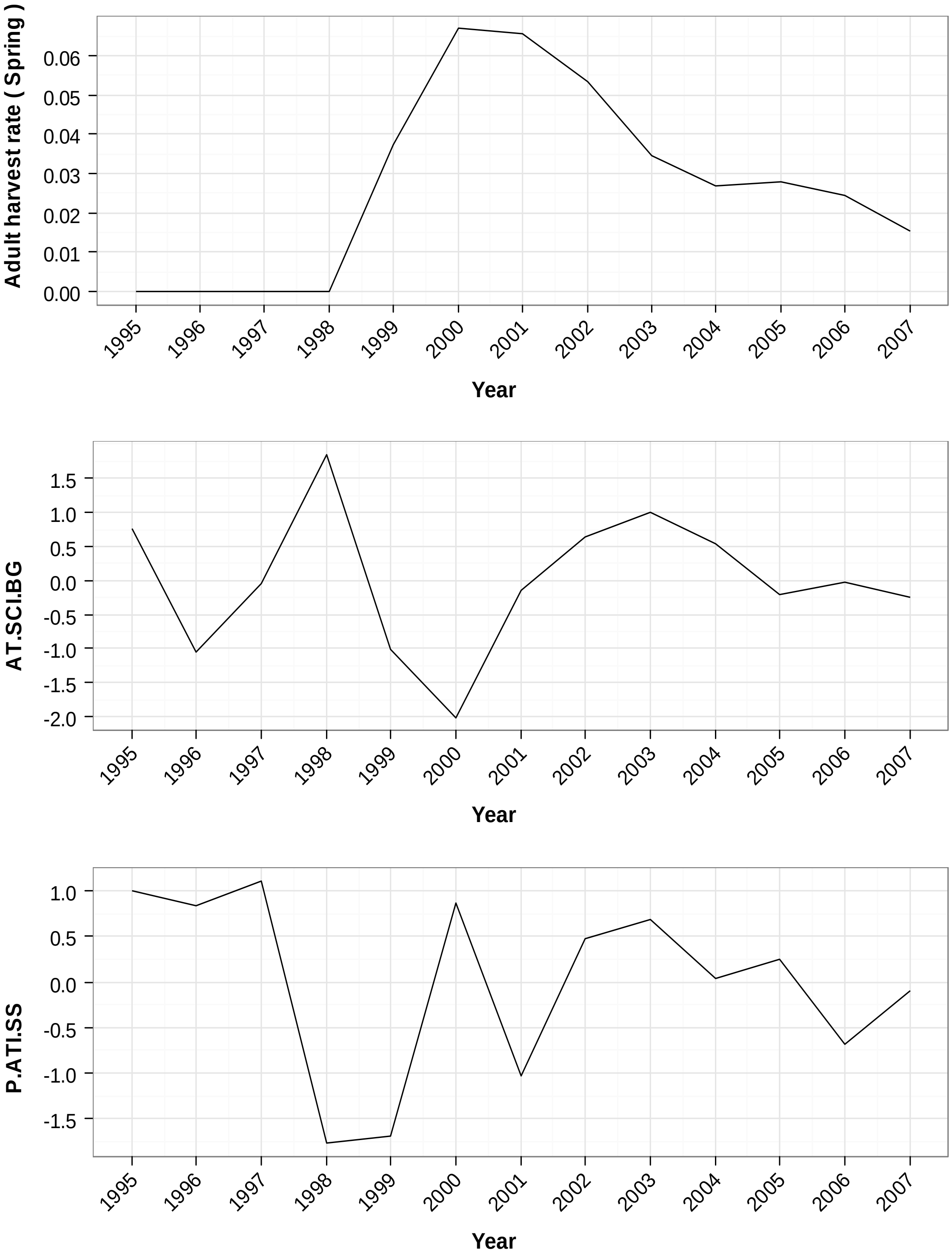

Figure 3.5 : Time series of the 3 explanatory variables retained in our analyses. Abbr.: AT.SCI.BG = Air Temperature and Snow Cover (June 5) Index on the Breeding Ground (noted CI_BG); P.ATI.SS = Precipitation and Air Temperature Index at Stopover Sites (noted CI_SS).

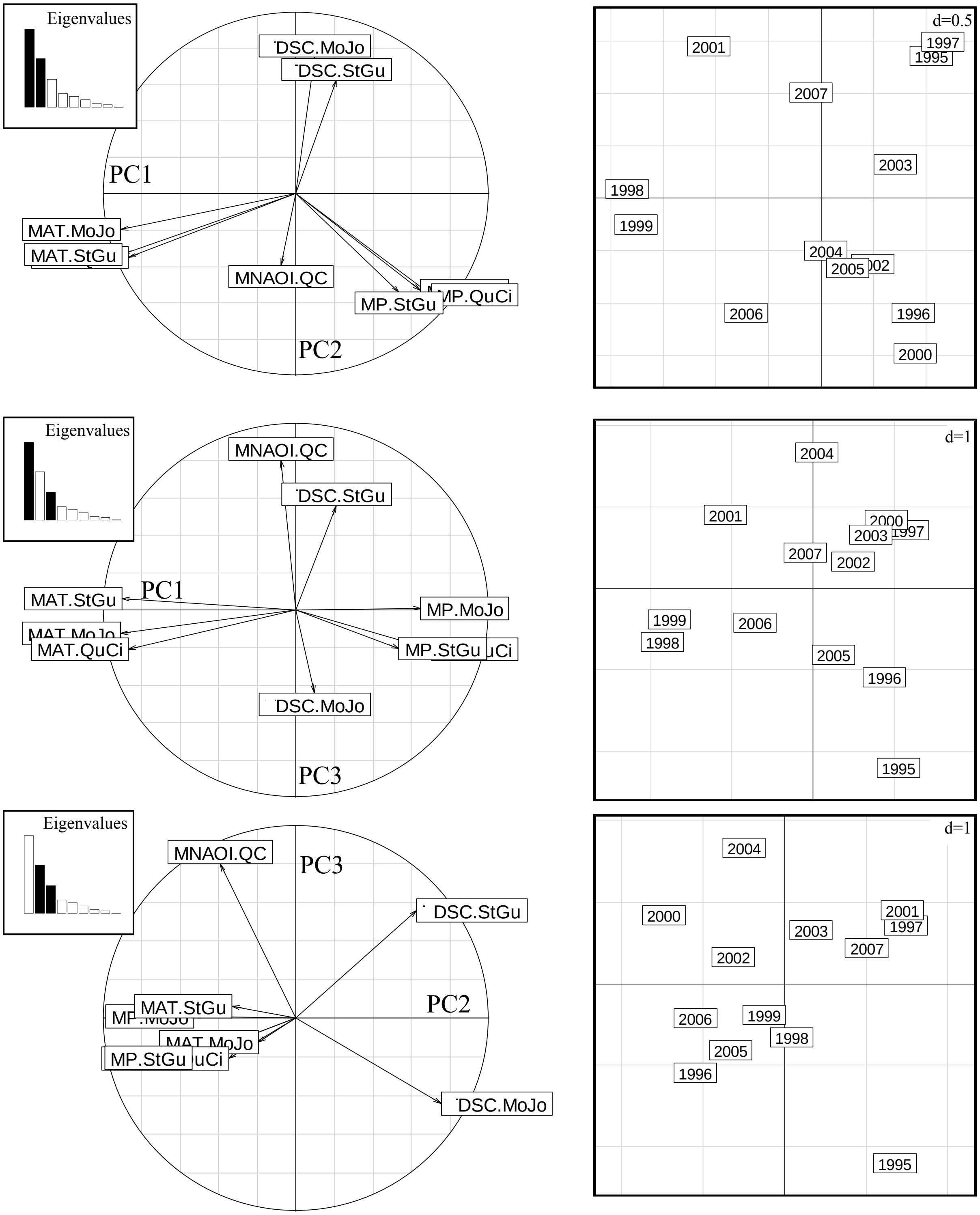
Eigenvalues
DSC.MoJo
DSC.StGu
PC1
MAT.MoJo
MAT.StGu
MNAOI.QC
MP.StGu
MP.QuCi
PC2
d=0.5
2001
1997
1995
2007
2003
1998
1999
2004
2005
2002
2006
1996
2000
Eigenvalues
MNAOI.QC
DSC.StGu
PC1
MAT.StGu
MP.MoJo
MAT.MoJo
MAT.QuCi
MP.StGu
MP.QuCi
DSC.MoJo
PC3
d=1
2004
2001
2000
2003
1997
2007
2002
1999
2006
1998
2005
1996
1995
Eigenvalues
MNAOI.QC
PC3
DSC.StGu
MAT.StGu
MP.MoJo
PC2
MAT.MoJo
MP.StGu
MAT.QuCi
DSC.MoJo
d=1
2004
2000
2003
2001
1997
2007
2002
2006
1999
1998
2005
1996
1995

Figure 3.6: Principal component analysis of all climatic variables relative to the staging period, from April 1 to May 19. The first three principal components explained 80% of the total variance (PC1 alone: 40%). Left: correlation circle; right: first plan (d = grid unit, number in boxes are years, axes cross at 0). Legend: DSC = number of Days with Snow Cover over the period, MAT = Mean Air Temperature, MNAOI = Mean NAO Index, MP = Mean Precipitations; QC = Québec City (QC), MoJo = Mont-Joli (QC), StGu = Saint Guillaume (QC).

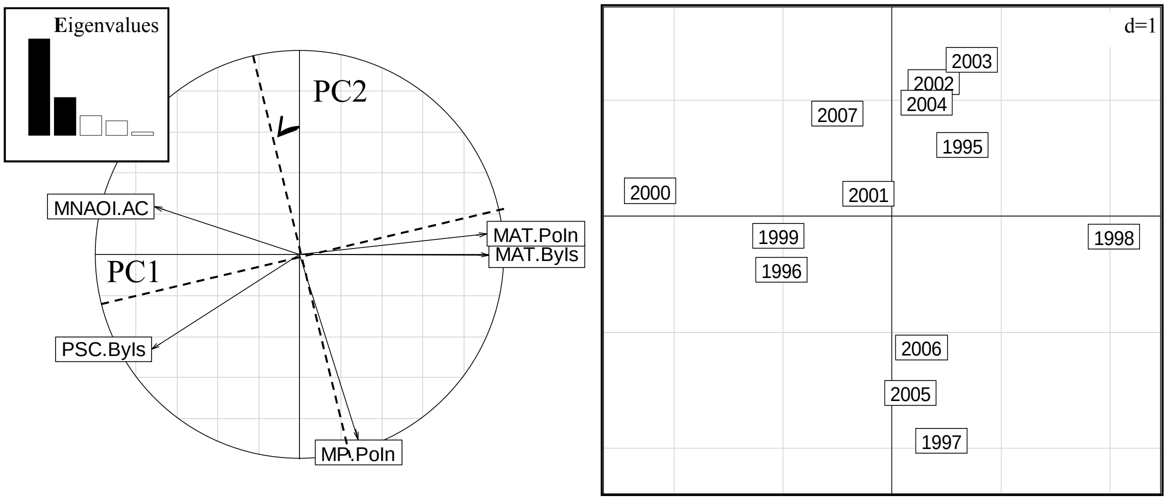

Figure 3.7: Principal component analysis of all climatic variables relative to the laying period, from May 20 to June 19. Left: correlation circle; right: space of the two principal axes (d = grid unit, number in boxes are years, axes cross at 0). The two main components retained explained 78% (PC1 alone after rotation: 38%) of the total variance. The dashed lines indicate the new relative position of the first 2 components after a 'varimax' rotation. Legend: MAT = Mean Air Temperature, MNAOI = Mean NAO Index, MP = Mean Precipitations, PSC = Percentage of Snow Cover (June 5); ByIs = Bylot Island (NU), PoIn = Pond Inlet (NU).

Chapitre 4
Carry-over effects of spring hunt and climate on recruitment to the natal colony in a migratory species.

C. Juillet, R. Choquet, R. Pradel and G. Gauthier

Résumé

Chez les espèces longévives, l'âge à la première reproduction peut varier considérablement au fil du temps, et est susceptible d'affecter le taux de croissance d'une population. Alors que la chasse, comme outil de gestion, devrait contrôler la taille de la population via une diminution de la survie, elle peut aussi agir en affectant le recrutement. Afin de contrôler la taille de la population de la Grande Oie des neiges (*Chen caerulescens atlantica*), une espèce surabondante nichant dans l'Arctique, une saison de chasse printanière a été mise en œuvre durant la halte migratoire à partir de 1999 en plus des saisons régulières de chasse à l’automne et à l'hiver. Nous avons étudié si la chasse printanière pouvait avoir un effet reporté sur le recrutement des femelles à leur colonie natale sur l'île Bylot, Nunavut, Canada, de 1992 à 2005. Nous avons également tenu compte de facteurs confondants potentiels, principalement des effets climatiques. Nous avons appliqué un modèle de recrutement multi-état de capture-marquage-recapture à un ensemble de données à long terme d’individus d'âge connu, combinant recaptures vivantes à la colonie de reproduction et récupérations des individus morts par les chasseurs. La variation annuelle dans les probabilités de recrutement a été mieux expliquée par un modèle incluant à la fois la chasse de printemps et une variable synthétique combinant les conditions climatiques lors de la migration (valeurs extrêmes de l'indice NAO régionale) et à l'arrivée à l'aire de reproduction (la couverture de neige). Ce modèle a expliqué 58% de la variation temporelle du recrutement, tandis que le taux de récolte à la chasse ou l'indice climatique pris seuls représentaient chacun 38%. Dans l'année où la pression de chasse au printemps a été maximale (taux de récolte des adultes autour de 6%), le recrutement a été réduit de près de 50% par rapport aux années sans chasse et présentant des conditions climatiques autour de la moyenne. L'effet est probablement dû à un effet reporté du dérangement causé par la chasse de printemps, dont on a déjà démontré l’effet néfaste sur la condition physique pré-reproductrice des oies. Nous concluons qu'il y a eu un effet considérable de la chasse de printemps sur le recrutement dans les Grandes Oies des neiges, qui s'ajoute à l'effet de conditions climatiques.

Abstract

In long-lived species, age at first reproduction may vary greatly over time, potentially affecting the growth rate of a population. While hunting, as a management tool, is generally expected to control population size via a decrease in survival, it may also act by affecting recruitment. In order to control the population size of the Greater Snow Goose (*Chen caerulescens atlantica*), an overabundant arctic-nesting species, a spring hunting season was implemented on the migratory staging area from 1999 onwards in addition to the regular fall and winter hunting seasons. We investigated the potential carry-over effect of spring hunting on recruitment of females to their natal colony on Bylot Island, Nunavut, Canada from 1992 to 2005 while accounting for other potential confounding factors, primarily climatic effects. We applied a multistate capture-mark-recapture recruitment model to a long-term dataset of known-age individuals, combining live recaptures at the breeding colony with dead recoveries from hunters. Annual variation in recruitment probabilities was best explained by a model including both spring hunt and a synthetic variable combining climatic conditions experienced during migration (extreme values of the regional NAO index) and upon arrival to the breeding grounds (snow cover). This model accounted for 58% of the temporal variation in recruitment, while the harvest rate or the climatic index taken alone accounted for 38% each. In the year with the highest spring hunting pressure (adult harvest rate around 6%), recruitment was reduced by up to 50% compared to years with no hunt and similar average climatic conditions. The effect is likely a carry-over effect of the disturbance caused by the spring hunt, which was previously shown to decrease the pre-breeding body condition of geese. We conclude that there was a considerable effect of the spring hunt on recruitment in Greater Snow Geese, which is additive to the effect of climatic conditions.

Introduction

In long-lived species with delayed maturity, recruitment into the breeding segment of the population is an important determinant of population growth (Cooch et al. 2001) because adult survival, which is theoretically most influential, exhibits a low temporal variability (Gaillard and Yoccoz 2003). Determining factors affecting age at first reproduction is thus critical to the understanding of population dynamics and for the management of wildlife populations. Recruitment is expected to be affected by both environmental factors and density-dependent effects (Gaillard et al. 1998). Anthropogenic perturbations such as harvest can be considered particularly severe environmental factors susceptible to significantly affect recruitment (Boyce et al. 2006, Schmutz 2009). However, few studies have examined the impact of hunting on recruitment in comparison to other vital rates like survival (Ward et al. 1997, Gauthier et al. 2001, Frederiksen et al. 2004). Long term studies based on the monitoring of marked individuals are ideally suited to examine this question and to reliably test biological hypotheses regarding factors affecting recruitment (Lebreton et al. 1992, Lebreton et al. 1993, Gaillard et al. 1998, Conroy 2009), especially when one can contrast different regimes of hunting following a change in hunting regulations.

In North America, several goose populations like the Greater Snow Goose (*Chen caerulescens atlantica*) are now considered overabundant because the exponential growth of their populations, linked to changes in agricultural practices during the second half of the 20th century (Gauthier et al. 2005), now threaten their natural habitats. Therefore, managers have decided to introduce special measures to stop the growth of the entire population (Batt 1998). Exceptional conservation measures, which involved a radical change in harvest strategy at the scale of the entire population, were implemented in Canada to stabilize the abundance of the Greater Snow Goose population. Bag-limits and season length were increased and hunting practices were liberalized, but the most spectacular action was the introduction of a special spring conservation harvest (hunt) during the migratory stopover in Québec, Canada, beginning in 1999. These special conservation measures are equivalent to a quasi-experiment (Williams et al. 2002) with the period before 1999 acting as the control and the period from 1999 onwards as the treatment, thereby providing an excellent opportunity to assess the effect of the new spring hunt on recruitment.

Previous studies have shown that the spring hunt had a negative impact on body condition of females upon departure from the staging ground for the Arctic (Mainguy et al. 2002, Féret et al. 2003). Because body condition is an important determinant of reproductive success in geese, including Greater Snow Geese (Bêty et al. 2003, Gauthier et al. 2003), we hypothesized that recruitment should be negatively affected by the spring hunt via a carry-over effect (Norris and Taylor 2006). Since we relied on a pseudo-experiment, *id est* in an uncontrolled environment, we had to consider other potentially confounding factors such as climate. Climatic factors may have a strong impact on many vital rates in vertebrates (Barbraud and Weimerskirch 2001, Ferguson et al. 2005, McMahon and Burton 2005), and this is especially true in arctic-nesting geese where either conditions encountered upon arrival in the Arctic or during spring migration (through a carry-over effect) may have a strong effect on reproduction (Skinner et al. 1998, Madsen et al. 2007, Dickey et al. 2008, Morrissette et al. 2010). Cyclic lemming populations, which are related to predation pressure on the arctic-nesting ground, are another potentially confounding factor. Reed et al. (2003c) showed that recruitment in Greater Snow Geese was reduced in years that lemming populations crashed in the Arctic because predation pressure on goose nests was much higher in those years due to prey switching by predators.

We examined recruitment in Greater Snow Geese using a capture-mark-recapture (CMR) model (Crespin et al. 2006, Votier et al. 2008) where the age-dependent probability of recruitment is estimated from females recaptured at least once as a breeder, hence conditional upon survival. We further used a mixture of information from live recaptures and dead recoveries from hunting (Henaux et al. 2007b), which allowed us to distinguish between permanent emigration and mortality. In a system such as ours where females are philopatric, recruitment is equivalent to the probability for a female born in a colony to return and to breed at her natal colony. In order to assess the effect of the spring hunt on the age-specific recruitment probabilities via a carry-over effect, we used a multiple inference framework (Anderson 2008). This allowed us to account for possible alternative climatic and ecological effects such as weather conditions experienced during migration and upon arrival to the breeding grounds and predation pressure experienced during breeding.

Material and methods

Study species and data collection

The Greater Snow Goose is a monogamous, migratory species wintering on the Eastern coast of the U.S.A. and breeding in the Canadian High Arctic. During migration, the population uses the Saint Lawrence River Valley in Québec, Canada, as a major stopover area during 6 to 8 weeks in spring and fall. All data presented in this paper originated from a long term marking study covering the period 1990 to 2005. Captures and marking occurred annually at the breeding colony on Bylot Island, Nunavut, Canada (73°N, 80°W). Several mass banding sessions were conducted at this location during a seven-day period in early August near the end of the brood rearing period. Adult geese, accompanied by their offspring of the year, are moulting and are thus flightless (Gauthier et al. 2001). Adults captured were primarily successful breeders because individuals that lose their nest before hatch leave the study site to moult and thus are not available for capture at the end of the summer (Reed et al. 2003a). Because philopatry is high but female-biased in this species (Reed et al. 2003c, Lecomte et al. 2008b), only females are considered in the analyses.

All birds were sexed by cloacal eversion and newly captured birds received an US Fish & Wildlife Service (USFWS) metal band. Goslings marked in a given summer were, by definition, of known age (n = 12 100) but all adults marked were of unknown age (≥ 2 year old). In addition, two thirds of the adult females were randomly selected and fitted with a plastic neck-band. Because plastic neckbands may affect breeding propensity (Reed et al. 2005), we only used non-collared adults in our analyses (n = 2 792). All young females receiving a collar at a subsequent recapture occasion were censored at this occasion.

Metal band recoveries of females considered in this study were reported by hunters to the Bird Banding Office of the US Fish and Wildlife Service/Canadian Wildlife Service (CWS), from which we retrieved the information (1 228 banded as juveniles and 302 as adults). The traditional hunting season occurs in fall in Québec, from fall to late winter in the USA and a light harvest by Native hunters occurs in the Arctic during the summer. Since 1999, the special spring hunting season was also introduced in Québec in April and May.

Multistate recruitment model

We used a multistate CMR recruitment model (Lebreton et al. 2003) with a mixture of live recaptures on Bylot Island and dead recoveries. In addition to individuals marked as juveniles (known age), we used individuals marked as adults (unknown age) to improve estimation of parameters other than recruitment. In this model, recruitment is defined as an age-dependent probability to move from the state ‘non-breeder’ to the state ‘breeder’, conditional upon survival (Henaux et al. 2007b).

In our multistate approach, individuals can move among 4 states, *alive and non-breeder* (NB; coded 1 in encounter histories), *alive and breeder* (B; coded 2), *newly dead* (ND; coded 3) and *dead* (†; coded 0). The difference between the states ‘newly dead’ and ‘dead’ stems from the fact that individuals can be retrieved the year they die (newly dead) through hunter’s recoveries but not afterwards (dead state). Individuals banded as goslings are coded 1 in encounter histories on that occasion and may be recaptured breeder (code 2) in the natal colony from age 2 and up (snow geese never breed at 1 year of age). Using dead recoveries allowed estimating real survival probability by separating permanent emigration from the breeding colony and mortality. Indeed, individuals of all ages can be hunted during the non-breeding season and hence be detected even if they did not recruit in the natal colony. Individuals recovered during the interval from occasion t to t+1 are newly dead at occasion t+1 (code 3).

We defined the matrix of transition Φ_t between states from t-1 to t where $S_{i,j}^{(t)}$ is the probability of survival from time t-1 in state i to time t in the state j; and $b^{(a_l,t)}$ is the probability of recruitment in the natal colony at age a_l (l being a given age class) during the interval t-1 to t conditional on survival. We defined the encounter vector E_t at time t where $p_B^{(t)}$is the probability of capture as breeder at time t; and $r^{(t)}$, is the probability of recovery from hunting conditional upon death (i.e. probability that an individual dies from hunting and that its band is reported) over the interval t-1 to t.

$$\Phi_t = \begin{bmatrix} S_{NB}^{(t)}.\left(1 - b^{(a_l,t)}\right) & S_{NB}^{(t)}.b^{(a_l,t)} & 1 - S & 0 \\ 0 & S_B^{(t)} & 1 - S_B^{(t)} & 0 \\ 0 & 0 & 0 & 1 \\ 0 & 0 & 0 & 1 \end{bmatrix}_t , \quad E_t = \begin{bmatrix} 0 \\ p_B^{(t)} \\ r^{(t)} \\ 0 \end{bmatrix}_t$$

Note that the transition from breeder to non-breeder is not allowed. Contrary to Reed, Gauthier et al. (2003c), we did not constrain an age of full breeding, allowing that some individuals never recruit, which is more realistic.

Goodness of fit tests

We applied *Goodness-of-fit* (GOF) tests on breeders only because such tests cannot be performed on the non-breeding segment (Crespin et al. 2006). We used the program U-CARE (version 2.3), which allows the inclusion of observable absorbing states (state newly-dead here) when data include a mixture of live and dead encounters (Choquet et al. 2009a). It performs the GOF tests for the full time-dependent model (Pradel et al. 2003).

Modeling of transition and encounter probabilities

We applied an age effect on survival by defining 3 age classes: juveniles (age 0-1), sub-adults (age 1-2) and adults (age ≥ 2). Survival is known to be lower for juveniles than for adults and we added a third age class (sub-adult) to allow for a progressive increase in survival (Francis et al. 1992). Based on preliminary analyses, we retained 4 age classes on probabilities of access to first reproduction (1, 2, 3, 4+ years old) and access at age 1 was fixed to 0. We distinguished live capture probabilities of individuals banded as goslings from those banded as adults. This allowed us to take into consideration the effect of philopatry because individuals banded as adults would be a mixture of immigrant and native birds (immigrants may be less faithful to the colony) and to account for any potential differences in the probability of detection due to breeding experience. This effect of age at banding was noted as '*gp*'. We defined 2 age classes for the probability of recovery by contrasting juveniles from the others because juveniles, due to lack of experience, are more susceptible to be killed by hunters than adults (Calvert et al. 2005). Finally, we considered temporal variability in the four kinds of parameters (survival, recruitment, recapture and recovery probabilities).

Covariates

We considered 5 covariates (Figure 4.1) that could explain temporal variation in recruitment rate. All covariates were computed for the period 1992 to 2005 because recruitment of the first banded cohort does not start before 1992. As an index of spring hunting pressure, we used the ratio of the estimated number of adult geese killed by hunters in Québec (from survey conducted by CWS among all registered hunters) to the estimated size of the population in spring of the previous year (from an aerial photo survey conducted by CWS every spring). By using the previous year population size, we considered only individuals which were susceptible to reproduce (because young born in the previous summer were excluded). We used a visual estimate of the snow cover taken annually on 5 June in the Qarlikturvik Valley of Bylot Island as an index of local environmental conditions at the breeding site (Reed et al. 2003c). This date is one week before the average date of peak egg-laying at the Bylot Island colony (Cadieux et al. 2008). To account for climatic conditions experienced during spring migration, we used a global climatic index, the North Atlantic Oscillation (NAO). This was preferred over local climatic data because the spring migration (including the staging period in Québec) covers a large geographical range (>3000 km). We computed a mean daily NAO index for the period 21 March to 20 May (http://www.nws.noaa.gov). This period covers the stopover along the Saint Lawrence River, where most of the fat accumulation takes place (Gauthier et al. 1992). We also computed a quadratic term for the NAO index to dissociate years with extremes values of NAO from years of intermediate values. The arctic fox is the main predator of Snow Goose eggs and levels of predation by arctic fox increase when lemmings (preferred prey) are absent (Bêty et al. 2002). We used a measure of predation pressure that took the value 1 in years of high lemming abundance (1993, 1996, 2000, 2004), -1 in years of lemming population crash (1995, 1999, 2002, 2003, 2005), and 0 the remaining years. We used data from a long term monitoring program conducted on Bylot Island, Nu to establish the level of lemming abundance (Gruyer et al. 2008).

To solve the problem of interdependence between temporal covariates in model selection, or multi-colinearity (Graham 2003), we used a principal component analysis (PCA) approach to create uncorrelated synthetic covariates (Jolliffe 2002, Grosbois et al. 2008). This method is also efficient in preventing multiplication of covariates used in analyses. To produce biologically interpretable synthetic covariates, we applied an orthogonal rotation method (varimax) on the principal components (Jolliffe 2002) using packages ‘psych’ in program R (Revelle 2010). We used the ANODEV approach (Skalski et al. 1993, Grosbois et al. 2008) to estimate the proportion of the variability explained by our synthetic covariates in the recruitment parameters. All CMR models were fitted using the E-SURGE program (v1.4.6) and we used the model notation from Choquet et al. (2009b). Model selection was based on Akaike Information Criterion corrected for overdispersion and sample size (QAICc) (Burnham and Anderson 2002).

Results

Fit of the model

The GOF tests of the global model for the two subsets of data (Table 4.3, Supplemental Material) indicated a slight overdispersion in both groups (breeders banded as adults: $\chi^2 = 240.1$, d.f. = 183, $P<0.01$; breeders banded as goslings, $\chi^2 = 54.3$, d.f. = 40, $P = 0.07$). The most significant deviation was found for breeders banded as adults in the subcomponent testing for trap-dependence (M.ITEC; overdispersion coefficient, $\hat{c}$=1.94). A detailed examination of the contingency tables did not allow for a clear biological interpretation. Considering that the overall coefficients of overdispersion were low in both groups ($\hat{c}$ of 1.31 and 1.36, respectively), we chose the highest of these two values for the model selection procedure.

Analysis of temporal covariates

We retained the first three rotated principal components from the PCA on our covariates dataset (eigenvalues >1, 84% of the global variation explained; Table 4.1 and Figure 4.4, Sup. Mat.). Spring NAO index and lemming abundance indices contributed the most to the first factor and were positively correlated with this factor (loading of 0.87 and 0.75 respectively), which accounted for 29 % of the global variation among covariates. Snow cover and quadratic spring NAO index were the two covariates loading the most on the second axis (0.90 and 0.74), which also explained 29 % of total variation. Finally, only adult spring harvest rate had a high loading on the third factor (0.98), which explained 26% of the global variation. Hence, we considered Factor 1 as a mixed spring climate/predation pressure index characterized by the NAO (high value indicative of cold spring temperature) and lemming abundance (high value indicative of low predation pressure on goose nests) and this factor was noted 'NAO/lemming'. Factor 2 was considered an index of poor climatic conditions, i.e. high snow cover at arrival upon the breeding ground and extreme NAO values during spring migration (NAO^2) and was noted 'snow/NAO^2'. The relationship between snow cover and NAO^2 was mostly driven by one year, 1992 (Figure 4.4, Sup. Mat.), and thus we interpreted Factor 2 primarily as a snow cover index at the breeding colony. Because Factor 3 was correlated at 0.98 with spring harvest rate of adults, and this was our covariate of main interest, we opted to use the original values of harvest rate in our analysis instead of the synthetic values of Factor 3. This procedure did not affect the results and interpretation of our model selection.

Effects of temporal covariates on recruitment

The best fitting model was $S_{a3+time}\, b_{a4+harvest\ rate+snow/NAO^2}\, p_{gp+time}\, r_{a2+time}$ (Table 4.2). In this model, recruitment was dependent upon age until 4 years of age, and included an additive negative effect of spring hunt and climatic conditions (snow cover/NAO^2 index) (slopes [95% Confidence Interval]: $\beta_{harvest\ rate}$ = -14.0 [-30.9, 2.9], β_{snow/NAO^2} = -0.58 [-1.17, 0.09] Figure 4.2). The combined additive effects of harvest rate and snow/NAO^2 explained 58% (ANODEV, $F_{2,11}$=8.07, P<0.01) of the temporal variability in the age-dependent probability of recruitment. The models where recruitment was affected only by harvest rate (ΔQAICc = 1.24, $\beta_{harvest\ rate}$ = -17.6 [-34.2, -1.0]), or only by the snow/NAO^2 index (ΔQAICc = 1.26, β_{snow/NAO^2} = -0.67 [-1.26, -0.09]), fitted the data less well. When considered alone, these covariates each explained 38% ($F_{1,12}$ = 3.37, P = 0.09 and $F_{1,12}$ = 3.36, P = 0.09 respectively) of the temporal variability. There was considerably less support for the model that included only the NAO/lemming index (ΔQAICc = 5.97, $\beta_{NAO/lemming}$= 0.23 [-0.21,0.66]) and this factor, which combined climatic conditions during migration and predation pressure at the colony, explained only 7% (ANODEV, $F_{1,12}$=0.41, P=0.53) of the temporal variability in recruitment probability. Models with either an additive effect of harvest rate and NAO/lemming (ΔQAICc = 0.39) or snow/NAO^2 and NAO/lemming (ΔQAICc = 1.42) were competitive but did not improve the fit to our data.

According to our best model, probability of recruitment was maximal at the age of 3 ($\bar{b}$ = 0.44, range: 0.24 to 0.72), lowest at 2 ($\bar{b}$ = 0.11; range: 0.03 to 0.27) and intermediate for individuals of 4 years of age and more ($\bar{b}$ = 0.20, range: 0.09 to 0.34; Figure 4.3).

Recruitment probability was inversely related to Adult harvest rate and snow cover/NAO^2 index (Figure 4.1), which indicates that recruitment was reduced during years of increased hunting pressure due to the special conservation hunt, and was also reduced in years of late snow-melt at the colony and poor weather conditions during migration (extreme NAO values).

Survival and encounter probabilities

Survival probabilities of adults were high, and above 0.8 in most years ($\bar{S} = 0.86$, range: 0.72 to 0.94, Figure 4.5, Sup. Mat.). Survival of juveniles was roughly half that of adult birds and showed considerable annual variability ($\bar{S} = 0.36$, range: 0.16 to 0.56). Survival of birds in their second year was much higher ($\bar{S} = 0.79$, range: 0.62 to 0.91) but still slightly lower ($\approx$ 8%) than that of older individuals. Capture probabilities on the breeding ground were slightly higher for female breeders banded as goslings ($\bar{p} = 0.07$, range: 0.02 to 0.12) than for those banded as adults ($\bar{p} = 0.06$, range: 0.02 to 0.09; Figure 4.6, Sup. Mat.). Finally, probability of band recovery conditional upon death was lower for juveniles ($\bar{r} = 0.10$) than for adults ($\bar{r} = 0.25$) and both presented large temporal variability (range: 0.02 to 0.21 and 0.02 to 0.44, respectively; Figure 4.7, Sup. Mat.).

Discussion

The special conservation measures originally introduced to decrease adult survival of the burgeoning Greater Snow Goose population also appear to have a major effect on age-specific recruitment probabilities. When controlling for climatic conditions, we detected a negative carry-over effect of the special conservation hunt occurring during spring staging on the probability of recruitment into the breeding population of females. As expected, climatic conditions also appeared to be an important determinant of accession to breeding status at the natal colony as recruitment probabilities decreased in years with a high snow cover at arrival on the breeding grounds and/or extreme regional climatic indices (NAO) during spring migration.

Special conservation hunt

The introduction of a special conservation hunt on the spring staging area of Greater Snow Geese was part of a large scale management strategy aimed at stopping the growth of the population. Previous studies showed that hunting had considerable impacts on several aspects of snow goose behaviour and life history traits other than just survival. Disturbance of geese due to spring hunting affected the distribution of the birds, increased the time spent flying, decreased feeding time and ultimately reduced the accumulation of body reserves in the first few years following implementation of the hunt (Féret et al. 2003, Béchet et al. 2004a). Reductions in body condition during spring has led to carry-over effects on reproduction of geese in the Arctic; breeding propensity was reduced, laying was delayed, clutch size was reduced and ultimately breeding productivity depressed (Mainguy et al. 2002, Bêty et al. 2003, Reed et al. 2004, Morrissette et al. 2010). Previous studies examining the impact of this spring hunt on reproduction simply contrasted years before *vs.* after the implementation of the spring hunt, limiting the ability to make strong inference about the effect of hunt. Here we used a more refined approach by using a continuous response variable (adult harvest rate) in our analysis, which decreased the likelihood of confounding the effect of hunt with other covariates that could have increased over time.

Our analysis provided strong evidence that the probability of recruitment of females is another life-history trait that was reduced by hunting activity in spring. These results are in accordance with previously documented effects of the spring hunt on goose reproduction. Our multiple inference approach allowed us to assess the relative importance of our covariate of interest among all the a priori identified potential effects. The special conservation harvest appeared to be the most important factor affecting recruitment over the period 1992-2005 followed by the climatic covariate indicative of poor conditions during migration and upon arrival to the breeding grounds. That there appears to be carry-over effects on recruitment from both increased harvest and poor climatic conditions during migration as well as an effect of local conditions at arrival to the breeding colony reflects well the mixed capital/income reproductive strategy of the Greater Snow Goose. As mixed capital/income breeders, snow geese depend upon resources acquired both at stopover sites and on the breeding grounds to produce their clutch (Gauthier et al. 2003). In contrast to climatic processes, which can affect resource acquisition at both the staging and breeding sites, hunting, which is more limited in time and space, likely affected resource acquisition at the stopover sites via disturbance, thereby reducing body condition (Féret et al. 2003, Béchet et al. 2004a). Because immature birds are mostly young and relatively inexperienced individuals, they may be more sensitive to factors negatively affecting body conditions than more experienced birds, and thus it is not surprising that their probability of recruitment was reduced.

Although survival was not the focus of our analysis, we noted a decrease in annual survival probability starting in 1999, *i.e.* at the time when conservation measures were put into effect. This is consistent with other studies investigating the effects of hunt on survival in Greater Snow Geese (Calvert and Gauthier 2005, Chapters 1 and 2)

Because all recoveries come from shot birds, we would have expected to recover more juveniles than adults since they are considered to be more susceptible to be killed due to a lack of experience (Calvert et al. 2005). Surprisingly, we found that recovery rates were lower in juveniles. This cannot be explained by differences in survival between the two groups because recovery rate was conditional upon death. A possibility may be that the primary causes of mortality differ between adults and juveniles. If the probability of dying from natural causes rather than from hunting is higher in juveniles than in adults, the reduced probability of dying from hunting could decrease the chance of being recovered. A large proportion of juveniles die from natural causes during the fall migration, before hunting takes place (Menu et al. 2005) . Another possibility is that a higher proportion of young are shot in the fall in Québec than in winter in the United States (Calvert and Gauthier 2005) and Québec hunters seem to have a lower probability of reporting bands than US hunters (Calvert et al. 2005, Zimmerman et al. 2009).

Climatic effects

It is well known that climatic conditions at the onset of the breeding season have a strong effect on the phenology and reproductive success of arctic-nesting geese (Skinner et al. 1998, Madsen et al. 2007, Dickey et al. 2008, Morrissette et al. 2010). Cool springs with late snow-melt delay laying date, reduce clutch size and depress the breeding propensity of experienced breeders (Reed et al. 2004, Dickey et al. 2008). Our results show that high snow cover at arrival on the breeding grounds also has a strong negative effect on the probability of recruitment of young females. As we argued above, young, inexperienced breeders are also likely to be the first affected by harsh environmental conditions at the onset of reproduction. A delayed snow-melt reduces habitat availability both in terms of nest site and feeding opportunities. Because of their mixed capital/income breeding strategy (Gauthier et al. 2003), the acquisition of nutrients via feeding on snow-free patches during the pre-laying period is essential for clutch completion in Greater Snow Geese (Bêty et al. 2003). This situation is analogous to the situation of the North American mallard (*Anas platyrhinchos*) where recruitment is strongly affected by the availability of ponds, a critical habitat for this species, which can fluctuate drastically in response to wet/dry cycles on the prairies (Dzus and Clark 1998).

Our results indicate that recruitment was nil in 1992. This event, occurring at the beginning of our study, could appear as an outlier, especially because only one cohort is concerned. Values of the quadratic spring NAO index and the snow cover were highest in 1992. This year was documented as being catastrophic for bird reproduction across the Arctic and was related to a volcanic eruption which cooled the climate globally (Ganter and Boyd 2000). Such an exceptional event could explain why extreme NAO values were more strongly linked to recruitment probabilities than the NAO value itself. In contrast, when conditions are favourable (e.g. very early snow-melt as in 1993 and 1994), recruitment probability can be very high, leading to strong cohort effects.

Recruitment is a 3-step process conditional upon survival: (1) pairing, (2) fidelity to the natal site, or philopatry, and (3) laying a clutch. In our case, the detection of breeders required a fourth step, successful hatching of a clutch, as failed nesters cannot be detected due to a moult-migration from the breeding site (Reed et al. 2003a). Snow geese are known to be a highly philopatric species and pair bonds generally form prior to arrival to the breeding grounds (Ganter et al. 2005), hence these two processes should not be influenced by snow cover upon arrival. Therefore, resource availability on the breeding grounds, in terms of nesting space and food availability, most likely explain the decision to delay breeding for the first time due to the mixed capital/income breeding strategy Our results also suggest that extreme climatic events experienced during migration (as indexed by the NAO in our analysis) may have influence the third process, laying and clutch completion, via a carry-over effect (Bêty et al. 2004, Descamps et al. 2010). However, because the NAO is a global index that can affect weather conditions in the Canadian Arctic, it is also possible that snow condition at the breeding colony in early June is partly affected by this index over the period of 21 March to 20 May.

Predation pressure

Crashes in cyclic lemming populations, used as an index of predation pressure, were identified as having a negative effect on recruitment in a previous study (Reed et al. 2003c). In our analysis, lemming abundance (which possibly had a positive effect on recruitment) was positively associated with the NAO index during spring (high NAO values are indicative of cool, late springs, which may negatively affect recruitment) in a synthetic covariate. There was low support in our analysis for the hypothesis that this covariate affected recruitment. The positive association between two variables with potentially antagonistic effects on recruitment may have prevented us from finding an effect of lemming abundance per se. Another confounding factor is that, in years of low lemming abundance, nesting success of geese decreases due to high predation pressure (Lecomte et al. 2008a) and it is conceivable that inexperienced breeders are especially vulnerable to predation. Thus, it is possible that an apparent effect of lemmings on recruitment is more associated with a reduced detection probability of newly recruited individuals in low lemming years than to a reduction in the probability of recruitment itself. In addition, it may be difficult to tease apart the effect of lemming abundance from that of climatic factors as the latter likely affect lemming abundance as well (Kausrud et al. 2008).

Management of harvested migratory species

Management decisions for our study population aimed at increasing hunting pressure in order to reduce survival (Gauthier and Brault 1998). Since the Migratory Birds Treaty of 1916 between Canada and the USA, pre-breeding hunting was not permitted on any migratory species, and thus the spring conservation hunt opened in Québec in 1999 was expected to be the measure with the strongest effect on Greater Snow Goose survival. The spring hunt has been an effective tool not only to reduce survival in Greater Snow Geese (Calvert and Gauthier 2005, Juillet et al. 2010, Chapter 2) but, as we show here for the first time, it also reduced the recruitment probability into the breeding population, likely due to a decrease in body condition due to hunting disturbance. When looking at recruitment probability at 3 years old, the age at which an individual is most likely to recruit, the probability to recruit was reduced by half from 0.51 in 1997 to approximately 0.25 in 2000 and 2001, all 3 years where the climatic conditions were similar and close to the mean for the period 1992-2005. This implies that, under average climatic conditions, each percentage point increase in the harvest rate could decrease recruitment probability by approximately 5%. Assessing the relative importance of such carry-over effects on overall population growth will require the use of a population matrix model approach to provide a more comprehensive comparison of the direct (via survival) versus indirect (via a carry-over on recruitment) effects.

Our study confirmed that climatic factors in spring also affected recruitment. In the absence of a spring hunt, recruitment probabilities (b) at 3 years old can also decrease by half when we compare a year with good climatic conditions such as 1994 ($b = 0.72$) and a year of poor climatic conditions such as 1995 ($b = 0.38$). For population management, the non-independence of climatic factors on a global scale renders the assessment of new conservation measures rather challenging. Ultimately such uncertainties in our mechanistic understanding can only be eliminated through controlled experiments but, unfortunately, we cannot control and manipulate confounding factors such as climate on a large scale. Future adaptive management programs will inevitably face the challenge of assessing interactive effects of conservation measures and climate in a changing environment. Spring snow melt in North America has been advancing over the last 3 decades of the XXth century (Dye 2002). If this trend continues, it is possible that managers may need to increase harvest in order to compensate for the potential positive effects, at least in the short term, of global warming on recruitment.

Table 4.1: Loadings of the five covariates on the first three factors from the rotated principal component analysis. Values of the two covariates contributing the most to each factor are in bold and are used to give a short descriptor of each factor. See methods for a detailed description of each covariate.

Covariate (1992 - 2005)	Factor 1 (NAO/Lemming)	Factor 2 (Snow/NAO^2)	Factor 3 (Hunt)
Adult spring harvest rate	0.00	0.08	**0.98**
Index of lemming abundance	**0.75**	-0.14	0.00
NAO (21 March – 20 May)	**0.87**	0.18	-0.08
NAO^2 (21 March – 20 May)	0.37	**0.74**	-0.52
Snow cover (5 June, breeding site)	-0.14	**0.90**	0.22

Table 4.2: Results of selection among models with various effects on survival (*S*), recruitment (*b*), capture (*p*) and recovery (*r*) probabilities. Models are presented in order of increasing ΔQAICc = (model QAICc) – (QAICc of best model). Rank = number of identifiable parameters in the model; a2, a3 and a4 correspond to models with respectively 2, 3 and 4 age-classes spanning 1 year except for the last one which has no upper limit; t = time; gp = group effect (age at banding: goslings *vs* adults).

Model				Rank	Deviance	ΔQAICc	QAICc Weights
S	*b*	*p*	*r*				
a3 + t	a4 + harvest rate +snow/NAO²	gp + t	a2 + t	54	909.88	0.00	0.35
a3 + t	a4 + harvest rate	gp + t	a2 + t	53	914.30	1.24	0.19
a3 + t	a4 + snow/NAO²	gp + t	a2 + t	53	914.32	1.26	0.19
a3 + t	a4 + harvest rate + NAO/lemming	gp + t	a2 + t	54	911.98	1.54	0.16
a3 + t	a4 + snow/NAO² + NAO/lemming	gp + t	a2 + t	54	914.16	3.15	0.07
a3 + t	a4	gp + t	a2 + t	52	922.13	5.00	0.03
a3 + t	a4 + NAO/lemming	gp + t	a2 + t	53	920.71	5.97	0.02
a3 + t	a4 + t	gp + t	a2 + t	65	901.54	16.00	0.00

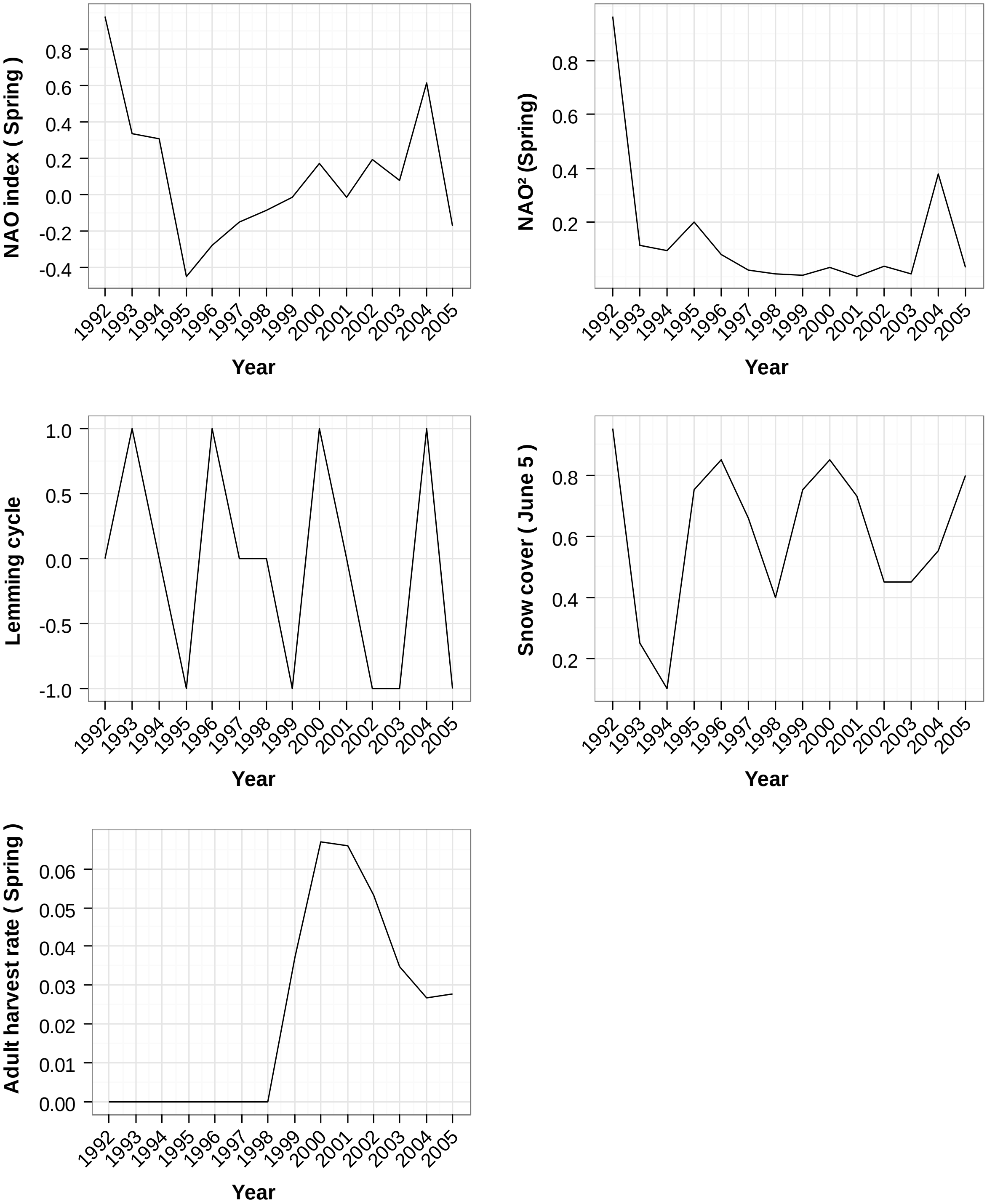

Figure 4.1: Time series of available explanatory variables.

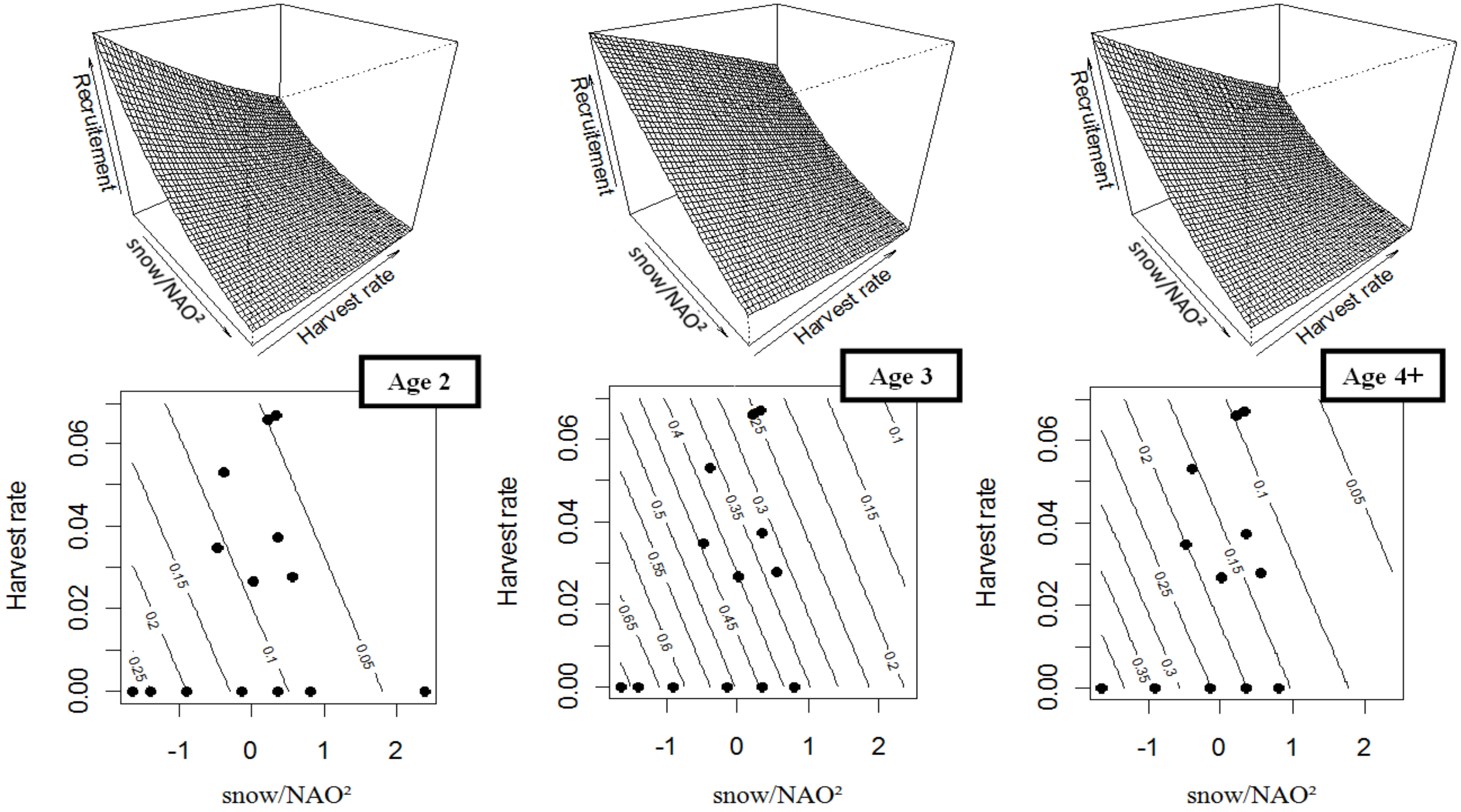

Figure 4.2: Representation of recruitment probability as a function of harvest rate, climatic conditions (snow/NAO^2) and age, estimated from our best model $S_{a3+time}$ $b_{a4+harvest\ rate+snow/NAO^2}$ $p_{gp+time}$ $r_{a2+time}$ (see Table 4.2). Isolines on the lower graphs indicate predicted recruitment probability and dots are observed values. Positive values of snow/NAO^2 indicate years with high snow cover at the breeding colony in spring and extreme positive or negative values of the NAO index during the pre-breeding migration over the period 1992-2005.

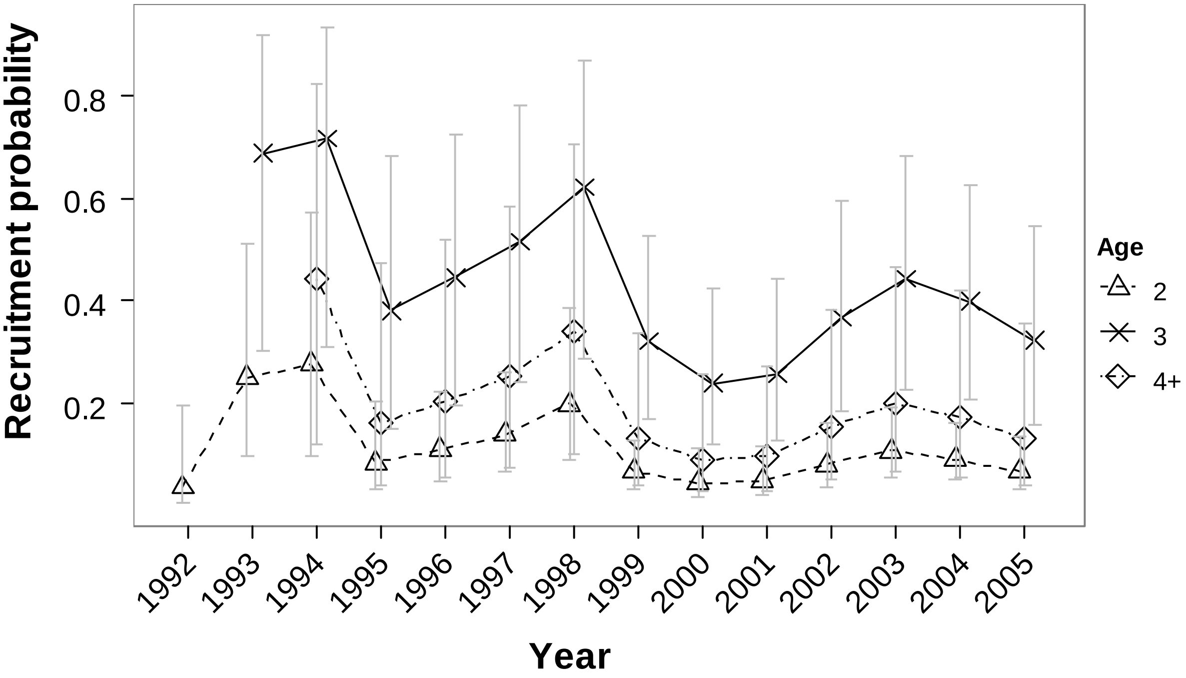

Figure 4.3: Annual variation in recruitment probability as a function of age estimated from our best model $s_{a3+time}\, b_{a4+harvest\ rate+snow/NAO^2}\, p_{gp+time}\, r_{a2+time}$ (see Table 2; estimate ± 95%CI).

Supplemental materials

Table 4.3: Results of the goodness-of-fit tests for the multistate recruitment model with mixture of information (recaptures and recoveries) of female breeders only ($\hat{c} = \chi^2 / d.f.$). Terminology of the test components follows Pradel et al. (2003).

	Banded as gosling				Banded as adult			
Test	d.f.	χ^2	P	$\hat{c}$	d.f.	χ^2	P	$\hat{c}$
3G.SR	8	9.44	0.31	1.18	14.00	5.75	0.97	0.41
3G.SM	3	2.87	0.41	0.96	28.00	19.60	0.88	0.70
M.ITEC	16	23.69	0.10	1.48	37.00	71.91	0.00	1.94
M.LTEC	13	18.28	0.15	1.41	104.00	142.85	0.01	1.37
Overall	40	54.27	0.07	1.36	183.00	240.10	0.00	1.31

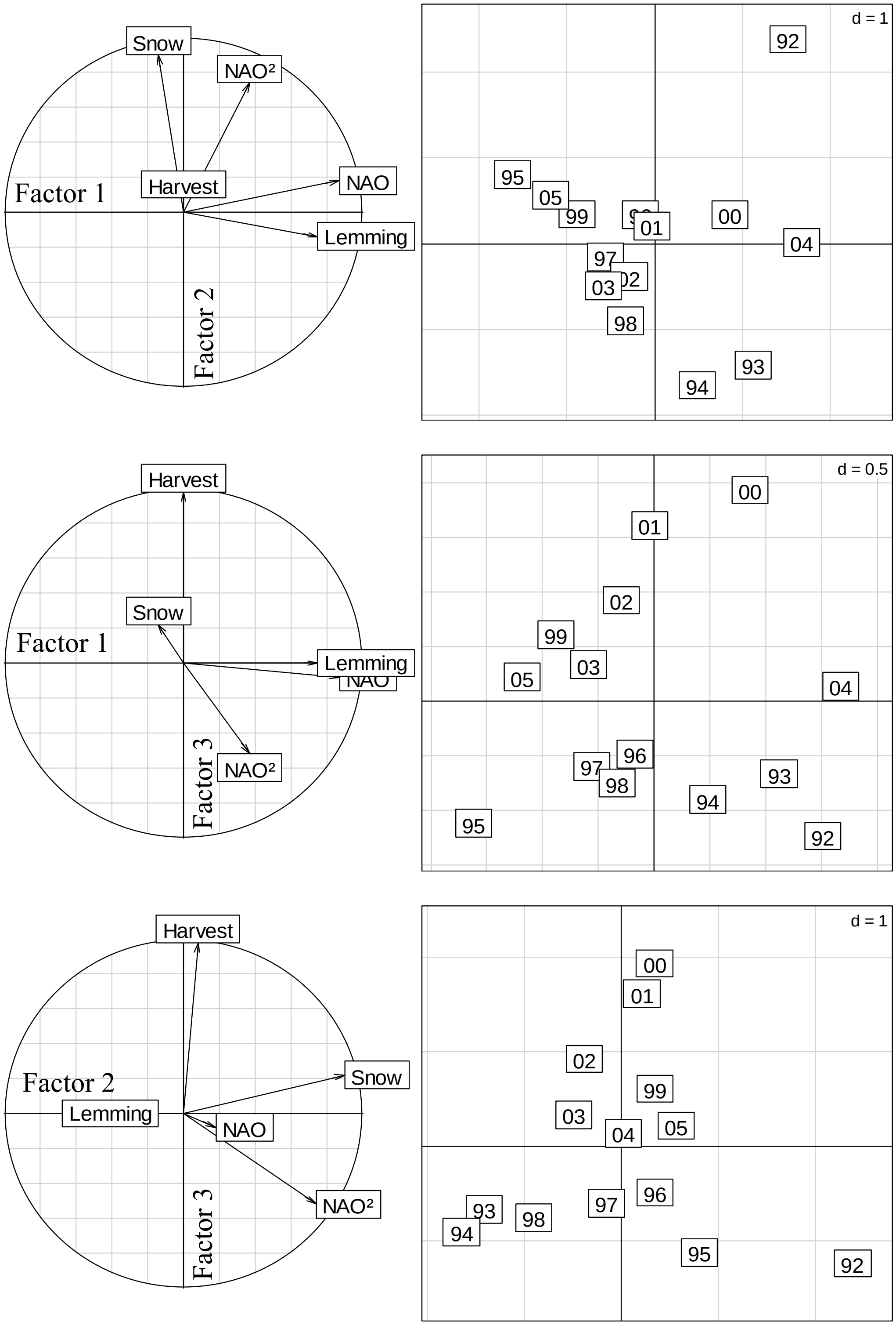
Snow
NAO²
Harvest
NAO
Lemming
Factor 1
Factor 2
d = 1
92
95
05
99
01
00
04
97
02
03
98
93
94
Harvest
Snow
Lemming
NAO
NAO²
Factor 1
Factor 3
d = 0.5
00
01
02
99
03
05
04
96
97
98
93
94
95
92
Harvest
Snow
Lemming
NAO
NAO²
Factor 2
Factor 3
d = 1
00
01
02
99
03
04
05
93
94
98
97
96
95
92

Figure 4.4 : Factorial maps with corresponding correlation circles after a ‘varimax’ rotation from the principal component analysis on our set of annual covariates (d = unit). Harvest = spring adult harvest rate; NAO = mean daily North Atlantic Oscillation Index during the period 21 March to 20 May; NAO² = quadratic mean daily NAO Index; Lemming = index of lemming abundance on Bylot Island, NU, Canada; Snow = Snow cover on 5 June on Bylot Island, NU. The last 2 digits of a given year are indicated in boxes.

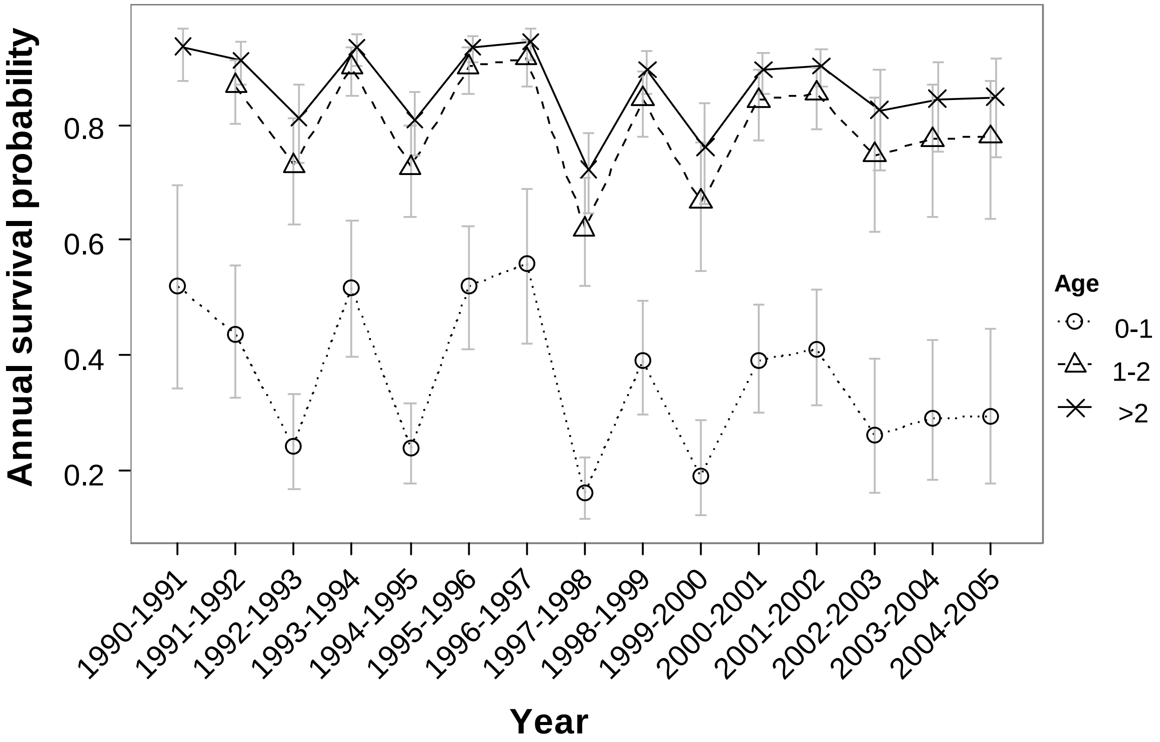

Figure 4.5: Annual variation in survival probability as a function of age estimated from our best model $S_{a3+time}\, b_{a4+harvest\ rate+\ snow/NAO^2}\, p_{gp+time}\, r_{a2+time}$ (see Table 2; estimate ± 95%CI).

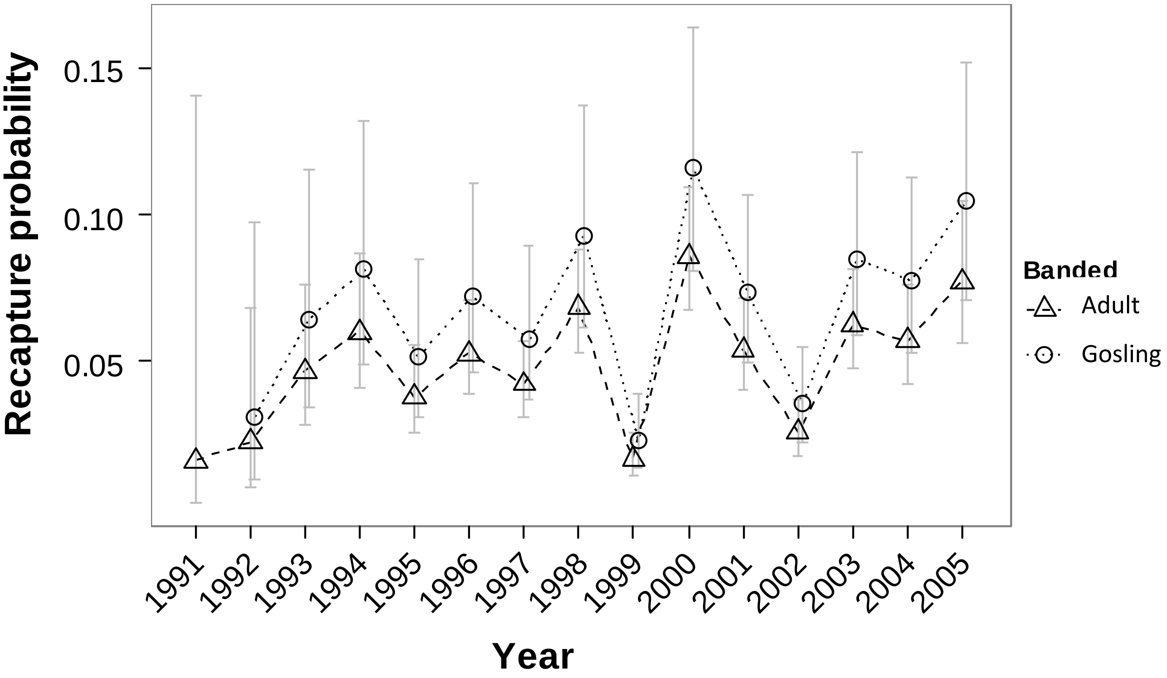

Figure 4.6: Variation in adult recapture probability as a function of age at banding estimated from our best model $S_{a3+time}\ b_{a4+harvest\ rate+\ snow/NAO^2}\ p_{gp+time}\ r_{a2+time}$ (see Table 2; estimate ± 95%CI).

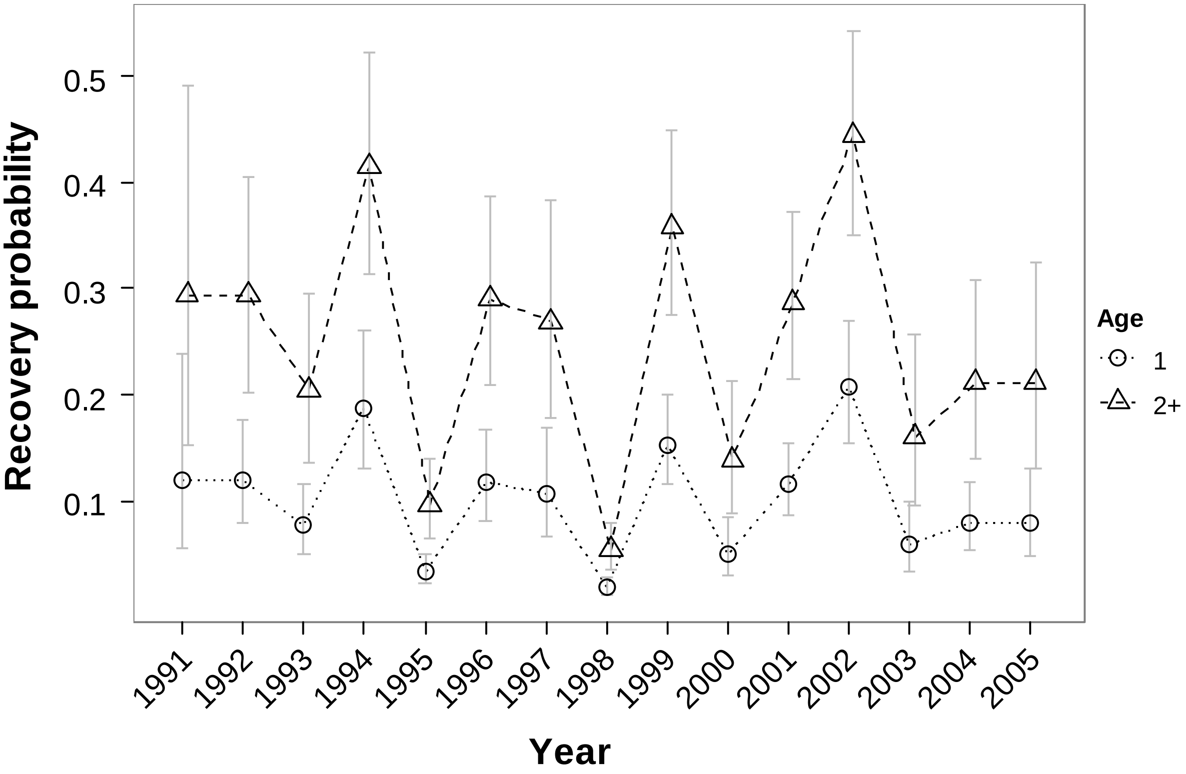

Figure 4.7: Annual variation in recovery probability as a function of age estimated from our best model $S_{a3+time}\, b_{a4+harvest\ rate+\ snow/NAO^2}\, p_{gp+time}\, r_{a2+time}$ (see Table 2; estimate ± 95%CI).

Conclusion

Rares sont les opportunités de pouvoir étudier les effets de la chasse comme outil de conservation pour contrôler l'effectif d'une population comme celle offerte par le cas de la Grande Oie des neiges. L'objectif des gestionnaires est de stabiliser la taille de population entre 500 000 et 750 000 individus. Grâce aux inventaires aériens conduits chaque printemps dans la vallée du Saint Laurent il est facile de pouvoir vérifier, après quelques années de recul, si la population diminue en association avec la mise en place des mesures et ainsi conclure que les mesures ont portées leur fruit. Ce qui est moins certain par contre est de savoir quels ont été les processus démographiques impliqués dans les changements de taille de populations en relation avec les changements de régimes de chasse. Réduire cette incertitude nécessite dans un premier temps d'évaluer les effets des mesures spéciales de conservation sur les paramètres démographiques que sont la survie, la reproduction et l'âge de première reproduction. La présente thèse concerne ce dernier point et les résultats propres à chaque paramètre démographique sont discutés ci-dessous.

Survie

Observer une diminution de survie entre les années qui précèdent l'introduction des mesures spéciales de conservation utilisant la chasse et les années où ces mêmes mesures sont appliquées et attribuer cette diminution à ces mesures de conservation est tout à fait naturel. Nous avons montré que la probabilité de survie annuelle des adultes avait bien diminuée en relation avec l'instauration des nouveaux règlements de chasse (baisse de 15%, de 0.876 à 0.747), tandis que chez les jeunes cela ne semble pas avoir eu d'impact sur la probabilité de survie annuelle. En conservation, les mesures de gestion appliquées aux espèces qui migrent sur de longues distances sont limitées dans le temps et l'espace relativement à l'ensemble du cycle de migration. Dans le cas de la Grande Oie des neiges les mesures appliquées différaient selon la saison et le lieu, automne et printemps au Québec, et hiver aux États-Unis. Ainsi, seule une approche saisonnière pouvait fournir le niveau de compréhension nécessaire pour distinguer l'impact sur la survie des différents régimes de chasse rencontrés par la population au cours de son cycle de migration. En utilisant les plus récentes avancées dans les modèles de CMR développés au premier chapitre, notre analyse fournit une évaluation fiable de l'effet saisonnier des mesures de conservation sur toutes les classes d'âge et les deux sexes de la population de la Grande Oie des neiges. Nous avons montré que les probabilités de survie des adultes ont diminué pendant les trois saisons de chasse (automne, hiver et printemps) après la mise en œuvre des mesures de conservation en 1999, mais pas de manière identique entre toutes les saisons. La baisse de survie a été moindre durant la portion du cycle de migration hivernale aux États-Unis en comparaison avec l’introduction des mesures durant les haltes migratoires automnale et printanière au Québec. Aucune diminution apparente de la survie n’a été documentée pour la partie nordique du cycle qui englobe principalement la partie de la migration dans l'Arctique et la saison de reproduction estivale. En revanche, il semble y avoir peu d'effet des mesures de conservation sur la survie des juvéniles durant leur premier automne et hiver et, de façon surprenante, la survie au cours de la seconde partie de la migration de printemps (du Québec au Haut Arctique) a augmenté après l’instauration des mesures de conservation.

Avec le développement du nouveau modèle de CMR présenté dans le premier chapitre, nous disposons maintenant pour nos analyses de survie d’un outil statistique qui utilise pleinement toute l’information qui a été recueillie sur le terrain. Il ne fait aucun doute que ce modèle général répond bien aux besoins du gestionnaire désireux d’acquérir une compréhension fine de l’effet des mesures de conservation mises en œuvre afin de mener une gestion éclairée de la population. Afin que le modèle puisse être facilement appliqué à d’autres systèmes biologiques, son implantation dans le logiciel E-SURGE (Choquet et al. 2009b), un programme gratuit relativement accessible aux non spécialistes, est documentée dans le premier chapitre. Un dernier point de développement important d’un point de vue statistique est la mise en œuvre de tests d’ajustement spécifiques à la classe des modèles multi-évènement. Ces tests, qui doivent être effectués avant toute modélisation, vérifient que les hypothèses initiales propres aux modèles de CMR sont bien respectées sur la base des données utilisées (Pradel et al. 2005a). Ce problème de tests d’ajustement qui restent à être développé n’est donc pas spécifique à notre modèle. Dans le second chapitre une approche conservatrice, et non répandue à ma connaissance, a été adoptée pour y remédier. Elle consiste à effectuer une série de tests d’ajustement sur des données partielles : données restreintes aux rencontres vivantes ou aux reprises d'individus morts ou encore données mélangées de rencontres vivantes et reprises correspondant à une seule saison. On se ramène ainsi à une situation connue, les modèles multi-état pour lesquels un test d'ajustement est disponible. Les modèles multi-état sont un cas particuliers des modèles multi-évènement et sont moins flexibles en termes de modélisation que ces derniers, ou autrement dit moins « capables » d'intégrer des particularités liées à un modèle biologique donné (dans notre cas l'absence d'information sur la présence de la marque auxiliaire, le collier). D'un point de vue théorique, un test d'ajustement d'un modèle multi-état à un jeu de donnée est donc plus susceptible d'être rejeté que si un test propre aux modèles multi-évènement avait été réalisé.

En termes de biologie, nos résultats présentés dans le second chapitre sont seulement les premiers pas réalisés dans l'application de notre modèle au cas de la Grande Oie des neiges. Jamais auparavant des estimés de survie n'avaient été présenté sur une base saisonnière et en considérant toute la population et le sexe des individus, aussi bien pour la Grande Oie des neiges que pour la Petite Oies des neiges, une espèce où les préoccupations en terme de conservation sont similaires. Un tel résultat est maintenant possible seulement en utilisant les plus puissants des ordinateurs personnels disponibles à ce jour, ce qui était donc impensable il y a encore à peine 2 ans. Cette contrainte technologique qui nous a forcé à ajuster un nombre restreint de modèles devrait s'atténuer dans un futur très proche. En parallèle, on peut espérer que les développements continuent au niveau des algorithmes pour les modèles complexes afin de les rendre plus facilement applicable (ou avec moins de temps de calcul), les progrès récemment accomplis dans ce domaine étant déjà spectaculaires. Ceci rendra alors possible un plus grand réalisme dans la modélisation de la survie chez la Grande Oie des neiges et d'autres espèces dans le but d'affiner encore nos connaissances biologiques.

Reproduction

Dans le cas de la reproduction, associer un changement des paramètres reproducteurs à un changement dans les pratiques de chasse durant la saison précédent la reproduction est moins évident car, contrairement à la relation entre chasse et survie, le lien invoqué ici est de nature indirecte. D'un point de vue conceptuel la relation négative entre chasse et reproduction est possible si 1) l'augmentation du dérangement par la chasse provoque une diminution de l'accumulation des réserves endogènes en graisse ou en protéines (moins de temps d'alimentation et/ou accès plus restreints aux habitats où la nourriture est la plus riche) durant les haltes migratoires précédant l'arrivée sur le site de reproduction, et 2) les ressources énergétiques utilisées pour la reproduction dépendent au moins partiellement des réserves endogènes accumulées durant la migration. Bien que ces deux points aient déjà été mis en évidence dans des études précédentes chez la Grande Oie des neiges (Béchet et al. 2003, Gauthier et al. 2003, Béchet et al. 2004a) la nouvelle étude sur la période 1995-2007 présentée dans le chapitre 3 ne permet pas de mettre en évidence un effet du taux de récolte des adultes durant la chasse de printemps au Québec sur différents paramètres de reproduction dans le Haut Arctique canadien (densité de nid, date et taille de ponte).

Même si un effet négatif associé à la présence de la chasse de printemps a été montré dans les études précédentes (Mainguy et al. 2002, Bêty et al. 2003, Dickey et al. 2008), cette étude est la première à utiliser un indice de pression de chasse quantitatif (taux de récolte) tout en contrôlant en même temps pour les conditions climatiques rencontrées durant la migration et à l'arrivée sur le site de nidification.

Morrissette et al. (2010) ont aussi trouvé une relation inverse entre productivité à l'automne (i.e. proportion de jeunes dans la population) et l'instauration de la chasse de printemps au Québec tout en contrôlant également pour les conditions climatiques. La productivité automnale à l'échelle de la population dépend de plusieurs paramètres dont principalement la propension des adultes à se reproduire, du succès de reproduction, de la proportion des juvéniles encore vivant à l'envol et de la survie des juvéniles jusqu'à la halte migratoire automnale. Le fait que nous ne détectons pas un effet de la chasse du printemps (tel que mesurée par le taux de récolte) sur les paramètres de la reproduction comme la date et la taille des couvées, mais qu'un effet ai été détecté sur la productivité, suggère que l'effet de la chasse pourrait se manifester essentiellement au niveau de la décision de se reproduire. Un tel effet sur la décision de reproduction a déjà été mis en évidence par le passé (Reed et al. 2004) basé sur les premières années où fut instaurée la chasse de printemps, mais aussi sur un plus grand nombre d'années dans le dernier chapitre de cette thèse. Nous avons ainsi quantifié la diminution de la probabilité de recrutement des jeunes adultes dans la population des reproducteurs avec l'augmentation du taux de récolte des adultes durant la chasse de printemps. Une fois que la décision de se reproduire est prise, les paramètres reproducteurs (date et taille de ponte) ne semblent pas être affectés par des effets reportés (*carry-over effects*) de la chasse au printemps mais par les conditions climatiques rencontrées à l'arrivée sur le site de nidification. Il est intéressant de noter que parmi les trois paramètres étudiés dans le chapitre 3 ce soit pour la densité de nid, un paramètre qui dépend de la décision de se reproduire, que l'absence d'un effet reporté de la chasse soit la plus incertaine. Seule une expérience permettant de manipuler la condition corporelle durant la migration, avant l'arrivée sur le site de reproduction, permettrait de clarifier la relation entre condition corporelle, et l'investissement dans la reproduction (décision de ponte, taille et date de ponte). Deux expéditions conduites par Josée Lefèbvre (SCF) sous l'égide du projet ArcticWOLVES et de l'Année Polaire internationale 2007-2009, ont permis le suivi de reproduction de Grandes Oies des neiges nichant à Eureka sur l'île d'Ellesmere au Nunavut. L'inscription dans le long terme du suivi d'au moins un autre site de nidification bénéficierait grandement aux analyses en augmentant la puissance statistique et en permettant de pouvoir généraliser les résultats à l'ensemble de la population. Malheureusement à cause de l'énorme coût financier des projets de recherche dans l'Arctique, ceci est difficilement faisable.

Recrutement

Avec le dernier chapitre nous apportons une forte évidence que la probabilité de recrutement est un autre trait démographique qui a été réduit par l'activité de chasse au printemps chez la Grande Oie des neiges. Ces résultats sont conformes avec les effets déjà documentés de la chasse de printemps sur la décision de se reproduire chaque année (Reed et al. 2004). Grâce à l'approche par inférence multiple, il a été possible d'évaluer l'importance relative de nos covariables d'intérêt parmi tous les facteurs potentiels identifiés a priori (conditions climatiques durant la migration printanière et à l'arrivée sur le site de nidification, indice de prédation sur le site de nidification). La pression de chasse durant la migration, représentée par le taux de récolte des adultes au printemps, est apparue comme le facteur le plus important touchant le recrutement au cours de la période 1992-2005, suivie par un indice climatique illustrant les mauvaises conditions rencontrés pendant la migration et à l'arrivée sur le site de reproduction. Que le recrutement soit clairement affecté par ces deux facteurs reflète bien la stratégie mixte d'allocation des ressources pour la reproduction avec une partie des réserves accumulées durant la migration complétée par les ressources acquises à l'arrivée sur le site de nidification (Gauthier et al. 2003). Nous démontrons ainsi que la décision de se reproduire dépend non seulement des conditions expérimentées par un individu au moment de se reproduire (liées aux conditions climatiques), mais que les conditions expérimentée dans la saison précédente (liées aux conditions climatique et à la chasse) peuvent aussi moduler cette décision. La littérature montre que l'intérêt pour de tel effets reportés ou avec délais (*carry-over effects*) sur la reproduction ne cesse de grandir depuis les dix dernières années aussi bien d'un point de vue des travaux théoriques (Norris et Taylor 2006, Harrison et al. 2010) que des travaux empiriques (Laaksonen et al. 2006, Inger et al. 2010, Morrissette et al. 2010). Par notre étude, en plus de démontrer empiriquement un effet avec délais, un phénomène souvent suggéré ou assumé mais rarement mis en évidence, c'est la première fois qu'une étude empirique permet de mettre clairement en évidence un effet de la chasse sur la probabilité de recrutement des jeunes adultes, mais également de quantifier cet effet reporté.

La chasse comme outil de conservation

La taille de population de la Grande Oie des neiges était estimée pour le printemps 2010 aux alentours de 800 000 individus, un chiffre légèrement inférieur à celui enregistré en 1999 (~1 000 000) au moment de l'instauration des mesures de gestion spéciales. La croissance exponentielle de cette population observée au cours la seconde moitié du XXème siècle a donc été interrompue. Si la survie des jeunes n'a pas diminuée avec l'instauration des mesures spéciales de conservation, il est probable que la diminution de 15% de la probabilité de survie annuelle des adultes (de 0.876 à 0.747) évoquée plus haut, ait été le principal facteur responsable de cette stabilisation. Si une baisse supplémentaire du taux de survie est nécessaire pour réduire encore davantage cette population, notre analyse sur une base saisonnière indique que les gestionnaires devraient cibler l'hiver aux États-Unis car c'est durant cette période que la survie a le moins changé depuis l'introduction de mesures spéciales de conservation en 1999.

Même si la chasse est utilisée pour manipuler la survie et ultimement la taille de population, nos résultats démontrent que la chasse peut affecter d'autres paramètres démographiques comme le recrutement. Même si la chasse a lieu en dehors de la saison de reproduction, des effets indirects reportés peuvent toutefois avoir lieu. J'espère ainsi que la publication de ces résultats encouragera un examen plus systématique pour d'autres espèces de potentiels effets indirects de la chasse sur la reproduction et pas seulement sur la survie afin de déterminer si nos résultats (Figure 1) sont une exception ou non. Chez les espèces migratrices, il est peut-être plus difficile de pouvoir anticiper et détecter des effets qui peuvent apparaitre après un certain délai car la population n'est pas accessible pour un suivi démographique tout au long de son cycle annuel. Toutefois, des effets indirects reportés devraient tout spécialement être anticipés lors de la mise en place de nouvelles mesures de conservation dans le cas des espèces présentant des stratégies mixtes d'allocation de ressources dans la reproduction (« capital/income breeder ») comme la Grande Oie des neiges.

Le rôle du climat comme facteur écologique majeur a été confirmé dans nos analyses sur la reproduction et le recrutement. Il apparait que le principal facteur impliqué dans les deux cas est un indice de la couverture de neige à l'arrivée sur le site de reproduction arctique, lequel exprime la disponibilité en habitat pour l'alimentation et la nidification. Concernant la survie, la relation entre climat et survie n'a pas encore été étudiée chez la Grande Oie des neiges. En théorie, cela devrait pouvoir être réalisé en appliquant le modèle du premier chapitre sur une base annuelle. Toutefois, une compréhension plus fine sur une base saisonnière afin de tenir compte du cycle migratoire annuel ne sera pleinement possible que lorsque les progrès liés aux ressources informatiques permettront une version dépendante du temps du modèle de CMR présenté dans le premier chapitre. Pour une gestion éclairée des populations sauvages et dans un contexte de changements climatiques, il est aujourd'hui essentiel de pouvoir mesurer avec exactitude les effets de nouvelles mesures de gestion.

Ultimement, il devient alors important de pouvoir comprendre qu'elle a été la contribution relative des effets directs sur la survie et indirects sur le recrutement, des mesures de conservation, aux changements de taille de population observés (Figure i). Pour y parvenir il sera nécessaire de recourir à un modèle matriciel de population. Un tel modèle de population s'avérera également fort utile afin de projeter la taille de population dans le futur (Caswell 2001). À l'exception de la propension à se reproduire, la présente thèse apporte des estimés pour tous les paramètres démographiques nécessaires à la construction d'un modèle matriciel. Un estimé de la propension à se reproduire chaque année peut être également très aisément produit en ajoutant un paramètre supplémentaire, la probabilité de se reproduire ou non chaque année, à la structure du modèle de survie présenté dans le premier chapitre. Mes analyses préliminaires ont montré que les données disponibles à la colonie de l`île Bylot, NU, étaient suffisantes pour obtenir une telle estimation à partir des femelles marquées avec un collier, la marque auxiliaire. Finalement, concernant l'influence du climat, il sera possible de contrôler celui-ci dans un modèle de projection en intégrant les tendances climatiques prédites par les travaux sur les changements climatiques (Jenouvrier et al. 2009).

Si la chasse s'est montrée un outil de gestion efficace dans le cas de la Grande Oie des neiges, une limitation à son utilisation provient de l'impossibilité pour les gestionnaires de contrôler précisément le taux de récolte (Walters et Hilborn 1978, Williams et al. 1996, Williams et al. 2002). Dans le cas de la Grande Oie des neiges, la diminution du taux de récolte des adultes (présentée dans les deux derniers chapitres) est associée à la diminution du nombre de chasseurs ce qui devrait rapidement conduire à un nouveau défi pour la gestion de la population si la tendance se poursuit.

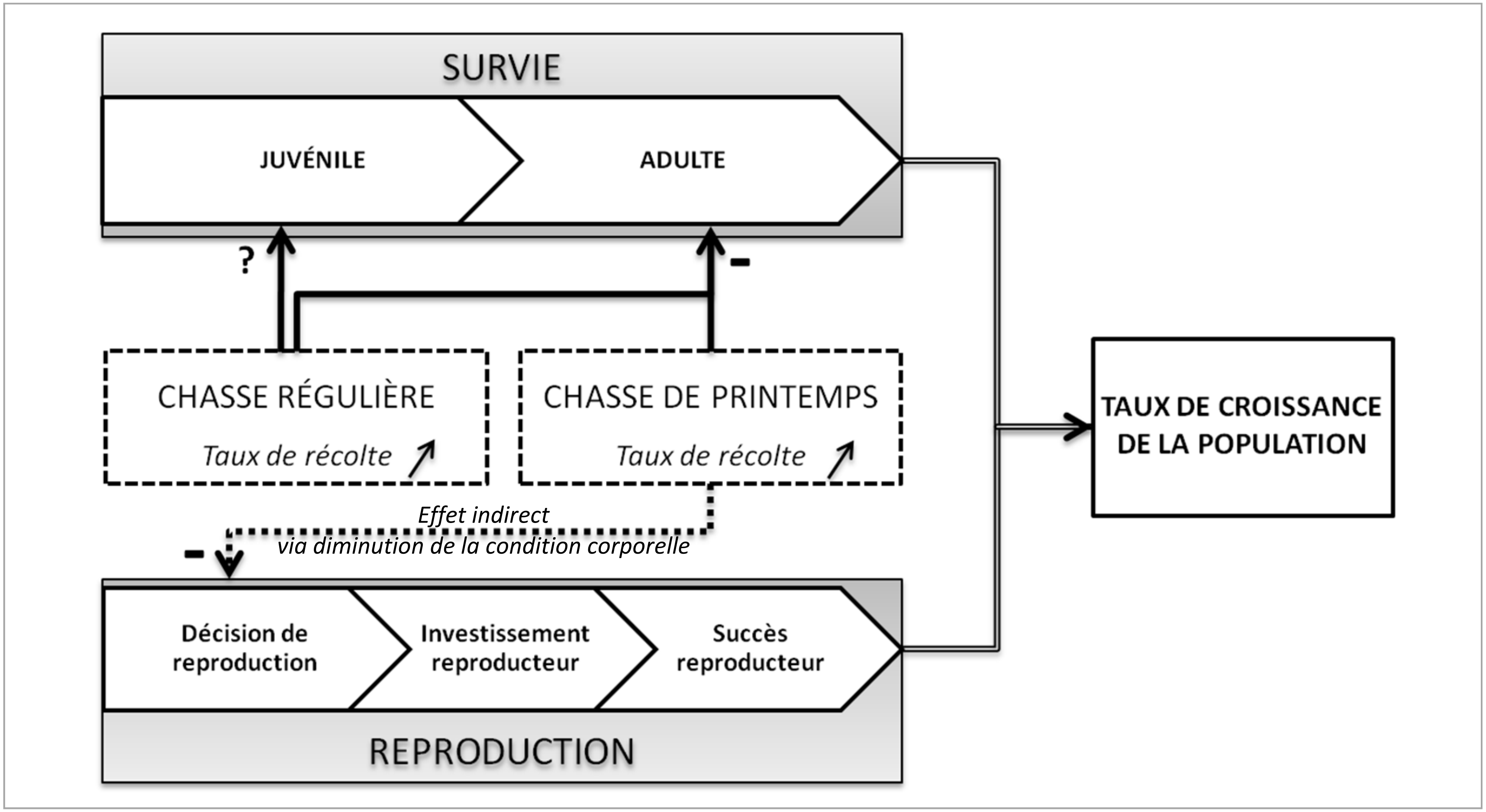

Figure 1 : Synthèse des effets de la chasse sur les paramètres démographiques. Les effets directs sont indiqués par des flèches solides. Le signe moins indique un effet négatif tandis que le point d'interrogation souligne une incertitude.

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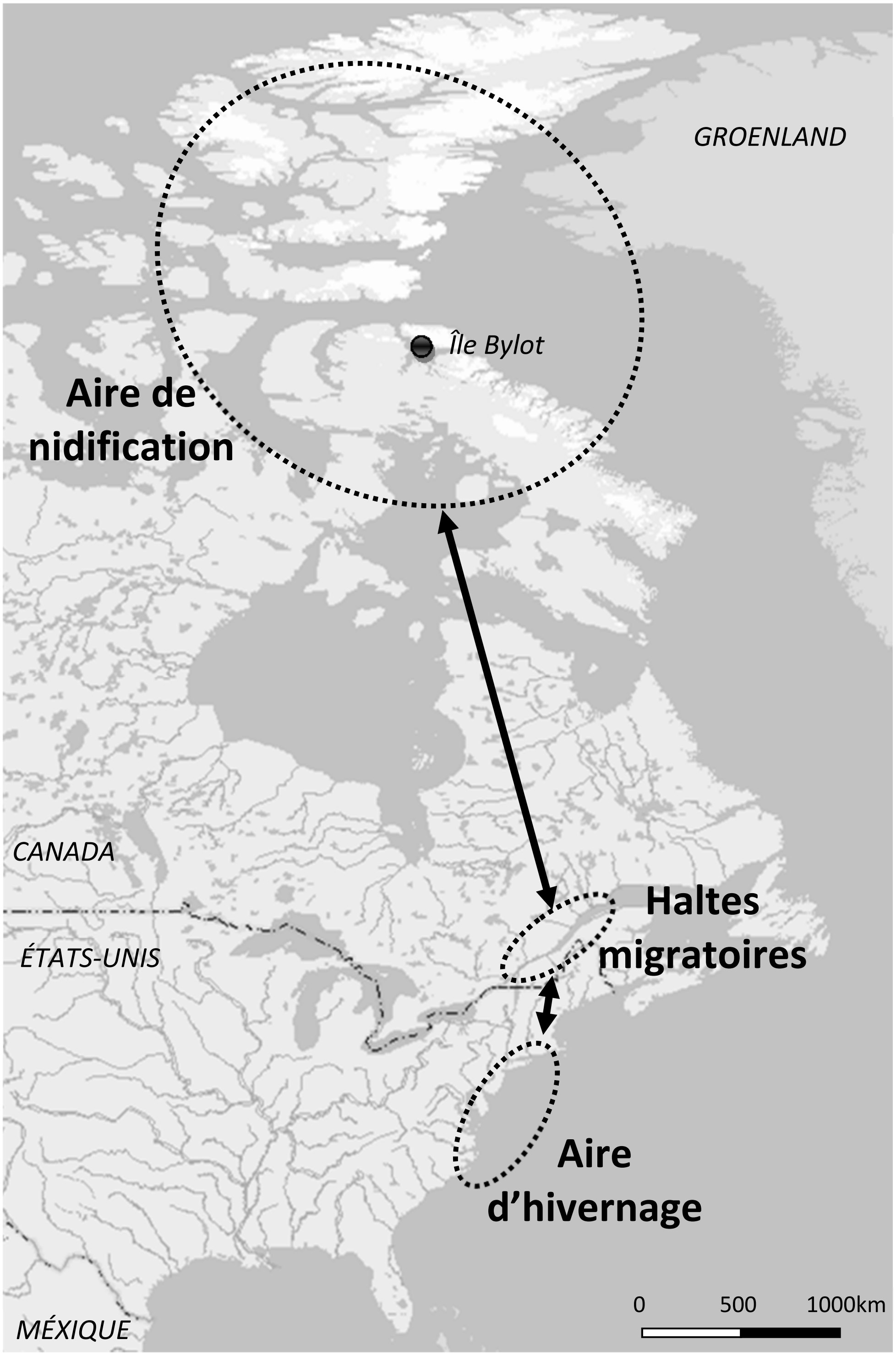
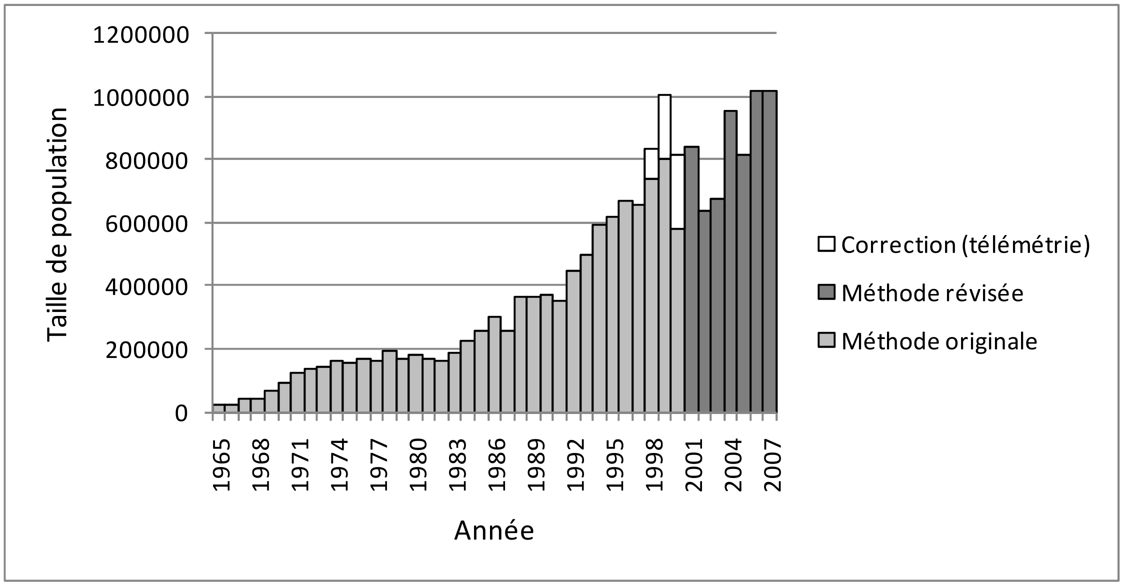
Annexe 1
Cycle de migration de la Grande Oie des neiges



Annexe 2
Taille de population de la Grande Oie des neiges



Évolution de la taille de la population de la Grande Oie des neiges sur la période 1965-2007. La taille de population est estimée chaque printemps au Québec, Canada, à partir de photographies aériennes (Service Canadien de la Faune, donnée non publiée). Pour le détail sur les méthodes utilisées pour estimer la taille de population, voir Béchet et al. (2004b).