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COÛTS DES SOINS PARENTAUX ET EFFETS DES CONDITIONS ENVIRONNEMENTALES SUR LA REPRODUCTION DE LA GRANDE OIE DES NEIGES

Thèse
présentée
à la Faculté des études supérieures
de l'Université Laval
pour l'obtention
du grade de Philosophiae Doctor (Ph.D.)

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

FÉVRIER 2003

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Résumé succinct

Notre objectif était de quantifier l'investissement et les coûts, en termes de survie et de reproduction future, associés aux soins parentaux prolongés et l'effet des conditions environnementales sur la démographie chez la Grande Oie des neiges (*Chen caerulescens atlantica*) nichant dans le Haut-Arctique canadien. Nous montrons que le taux de séparation des familles entre la halte migratoire printanière et les sites de reproduction est élevé. De plus, la survie des femelles associées à leurs jeunes pour une longue période est réduite. La date de naissance d'un individu est négativement reliée à sa survie, indiquant que les conditions ontogéniques peuvent affecter le recrutement. Des interactions trophiques indirectes causées par des prédateurs communs font aussi en sorte que le recrutement d'individus est presque nul à faible densité de lemmings. La probabilité de reproduction des adultes montre de fortes variations annuelles, expliquées en partie par la couverture de neige printanière.

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Résumé long

L'objectif de cette thèse était de quantifier l'investissement et les coûts (survie et reproduction future) associés aux soins parentaux prolongés et l'effet des conditions environnementales sur la démographie chez la Grande Oie des neiges (*Chen caerulescens atlantica*) nichant dans le Haut-Arctique canadien. Les données ont été récoltées de 1990 à 2001 à l'Île Bylot (Nunavut), sur les haltes migratoires (Québec) et sur les aires d'hivernage (États-Unis). J'ai quantifié les variations individuelles dans la durée des soins parentaux et les coûts qui y sont associés. Mes résultats indiquent que les bris de familles entre l'automne et le printemps sont majoritairement dus à la mortalité des jeunes mais que les séparations de familles sont importantes entre le printemps et l'été. Je présente des évidences empiriques démontrant que la survie, mais non la probabilité de reproduction, des femelles associées à leurs jeunes pour une période de 10 mois ou plus est réduite par rapport à celles sans jeunes. Je me suis ensuite intéressé à la migration de mue. La majorité des adultes non-reproducteurs ainsi que ceux dont les nids sont prédatés quittent l'Île Bylot pour la mue. L'effet potentiellement négatif d'un marqueur auxiliaire (colliers) a ensuite été examiné. Les femelles avec colliers avaient une probabilité de reproduction et une taille de ponte réduite mais leur survie n'était pas affectée. Cet effet négatif est probablement dû à une dépense énergétique accrue lors du vol. Finalement, j'ai étudié l'effet des conditions environnementales sur les paramètres démographiques. Mes résultats démontrent que la survie juvénile est négativement reliée à la date de naissance d'un individu. La survie juvénile varie considérablement entre les cohortes mais ne pouvait être expliquée par les variables environnementales à l'étude. Des interactions trophiques indirectes causées par des prédateurs communs font aussi en sorte que le recrutement d'individus est presque nul à faible densité de lemmings. Finalement, la probabilité de reproduction des adultes montre de fortes variations annuelles, expliquées en partie par la couverture de neige printanière. Ces résultats démontrent la présence de coûts liés aux soins parentaux et l'importance des conditions environnementales sur la dynamique de cette population.

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Abstract

This thesis' objective was to quantify investment and costs (reduced future survival or reproduction) associated with prolonged parental care, as well as the effects of environmental conditions on the demography of Greater Snow Geese (*Chen caerulescens atlantica*) nesting in the Canadian High Arctic. Data were collected from 1990 - 2001 at Bylot Island (Nunavut), on staging areas (Québec) and on the wintering grounds (USA). We first quantified individual variation in the duration of parent-offspring association and the costs associated with prolonged parental care. Our results indicate that family break-up between fall and spring was mostly due to mortality of offspring whereas separations of families became important between spring and summer. We present empirical evidence of a survival cost for females providing care for 10 months or more but no cost on future reproduction. We next looked at moult migration. The majority of adult non-breeders and failed nesters left Bylot Island for the moult. The potential negative effect of an auxiliary marker (neck bands) was also examined. Neck-banded females had reduced breeding probabilities and clutch size but their survival was not affected. This negative effect is likely due to increased energetic expenditure during flight. Finally, we studied the effects of environmental conditions on demographic parameters. Our results indicate that juvenile survival, hence recruitment of individuals in the breeding population, was negatively related to an individual's hatching date. Juvenile survival was also highly variable among cohorts but this variation could not be explained by the environmental variables considered. Indirect trophic interactions caused by common predators resulted in almost null recruitment of individuals in lemming crash years. Finally, reproduction probabilities of sexually mature adults were highly variable among years, and this variation could be explained in part by spring snow cover. These results show costs associated with long-term parental care and the importance of environmental conditions on the dynamics of this population.

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Avant-Propos

Cet ouvrage comprend 6 chapitres principaux rédigés sous forme d'articles scientifiques. La thèse inclue aussi une introduction générale et se termine par une conclusion générale. Chacun des chapitres est complet et ne nécessite pas la lecture des autres chapitres pour être compris. Dans tous les cas, je suis l'auteur principal de ces articles. En plus de mon directeur de thèse, Gilles Gauthier, les co-auteurs Joël Bêty, Julien Mainguy, Austin Reed, Jean-François Giroux, Roger Pradel et Jean-Dominique Lebreton ont contribué à l'élaboration des objectifs ou au moment de la rédaction. Joël Bêty, Julien Mainguy et Austin Reed ont aussi contribué avec des données personnelles (Chapitres 1 et 3). Les Chapitre 3 et 5 sont présentement acceptés comme publication dans les revues *Arctic* et *Ecology*. Le chapitre 1 sera soumis à la revue *Auk*, le chapitre 2 à *Animal Behaviour*, le chapitre 4 à *Journal of Wildlife Management* et le chapitre 6 à *Oikos*.

Il est rare d'avoir la chance de travailler avec une base de données à long-terme aussi complète que celle qui a été accumulée à l'Île Bylot et le long de l'estuaire du Saint-Laurent. Pour cela, je veux féliciter la vision et la passion des initiateurs de cet ambitieux projet, Austin Reed et Gilles Gauthier. Ils ont su développer un programme de recherche très rigoureux, qui apporte des dividendes de plus en plus importantes à mesure que s'accumulent les données. Peut-être plus important encore, ils ont permis à toute une génération d'étudiants d'acquérir une expérience exceptionnelle dans un environnement de travail non moins exceptionnel, l'Île Bylot. Je ne saurais passer sous silence la collaboration de Jean François Giroux à cet ambitieux projet. Il est le maître d'oeuvre et superviseur du projet de suivi télémétrique mis en place le long du fleuve Saint-Laurent et a l'Île Bylot. J'aimerais le remercier pour son intérêt dans mon projet ainsi que les nombreux conseils qu'il a su me prodiguer au cours de mon cheminement.

Évidemment, ces travaux à long-terme n'auraient jamais été possibles sans la participation de nombreuses personnes, envers qui j'ai beaucoup de reconnaissance. J'aimerais d'abord et avant tout remercier Gérald Picard pour son dévouement et son sérieux au travail, mais plus particulièrement pour son manque de sérieux après le travail et la grande amitié qui s'est développé entre nous. Amos et Joasie Ootovak se sont aussi avérés de très bons amis.

J'ai eu l'occasion de côtoyer certaines personnes qui m'ont été très importantes au cours de mes études, des personnes avec qui j'ai partagé certaines passions et envers qui j'ai beaucoup de reconnaissance: Christopher Ellis, Jean-Pierre Tremblay, Louis Lesage, Hélène Massé, Arnaud Béchet, Josée Lefebvre et Francis St-Pierre. Plusieurs autres personnes ont participé au marquage des oies et à la récolte de données sur le terrain, soit Joël Bêty, Jonatan Blais, Grégory Bourguelat, Isabelle Chouinard, Frédéric Demers, Réjean Deschênes, Johanne Dussureault, Dominique Fiset, Julie Lambert, Diane Leclerc, Julien Mainguy, Bernard Maktar, Stéphane Menu, Nadia Nadeau, Jonathan Olson, Sam Ootovak, Pascale Otis, Natalie Piedboeuf, Florence Portal, Mohamed Righi, Stéphanie Rioux, Nathan Tigalurak. J'aimerais particulièrement souligner le travail acharné de Diane Dauphin qui, au fil des ans, a réussi a accumuler une importante quantité d'information sur les femelles marquées de colliers sur la rive sud du Saint-Laurent lors de la migration. Évidemment, j'aimerais remercier tous les étudiants qui ont travaillé avant moi soit sur les sites de nidifications ou les haltes migratoires et qui m'ont permis d'avoir accès a une base de données aussi complète.

Des échanges constructifs avec plusieurs personnes m'ont permis d'améliorer considérablement le contenu des chapitres de ma thèse. Je voudrais particulièrement souligner le travail de Gilles Gauthier pour sa supervision et son sens de la minutie. Jean-François Giroux a aussi largement contribué a améliorer la qualité de ma thèse par ses nombreux commentaires sur certains chapitres. J'ai reçu un très bon accueil en France de la part de Jean-Dominique Lebreton et la collaboration avec lui et Roger Pradel s'est avérée très positive. Ils m'ont permis de parfaire ma formation et de rehausser la qualité de cet ouvrage. Cyrille Barrette, Arnaud Béchet, Austin Reed et Gary White ont lu et apporté des critiques très constructives à un ou des chapitres de ma thèse. Enfin, je remercie tous les membres du département de biologie de l'Université Laval qui ont fait partie de mon comité de supervision pour une partie ou pour la totalité de mes études, soit Cyrille Barrette, Steeve Coté, Julian Dodson et Jean Huot, ainsi que l'examinateur externe de la thèse, James D. Nichols.

Le support logistique offert par les membres du l'organisme fédéral 'Étude du Plateau Continental Polaire' a grandement facilité le travail de terrain a l'Île Bylot. Ted Nichols et Serge Labonté ont aussi aidé lors de mes travaux sur les aires d'hivernage (New Jersey, Delaware, Maryland, Virginie) et au Cap Tourmente respectivement. J'aimerais aussi remercier Olivier Gimenez pour avoir rendu mon arrivée a Montpellier plus aisée ainsi que Marie-Pierre Castanié qui a bien voulue m'héberger chez elle pendant mon séjour en France.

En terminant, j'aimerais remercier mes parents, qui m'ont toujours fourni un support inconditionnel tout au long de mes études. Ils ont été une grande source d'inspiration pour moi et m'ont transmis leur passion de l'histoire naturelle et des espaces sauvages dès mon plus jeune âge. Je leur en suis extrêmement reconnaissant. Mon dernier mot de remerciement va à Isabelle, pour sa passion (qu'elle veut bien partager avec moi), sa compréhension et surtout son sourire.

Cette recherche a été réalisée grâce au généreux support logistique et financier de :
Conseil de Recherche en Sciences Naturelles et en Génie du Canada (subvention à GG)
Arctic Goose Joint Venture (Service Canadien de la Faune) (subvention à GG et à JFG)
Fonds pour la Formation des Chercheurs et l'Aide à la Recherche (FCAR, Ministère de l'Éducation du Québec) (bourse à ETR et subvention d'équipe à G. Gauthier)
Département des Affaires Indiennes et du Nord Canada (subvention de voyage à ETR)
Fondation de l'Université Laval (bourse à ETR)
Centre d'Études Nordiques (bourse à ETR)
Dennis Raveling Scholarship Fund (bourse à ETR)
Fonds Richard Bernard (bourse à ETR)
Étude du Plateau Continental Polaire
Hunters and Trappers Association of Pond Inlet, Nunavut Territory
Centre d'Écologie Fonctionnelle et Évolutive de Montpellier, France
Institute for Wetlands and Waterfowl Research (subvention à J.-F. Giroux et G. Gauthier)

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Introduction

La théorie des traits d’histoire de vie (*life history*) nous permet de relier divers champs de la biologie et améliore la compréhension de l’action de la sélection naturelle. Cette théorie assume qu’à chaque phénotype ou stratégie est associée une combinaison de traits qui ont été façonnés par des contraintes environnementales et des compromis (Roff 1992, Stearns 1992). L’interaction entre ces traits déterminera ultimement le fitness individuel, alors que la combinaison de ces traits pour l’ensemble des individus détermina la dynamique de la population. Parmi les principaux traits d’histoire de vie on note : la taille corporelle à la naissance; le patron de croissance; l’âge de la maturité sexuelle; la taille corporelle à maturité; le nombre et le ratio des sexes de la progéniture; l’investissement reproducteur en fonction de l’âge et de la taille; les cédules de mortalité spécifique à l’âge et à la taille; et la durée de vie (Stearns 1992). Ces traits sont contraints par divers compromis tels la reproduction actuelle versus la survie et la reproduction future, et le nombre, la taille et le sexe de la progéniture (Stearns 1992). Il est donc important d’être en mesure de quantifier précisément les différents traits démographiques, mais aussi de comprendre les facteurs comportementaux et environnementaux qui influencent la variabilité de ces traits.

La théorie prédit que l’énergie dont les individus disposent est limitée et que l’investissement dans un trait d’histoire de vie peut se faire au détriment des autres. Un des compromis évolutifs le plus étudié est celui entre l’investissement des individus dans leur reproduction actuelle et leur survie ou reproduction future (ex. Trivers 1972, Bell 1980, Linden et Møller 1989, Pugesek et Diem 1990, Clutton-Brock 1991). Le concept de coût de la reproduction est central à la théorie des cycles-vitaux et bien que plusieurs études aient tenté d’évaluer les coûts associés à la reproduction, ces coûts sont difficiles à mesurer et leur importance demeure un sujet de controverse (voir Stearns 1992, Appendix 2 pour une revue de la littérature). Le principal coût relié à la reproduction, chez les oiseaux et les mammifères, est associé aux soins parentaux. S’il existe effectivement un coût à la reproduction, on devrait voir l’apparition d’un optimum dans l’effort reproducteur des parents, lequel serait un compromis entre la production et la survie des jeunes actuels et la survie et la fécondité future des parents. Cet optimum risque d’être différent du point de vue des parents et des jeunes, menant à un conflit parental (Trivers 1974, Lazarus et Inglis 1986).

Les conditions environnementales rencontrées par les individus au cours de leur vie peuvent aussi avoir des répercussions sur l'ensemble de leurs caractères. Les conditions rencontrées en début de vie ont, chez plusieurs espèces, des conséquences sur la croissance des individus et éventuellement sur plusieurs traits d'histoire de vie (taille adulte: Larsson et Forslund 1991; reproduction et survie: Spear et Nur 1994, Sedinger et al. 1995, Prévot-Julliard et al. 2001). Les conditions rencontrées durant la vie adulte peuvent aussi avoir un impact sur les traits d'histoire de vie. Plus particulièrement, les conditions rencontrées durant la période de reproduction peuvent affecter la productivité et l'optimisation de l'effort reproducteur (Boyce et Perrins 1987, Prop et de Vries 1993, Nur et Sydeman 1999). Les conditions environnementales, couplées aux coûts de la reproduction, peuvent avoir une profonde influence sur l'évolution des traits d'histoire de vie d'une espèce et favoriser la plasticité des paramètres les plus sensibles à ces forces sélectives.

Investissement reproducteur et coûts des soins parentaux

D'un point de vue évolutif, les coûts associés à la reproduction se mesurent en terme de survie plus faible et/ou de fécondité future réduite (Clutton-Brock 1991). Les mécanismes responsables des coûts en terme de survie future sont multiples mais on peut en cibler quelques-uns des plus importants: augmentation des risques de prédation (Magnhagen 1991), réduction de la capacité immunitaire résultant en une diminution de la résistance aux infections et parasites (ex. Festa-Bianchet 1989, Møller 1993, Norris et al. 1994, Deerenburgh et al. 1997) et mortalité accrue à la chasse (Prevett et MacInnes 1980). Les coûts en terme de reproduction future seraient davantage liés à des facteurs énergétiques, la reproduction courante ayant un effet négatif sur la condition corporelle des parents lors du prochain épisode de reproduction (Drent et Daan 1980).

L'évaluation des coûts de la reproduction est un des défis principaux de l'application de la théorie d'histoire de vie aux populations sauvages. Chez des espèces ou des populations vivant dans des habitats hétérogènes, les coûts de la reproduction risquent d'être variables d’une année à l’autre suite à des fluctuations dans les conditions environnementales. Ainsi, les coûts de la reproduction sont difficiles à mesurer car il y a souvent une variété de facteurs environnementaux (biotiques et abiotiques) qui peuvent masquer les coûts réels (Williams 1966, Stearns 1992, Cam et al. 1998) et parce que l’estimation des paramètres démographiques tels la survie et la probabilité de reproduction (*breeding propensity*) requièrent un suivi temporel des individus pendant une période relativement longue. Les corrélations phénotypiques entre l’effort reproducteur et le fitness des individus ont été critiquées car les facteurs génétiques et environnementaux y sont confondus (Reznick 1985, 1992; van Noordwijk et de Jong 1986). Malgré leurs limitations, les études de corrélations phénotypiques peuvent permettre une évaluation des coûts liés aux soins parentaux et permettre d’étudier, dans un cadre évolutif, des comportements qui sont difficiles à manipuler en situation naturelle (Linden et Møller 1989; Partridge 1992). La période d’association entre parents et jeunes chez des espèces qui ont des capacités de reconnaissance individuelle (ex. Radesäter 1976) est un exemple de comportement difficilement manipulable en nature.

Malgré un grand nombre d’études sur le sujet, la difficulté d’estimer les paramètres démographiques d’intérêt pour la question des coûts liés à la reproduction en milieu naturel fait que l’importance évolutive de ces coûts est encore mal connue. Les coûts de la reproduction semblent relativement importants chez certaines espèces d’oiseaux marins, comme en fait foi le cycle bisannuel de reproduction chez plusieurs espèces de Procellariiformes (Tickell et Pinder 1967), alors qu’ils n’ont pu être détectés chez plusieurs autres espèces (ex. Chastel 1995, Tombre et Erikstad 1996).

Le principal coût associé à la reproduction chez les vertébrés terrestres est lié aux soins parentaux prodigués par les adultes à leur progéniture (coûts post-reproduction : Jönsson et al. 1998). La quantité et la qualité des soins parentaux vont déterminer en grande partie le succès reproducteur d’un individu. Les soins parentaux sont définis comme étant tout soins apportés aux oeufs et aux jeunes lorsqu’ils ne sont plus dans le corps de la mère (Clutton-Brock 1991). Deux catégories de soins parentaux sont reconnues (Altmann et al. 1977): les soins dépréciables (synonymes: “shareable” [Wittenberger 1979] et “shared” [Lazarus and

Inglis 1986]), où les bénéfices des jeunes diminuent avec une augmentation de la taille de la couvée, et les soins non-dépréciables (syn.: “nonshearable” [Wittenberger 1979] et “unshared” [Lazarus and Inglis 1986]), où les bénéfices sont indépendants de la taille de la couvée. L’alimentation des jeunes au nid est un exemple de soin dépréciable alors que la vigilance est non-dépréciable.

Les résultats d’études empiriques chez les oiseaux suggèrent que l’intensité ou la durée des soins parentaux que les femelles sont capables de prodiguer sont souvent dépendantes de la condition des individus, les femelles en mauvaise condition ayant tendance à abandonner leurs couvées plus tôt (Monaghan et al. 1992, Kilpi et al. 2001). Ce patron d’abandon serait en accord avec l’hypothèse d’une stratégie compensatoire, par laquelle le stress énergétique de la ponte et de l’incubation limite la capacité des femelles à prodiguer des soins à sa progéniture (Bustnes et Erikstad 1991). Les jeunes abandonnés tôt auraient une survie plus faible, ce qui suggère qu’il y a un coût sur la fécondité des parents qui abandonnent leur couvée (Bustnes et Erikstad 1991, mais voir Pöysä 1995). Les bénéfices associés à des soins de longue durée incluraient une augmentation de la survie, du recrutement ou de la fécondité de la progéniture, ainsi qu’une amélioration du rang social des familles (Conover et al. 2000, Ekman et al. 2000, Raveling et al. 2000, Green et Cockburn 2001).

Chez les oiseaux nidicoles, la taille de couvée (i.e. le nombre de jeunes qui doivent être nourris) devrait être un bon indice de l’investissement parental mais chez les espèces nidifuges, la durée des soins devrait être un meilleur indice d’investissement dans les cas où ces soins sont majoritairement non-dépréciables (i.e. indépendants de la taille de la couvée). Il est donc surprenant de voir que la majorité des études qui ont tenté de quantifier les coûts des soins post-reproductifs chez des espèces nidifuges aient utilisé la taille de la couvée et non la durée des liens entre parents et jeunes comme indice d’investissement (ex. Dow et Fredga 1984, Black et Owen 1989a, Loonen et al. 1999)

Si la reproduction et les soins parentaux sont coûteux, l’âge où les individus atteignent la maturité devrait être retardée chez les espèces longévives. L’âge de la maturité, défini comme étant l’âge à laquelle un individu parvient à se reproduire pour la première fois (Stearns 1992), est d’une importance majeure dans l’étude des stratégies vitales (*life-history* *strategy*) car le fitness est habituellement plus sensible à un changement dans ce trait que dans la fécondité annuelle. Un délai de la maturation sera bénéfique si: 1) il permet à l'individu d'atteindre une taille plus grande et si sa fécondité augmente avec sa taille; 2) la qualité de la progéniture ou les soins parentaux prodigués sont supérieurs, résultant en une meilleure survie des jeunes; 3) un délai permet à l'organisme de vivre plus longtemps et d'avoir plus d'occasions de reproduction durant sa vie. L'âge optimal à la maturité est donc un compromis entre les bénéfices et les coûts de la maturation à différents âges et/ou tailles corporelles.

Un délai dans l'accession à la reproduction est commun chez les espèces longévives (Wooler et Coulson 1977, Pradel et al. 1997, Cooch et al. 1999a) et la première reproduction d'un individu est souvent la plus coûteuse (Viallefont et al. 1995a). Ce délai dans l'âge à la première reproduction a été entre autres imputé à des différences dans la qualité des individus qui subiraient des coûts différentiels de reproduction (Curio 1983, Forslund et Pärt 1995) et à l'amélioration progressive des compétences reproductrices ou de quête alimentaire avec l'âge (Recher et Recher 1969, Desrochers 1992). Un délai dans l'accession à la reproduction lorsqu'il y a des coûts associés à la reproduction peut ainsi augmenter le succès reproducteur à vie d'un individu (Tavecchia et al. 2001).

Environnement stochastique et traits d'histoire de vie

L'investissement reproducteur et les coûts de la reproduction sont étroitement liés aux conditions du milieu. L'intensité de l'investissement et les coûts qui s'y rattachent peuvent donc varier en fonction des conditions présentes, mais aussi en fonction des conditions rencontrées en tout début de vie. Les conditions rencontrées durant l'ontogénie peuvent avoir un effet permanent sur les individus. Par exemple, une réduction du taux de croissance pendant cette période, due à des conditions inclémentes, peut avoir des conséquences sur la taille corporelle à maturité (Larsson et Forslund 1991) et ainsi influencer la survie ou l'âge à la première reproduction (Spear et Nur 1994, Sedinger et al. 1995, Prévot-Julliard et al. 2001). Dans les environnements saisonniers où des périodes d'abondance de nourriture alternent avec des périodes de faible abondance, la date de naissance d'un individu est souvent un bon indice de la qualité de son environnement durant sa croissance (Lepage et al. 1998). Les besoins nutritifs des jeunes sont à leur apogée au début de la croissance si bien que les individus devraient synchroniser leur reproduction pour que leurs jeunes profitent de conditions d'alimentation optimales (Blondel et al. 1993). Plusieurs études chez les oiseaux ont démontré l'importance de la date de naissance sur la croissance des jeunes et leur taille adulte finale (Cooch et al. 1991, Larsson et Forslund 1991, Lepage et al. 1998). La date de naissance peut donc influencer la survie et le recrutement d'une variété d'espèces aviaires (ex. Spear et Nur 1994, Verboven et Visser 1998, Dawson et Clark 2000, Prévot-Julliard et al. 2001).

Les conditions environnementales rencontrées par les individus au moment de la reproduction ou durant la période précédant un épisode de reproduction peuvent aussi avoir des effets importants sur celle-ci. Par exemple, des contraintes énergétiques rencontrées entre les épisodes de reproduction chez certaines espèces d'oiseaux marins expliqueraient leur cycle de reproduction bisannuel (Chastel 1995). De même, il est suspecté depuis longtemps que les conditions climatiques printanières peuvent avoir des conséquences sur la probabilité de reproduction des oies nichant dans l'Arctique (Barry 1962), même si peu d'études aient été en mesure de le confirmer directement (voir Prop et de Vries 1993 pour une exception). Les réserves accumulées sur les haltes migratoires printanières, tout comme celles accumulées en période de pré-ponte sur les sites de reproduction, peuvent influencer la date de ponte et le nombre d'œufs produits (Ankney et MacInnes 1978, Ganter et Cooke 1996, Lepage et al. 2000). De plus, un retard de la fonte de neige peut retarder l'atteinte d'un seuil minimal de condition permettant la reproduction (Rowe et al. 1994, Bêty 2001).

Finalement, les interactions trophiques peuvent aussi avoir un effet sur les coûts de la reproduction et même l'investissement reproducteur. Ainsi, une augmentation de la pression de prédation sur les nids peut diminuer considérablement la probabilité de succès d'une reproduction et même en augmenter les coûts si les adultes sont aussi susceptibles à la prédation. Des fluctuations considérables dans l'abondance et la productivité des espèces d'oiseaux nichant dans les milieux nordiques ont été notées, parallèlement aux variations d'abondance de petits mammifères (Summers et Underhill 1987, Ebbinge 1989). Ceci est dû à des effets indirects entre oiseaux et mammifères ayant des prédateurs communs (Bêty et al. 2002). D’autre part, il a été démontré que la simple présence de prédateurs sur les sites de nidification en période pré-reproductrice pouvait être suffisante pour empêcher certaines espèces d’oies Arctiques de nicher, et donc de réduire leur investissement reproducteur (Spaans et al. 1998).

Même si plusieurs chercheurs se sont intéressés à l’influence de la variabilité environnementale sur différents traits d’histoire de vie (ex. Boyce et Perrins 1987, Sedinger et al. 1995), l’effet de cette variabilité sur la proportion d’individus entrant dans le segment reproducteur de la population (recrutement) ou sur les probabilités de reproduction d’adultes sexuellement matures est encore très mal connu (mais voir Prop et deVries 1993, Anderson et al. 2001, Sedinger et al. 2001).

Objectifs de la thèse

Les principaux objectifs de cette thèse sont de quantifier l’investissement et les coûts associés à la reproduction ainsi que l’effet des conditions environnementales sur la démographie d’une population d’oiseaux migrateurs nichant dans le Haut-Arctique, un environnement hautement variable. D’une part, j’aborde certains aspects des coûts de la reproduction en examinant à quel point l’investissement dans la reproduction actuelle est un compromis par rapport à la survie et à la reproduction future des parents (Williams 1966, Stearns 1992). D’autre part, je traite de l’effet des conditions environnementales sur la démographie, plus particulièrement sur le recrutement d’individus dans le segment reproducteur de la population et sur la probabilité de reproduction des individus matures sexuellement. Ma thèse intègre donc des aspects évolutifs et démographiques qui sont essentiels à la compréhension des forces évolutives qui façonnent les traits d’histoire de vie et la dynamique des populations.

Système à l’étude

L’espèce à l’étude dans ma thèse, la Grande Oie des neiges (*Chen caerulescens atlantica*), représente un bon modèle pour l’étude des coûts de la reproduction et des traits d’histoire de vie. La Grande Oie des neiges est une espèce longévive dont l’espérance de vie est d’environ 6 ans après la première année. Les Anserinae sont monogames et accouplés pour la vie, le taux de divorce étant généralement peu élevé (Owen et al. 1988). Les deux parents participent aux soins parentaux, et ce durant les périodes de pré-ponte, d'incubation (Gauthier et Tardif 1991), et d'élevage des jeunes avant (Sedinger et Raveling 1990) et suivant l'envol (Turcotte et Bédard 1989a). Bien qu'il s'agit d'une espèce nidifuge, elle prodigue des soins de longue durée à ses jeunes, s'échelonnant jusqu'à un an (Prevett et MacInnes 1980, Gauthier et Tardif 1991, Reed 1993), et parfois plus (Ely 1993, Warren et al. 1993), contrairement à la majorité des espèces d'oiseaux. Ainsi, la période des soins parentaux se prolonge fréquemment jusque dans la période pré-reproductrice suivante.

Les soins parentaux se présentent sous plusieurs formes: vigilance, défense active des jeunes contre les prédateurs, utilisation des sites propices à l'apprentissage des jeunes, etc. Cet investissement parental se répercute sur le budget d'activité des adultes, laissant une moins grande proportion du temps disponible pour l'alimentation (Black et Owen 1989a et b, Lazarus et Inglis 1978, Lessells 1987). Chez les Anserinae, la majorité des soins parentaux, sous forme de vigilance et d'apprentissage, sont non-dépréciables (Lazarus et Inglis 1986). Ainsi, le niveau d'investissement associé à ces soins est indépendant de la taille de la couvée. Par contre, le chevauchement entre les soins parentaux et la période pré-reproductrice subséquente peut représenter un coût qui est absent pour des espèces où les soins parentaux se terminent plusieurs mois avant cette période.

À l'intérêt académique de cet ouvrage s'ajoute un aspect appliqué de grande importance. À l'instar de plusieurs autres espèces d'oies à travers le monde, la population de la Grande Oie des neiges a augmenté considérablement au cours des dernières décennies. D'environ 50 000 individus à la fin des années 1960, elle atteint aujourd'hui près de 800 000 individus (Reed et al. 1998). L'intensification de l'agriculture sur les aires d'hivernage et de migration est identifié comme un des principaux facteurs responsable de cette récente croissance démographique (Batt 1998). Cette explosion démographique est associée à une pression de broutement accrue sur les sites de reproduction et les haltes migratoires de l'espèce. De plus, les oies peuvent avoir un impact majeur sur la dynamique des communautés végétales de ces habitats fragiles (Giroux et Bédard 1987, Giroux et al. 1998). Les décisions de gestion associées à cette population sont en large partie basées sur des modèles de populations utilisant les connaissances acquises sur les différents paramètres démographiques de l'espèce (Gauthier et Brault 1998). Ma thèse comblera certaines lacunes dans les connaissances liées à la dynamique de la population de la Grande Oie des neiges, plus particulièrement en ce qui a trait au recrutement d'individus dans la population reproductrice et l'estimation de la probabilité de reproduction des adultes.

La présente étude se base sur un programme de marquage à long-terme (bagues et colliers) avec des recaptures l'été et des réobservations à toutes les saisons.

Importance de l'approche méthodologique

La majorité des études en biologie évolutive requièrent l'estimation de paramètres démographiques tels la survie, la probabilité de reproduction, l'âge à la maturité, etc. Ces paramètres sont difficiles à estimer dans les populations sauvages et ce n'est que récemment que des méthodes permettant d'obtenir des estimations non-biaisées à partir de données de capture-marquage-recapture (CMR), ont été développées (Lebreton et al. 1992). Parce qu'il est pratiquement impossible d'échantillonner les individus d'une manière exhaustive sur le terrain, il est essentiel de prendre en compte l'intensité d'échantillonnage (probabilités de recapture ou de réobservations), et c'est justement ce que la méthodologie de CMR permet de faire. Malheureusement, très peu d'études ont jusqu'à maintenant utilisées ces méthodes pour tester des hypothèses évolutives comme celle du coût de la reproduction, et ce malgré le fait qu'il ait été clairement démontré que de ne pas utiliser ces méthodes peut mener à des conclusions erronées (Clobert 1995).

L'approche de CMR classique permet l'estimation de paramètres démographiques d'individus marqués et capturés à un seul site (e.g. Pollock et al. 1990). Cependant, des développements récents dans les outils de modélisation et les logiciels (White et Burnham 1999) permettent maintenant de recapturer / réobserver les individus dans plusieurs états (locations géographiques ou état physiologique, reproducteur, etc.). Il est ainsi possible d'étudier les mouvements entre ces états (Hestbeck et al. 1991, Brownie et al. 1993, Nichols et al. 1994). Ces modèles multi-états sont bien adaptés à l'étude comparative de différents comportements ou traits d'histoire de vie dans un contexte d'écologie évolutive

(Nichols et Kendall 1995). L’utilisation d’information provenant de diverses sources dans des modèles de CMR, bien qu’encore peu répandue, représente aussi une autre approche qui a un fort potentiel pour l’étude de certains paramètres démographiques (Lebreton et al. 1999). Bref, les développements récents dans les méthodologies de CMR nous permettent maintenant d’étudier des paramètres démographiques qui demeuraient jusqu’ici difficiles à quantifier.

L’application de méthodes de CMR à l’étude des traits d’histoire de vie requiert qu’on puisse reconnaître (recapturer ou réobserver) des individus d’identité connue. À cette fin, plusieurs types de marqueurs, portant des codes individuels, ont été développés. Chez la sauvagine, certains types de marqueurs externes permettent aux observateurs de déterminer l’identité d’un individu à distance, sans qu’une recapture “physique” soit nécessaire. Ainsi, l’utilisation de colliers de plastique portant un code alphanumérique individuel a pris une importance considérable dans l’étude des populations d’oies en Amérique du Nord (Fjetland 1973, Hestbeck et al. 1991). L’utilisation de colliers est avantageuse comparé à d’autres types de marquers comme les bagues car elle permet d’obtenir beaucoup plus de données à partir des réobservations des individus marqués.

L’application de marqueurs sur les individus, bien qu’essentielle pour des analyses de CMR, n’est pas sans comporter certains risques. En effet, une prémisse importante des modèles de CMR est que le comportement et la survie des individus marqués ne diffèrent pas du reste de la population (Jolly 1965, Seber 1965, Brownie et al. 1985). Les effets négatifs potentiels des marqueurs sur les individus ont souvent suscité des débats, notamment chez les oies (ex. Samuel et al. 1990) et les manchots (Jackson 2002). Il a été démontré que, dans certains cas, les colliers réduisaient la survie (Ballou et Martin 1964, Ankney 1975, Castelli et Trost 1996, Schmutz et Morse 2000), ainsi que la probabilité de nicher (Lensink 1968) chez certaines espèces d’oies. La présence d’une telle hétérogénéité risque donc de biaiser les résultats obtenus si elle n’est pas prise en compte. Pour évaluer ce problème, il est suggéré d’utiliser un groupe témoin marqué avec des bagues tarsales, dont l’innocuité est reconnue, en parallèle avec un groupe portant des colliers afin de pouvoir comparer les deux (Castelli et Trost 1996, Alisauskas et Lindberg 2002).

Division de la thèse

Dans un premier chapitre, j'aborde une question importante à la compréhension des stratégies d'investissement dans la reproduction. Parce que la durée des soins parentaux suivant l'envol des jeunes peut s'avérer une composante importante du coût de la reproduction chez les oies, il est essentiel de mieux connaître la variabilité individuelle dans la durée de ces soins. En utilisant une approche de suivi individuel de femelles marquées et de décomptes dans la volée, je quantifie la probabilité de bris de familles à l'intérieur d'une année ainsi que les variations inter-annuelles. Ceci me permet d'identifier la période à laquelle les conflits parentaux dans l'allocation des soins apparaissent. J'étudie aussi la relation entre des indices de qualité des parents et des jeunes pour déterminer s'ils peuvent expliquer la variabilité individuelle dans la durée des soins parentaux. Je teste l'hypothèse que la séparation des membres d'une famille (parents et jeunes) sera plus importante à l'approche de la prochaine saison de reproduction.

À l'intérieur du deuxième chapitre, j'aborde une des hypothèses centrales à la théorie des histoires de vie, soit la présence possible de coûts, en terme de reproduction et de survie future réduite pour les parents, associés aux soins parentaux prolongés. Je teste la prédiction que les coûts pour les parents seront additifs à la durée des soins qu'ils prodiguent et donc que les coûts seront plus importants pour les femelles encore associées à des jeunes au printemps (10 mois après la naissance des jeunes) que pour celles associées à des jeunes à l'automne (3 mois après la naissance).

Le troisième chapitre aborde un aspect écologique important qui constitue une des prémisses de base de la majorité de mes analyses. Ce chapitre porte sur la migration de mue de femelles adultes en relation avec leur statut et leur succès reproducteur. Pour plusieurs études démographiques faisant appel à des données de capture-recapture, il est essentiel de savoir quel segment de la population est échantillonné. En utilisant des données de femelles marquées avec des émetteurs radios, il m'est possible de déterminer la probabilité qu'une femelle adulte quitte l'aire d'étude et entreprenne une migration de mue en fonction de son effort reproducteur et de son succès de nidification à différents moments de la saison de reproduction.

Le quatrième chapitre traite de l’effet possible du collier sur la probabilité de survie et de reproduction des femelles adultes. Une première étude chez la Grande Oie des neiges n’a pas révélé d’effets sur la survie mais a fourni des évidences indirectes que le collier pourrait interférer avec la reproduction (Menu et al. 2000). La présence d’un effet négatif du collier sur la reproduction, si elle s’avérait fondée, peut quand même présenter certains avantages, comme celui d’être vu comme une manipulation expérimentale augmentant le coût de la reproduction (Schmutz et Morse 2000). Je teste donc l’hypothèse que le collier pourrait réduire l’effort reproducteur des femelles, possiblement en augmentant la dépense énergétique lors de la migration. Cette analyse peut donc nous aider à mieux comprendre le processus d’allocation optimale des ressources dans la reproduction et la survie chez les oiseaux.

Le cinquième chapitre porte sur l’effet des conditions environnementales rencontrées durant la première année de vie des individus et lors de leur première reproduction sur la probabilité de recrutement et l’âge à la première reproduction. Le processus de recrutement est encore très mal connu chez les vertébrés dû à la difficulté d’estimer les différentes composantes de ce trait d’histoire de vie en milieu naturel. Des conditions environnementales difficiles rencontrées tant en début de vie qu’au moment où les individus commencent à se reproduire, peuvent mener à un report de la première reproduction. J’ai donc étudié l’effet de la date de naissance individuelle et de la qualité de l’année de naissance (date de ponte médiane), ainsi que la couverture de neige et la densité de lemmings au moment de se reproduire, sur la survie juvénile et l’âge à la première reproduction chez l’oie des neiges.

Finalement, le sixième et dernier chapitre traite de la variabilité annuelle dans la probabilité de reproduction de femelles matures, et des facteurs environnementaux qui influencent cette variabilité. Si la reproduction est coûteuse, une plus grande proportion de femelles ne devrait pas se reproduire durant les années où les probabilités de reproduction avec succès sont réduites ou lorsque leur condition corporelle est réduite. Dans cette analyse, je teste l’effet des conditions climatiques sur les aires de reproduction et l’effet d’une chasse de printemps qui a mené à une réduction de la condition corporelle des oies lors de leur halte migratoire. Mes prédictions sont que la probabilité de reproduction sera négativement corrélée à la couverture de neige sur les sites de reproduction en période de pré-ponte et à l’occurrence d’une chasse sur la halte migratoire printanière.

CHAPITRE 1

DURATION OF FAMILY BONDS IN GREATER SNOW GEESE: A MARK-RESIGHT APPROACH

Eric T. Reed, Gilles Gauthier, Austin Reed.

Résumé

L'étude des relations parents-jeunes est souvent biaisée par une survie ou une probabilité d'observation différente des parents et des individus non-parentaux. Nous avons utilisé un mélange de modèles de capture-réobservation multi-états et de décomptes dans la volée pour déterminer la durée d'association entre parents et jeunes chez la Grande Oie des neiges (*Chen caerulescens atlantica*) durant deux années successives. Nous avons examiné la variation annuelle dans le bris des familles ainsi que tenté d'expliquer les différences individuelles dans la durée de ces liens. Le taux de bris de famille était modéré entre l'automne et l'hiver (0.41 ± 0.08, moyenne ± 1SE), faible entre l'hiver et le printemps (0.32 ± 0.09), et élevé entre le printemps et l'été (0.69 ± 0.12). La proportion de jeunes seuls dans la volée ne variait pas (0.14 ± 0.02) alors que la proportion de couples accompagnés de jeunes diminuait de plus du deux tiers entre l'automne et le printemps (0.63 ± 0.04 à 0.19 ± 0.08). Il n'y avait pas de variation détectable du taux annuel de bris de famille. La durée de l'association entre les parents et leurs jeunes était indépendante de la taille de la couvée à l'automne, de l'âge de la mère et de la date de naissance des jeunes (un index de la qualité des jeunes). Les adoptions observées étaient rares et résultaient sans doute plutôt de mauvaises identifications du statut familial que de vrais adoptions. Nous suggérons que le bris de famille entre l'automne et le printemps était surtout due à la mortalité des jeunes, alors que la séparation des parents et des jeunes augmentait entre le printemps et l'été. Ceci suggère l'apparition d'un conflit parental à l'approche de la prochaine saison de reproduction des parents.

Abstract

Studies of parent-offspring relationships are often biased by differential survival or sighting probabilities of parental and non-parental birds. We used a mixture of multistate mark-resight models and group counts to determine the length of parent-offspring association in Greater Snow Geese (*Chen caerulescens atlantica*) in two consecutive years. We searched for correlates of parental care and examined annual variation in family break-up. Rate of family break-up was moderate between fall and winter (0.41 ± 0.08, mean ± 1SE), lower between winter and spring (0.32 ± 0.09), and highest between spring and summer (0.69 ± 0.12). The proportion of lone juveniles in the flock remained stable (0.14 ± 0.02) but the proportion of pairs with young decreased more than three-fold between fall and spring (0.63 ± 0.04 to 0.19 ± 0.08). There was no annual variation in the rate of family break-up. Length of parent-offspring association was independent of fall brood size, age of parental females and hatch date of offspring (an index of offspring quality). Observed adoptions were rare and likely resulted from misidentification of family status rather than true adoptions. We suggest that family break-up between fall and spring was mostly due to offspring mortality, whereas separation of parents and offspring increased between spring and summer, indicative of parent-offspring conflicts prior to the parents' upcoming breeding attempt.

Introduction

The amount of care that a parent invests in its offspring represents a trade-off between increased survival and recruitment of offspring and decreased future survival and reproduction of the parent (Trivers 1974). Because parents are only half as related to an offspring as the offspring is to himself, selection should favor a greater optimum value of parental investment for offspring than for parents, resulting in parent-offspring conflicts over the amount of parental investment provided (Lazarus and Inglis 1986).

In the wild, parents may cease to be associated with their offspring for several reasons: offspring could die or become separated accidentally from their parents (e.g. Prevett and MacInnes 1980), they could leave the family group voluntarily (e.g. Bustamante 1994), or parents could terminate the association by chasing away their young (Prevett and MacInnes 1980, Black and Owen 1989b). Only the latter response would be adaptive on the part of parents. It is thus important, in an evolutionary perspective, to describe the process of family break-up and associated causes in wild populations.

Geese are unique among precocial birds in that they provide long term care to their offspring with family bonds lasting for up to one year (Prevett and MacInnes 1980, Turcotte and Bédard 1989a, Reed 1993) and sometimes beyond (Ely 1993, Warren et al. 1993). Although family break-ups may occur throughout the annual cycle, it possibly increases during spring migration or at the start of breeding (Prevett and MacInnes 1980, Black and Owen 1989a, Gauthier and Tardif 1991). Because providing parental care in spring overlaps with the period of nutrient storage essential for the forthcoming migration and reproduction (Ankney and MacInnes 1978, Choinière and Gauthier 1995, Ebbinge and Spaans 1995, Gauthier et al. 1992) and with pre-breeding activities, parental care may be more costly at that time than at any other time of the year for females.

Previous studies that have investigated the process of family disintegration in geese have relied solely on group counts (e.g. Jones and Jones 1966, Lambeck 1990, Gauthier and Tardif 1991) or a combination of observations on marked birds and group counts (Prevett and MacInnes 1980, Ely 1993, Reed 1993, Black and Owen 1989a). These methods may however suffer from several biases. For instance, group counts may be subject to observer bias or may be affected by differential migratory behavior of social classes (e.g. breeders vs. non-breeders). Studies relying on marked birds are more robust but biases may occur if differences in sighting or survival probabilities between parents and non-parents are not accounted for.

Recent developments in mark-resight data modeling provide robust tools for addressing questions of interest to evolutionary ecology (Nichols and Kendall 1995). In particular, multistate mark-resight models can be used to estimate survival, sighting and transition probabilities in a population stratified by state variables (Arnason 1973, Brownie et al. 1993, Nichols et al. 1994). We used this approach to quantify seasonal family break-up in Greater Snow Geese (*Chen caerulescens atlantica*) in two consecutive years. We also searched for correlates of parental care in terms of female experience and gosling recruitment prospects. These data were supplemented by group counts in unmarked flocks in order to quantify seasonal changes in brood size, proportion of paired adults accompanied by young and lone juveniles (orphans) in the population. Because Greater Snow Geese provide mostly unshared parental care (i.e. independent of brood size, Lazarus and Inglis 1986) in the form of anti-predator defense, teaching feeding techniques and migratory routes, and access to prime food patches through intraspecific aggressive interactions, we focused on complete family break-up independently of brood size.

Methods

Study area

In 1997-1998, observations were conducted on the breeding and fall and spring staging areas. In 1998-99 observations were also extended to wintering areas. Fall observations were made along the St-Lawrence River estuary, Canada, and adjacent farmlands between 1 October and 5 November (36 days, median date of observations: 15 October) (see Figure 1 for map of study area). Winter observations were conducted in the core of the winter range, in the states of Delaware, Maryland, New Jersey and Virginia, USA, between 4 and 28 January (24 days, median: 20 January). Spring observations were also conducted along the St-Lawrence estuary and adjacent farmlands between 1 April and 24

May (53 days, median: 28 April). Finally, summer observations were conducted on Bylot Island, Nunavut Territory, Canada, between 27 May and 17 July (45 days, median: 22 June), during the pre-nesting and nesting periods. The summer sample is biased towards breeders because most non-breeders or failed-nesters, including yearlings, emigrate from the study area prior to molting (Abraham 1980, Reed et al. 2003a).

Observations of marked individuals

Adult breeding females were captured in late summer and fitted with coded plastic neck bands between 1989 and 1998 on Bylot Island (see Menu et al. 2001 for details). Goslings were also marked with coded plastic leg bands in 1998. All geese were sexed and aged (gosling/adult) at marking and morphometric measurements (culmen, head, tarsus and 9th primary length) and body mass were taken on most goslings.

Telescopes (20-60X) were used to determine age class of individuals, identify family units, and read coded neck bands or tarsal bands at all study sites. Juveniles were easily identified by their gray plumage throughout their first year of life. We considered as families small groups consisting of two (occasionally one or three) adults and 1-8 juveniles showing strong cohesiveness in their movements, in which one or both parents engaged in agonistic interactions with other geese in apparent defense of young, or in which adults displayed behaviors indicative of long term bonding such as the triumph ceremony (Black and Owen 1989b, Reed 1993). Our data set consisted of observations of neck-banded females and their family status, and observations of juveniles with tarsal bands and their family status (1998-99 only) in each of the 4 seasons.

Neck-banded females were observed for as long as needed to determine association with young of the year. Because sighting periods spanned a long period and family break-up could occur within periods, a marked female was considered as being associated with young during that period if it was confirmed once in that state even if it was seen later without young. An analysis of multiple observations of marked females (fall 1998 data) indicated that the probability of assigning the wrong family status to a female was between 3.8 and 5.9%, such that using single observations of a female should not result in serious biases (Chapitre 2).

Group counts

Group counts were conducted in early fall 1997 and 1998 (between 1 and 23 October and 5 to 15 October, respectively), before the disruptive effects of hunting on social group integrity. Group counts were also performed in winter and in spring 1999 in order to document changes in social group structure over a year. Group counts on the breeding grounds were not used because the sample of geese there is strongly biased towards breeders and hence is not representative of the entire population.

Flocks of unmarked Greater Snow Geese were scanned and all social groups noted in undisturbed situations. Typically, counts were conducted when geese were arriving at or, less frequently, departing from a feeding or roosting site (Lynch and Singleton 1964). To avoid double counting, only groups or individuals seen landing or departing were noted at a given site. Observations ceased when a disturbance occurred and the flock took flight.

The number of families and their associated brood size were noted as well as all other recognizable social groups (pairs without young, single adults, lone juveniles, one and three parent families). When it was not possible to differentiate social groups (e.g. in large multi-family flocks), we tallied the number of young and adults. Data from group counts thus provided information on brood sizes, percent juveniles in the flock, proportion of paired adults with young and proportion of unattached juveniles (orphans). Only data from identifiable social groups were used.

We analyzed group count data with linear models when the dependent variable was a proportion (e.g. proportion of orphans in the flock), modeling our data following a Poisson distribution (GENMOD procedure, SAS Institute 1996). We assessed the significance of an effect with Likelihood Ratio statistics for type3 analysis. When the dependent variable followed a normal distribution, we used an ANOVA for unbalanced design (GLM procedure).

Analysis of family break-up

We quantified intra-annual family break-up by analyzing the 1998-1999 resight data with multistate mark-recapture models (Brownie et al. 1993, Nichols et al. 1994). These models allow the estimation of transition probabilities (from one state to another), survival, and sighting probabilities for each period. The state variable was the family status (presence or absence of young) of a marked female and transition probabilities represented the probability that a female will lose her young (family break-up) or alternatively that she will adopt young from one season to the next (adoption). Since transition probabilities from a given state sum up to 1, we could also derive the probabilities for a female to keep her young or to remain unassociated with young.

The factorial structure of a model was represented by subscripting survival (S), transition (Ψ), and sighting rate (p). Our base model (S_{g*t}, Ψ_{g*t}, p_{g*t}) included family status (g), season (t) effects and their interaction on survival, transition and sighting probabilities.

There are no goodness-of-fit (GOF) tests for multistate models. We thus assessed the fit of our general model by pooling all data into one state with classic GOF tests developed for the Cormack-Jolly-Seber model using program RELEASE (Burnham et al. 1987).

We analyzed the data using program MARK v1.9 (White and Burnham 1999). The time series ran from fall to early summer and unequal time intervals between sighting periods were taken into account for survival probabilities. However, because transition probabilities are for the whole time interval independently of its length, models where transition probabilities were constant across periods or followed a linear trend through time had no clear biological interpretation and were thus not considered.

We used AICc to select the best model based on the principle of parsimony (Burnham and Anderson 1998). When differences in AICc were small, we computed a weighed average of the parameter of interest using AICc weights (ωAICc), which represent the weight of evidence in support of each model in the set of candidate models (Burnham and Anderson 1998).

Inter-annual differences in family break-up (i.e. 1997-1998 vs. 1998-1999) were evaluated in a separate analysis because no observations were conducted in winter 1997-98. Therefore, we had to ignore this occasion and examined for differences in family break-up probabilities between fall - spring and spring – early summer. We included a year effect (and interactions with other variables) on survival (*S*), transition (Ψ) and sighting rates (*p*) in our general model. Years were treated as two separate groups because capture histories started in fall and ended in summer. To avoid pseudoreplication, we retained only one time series per individual, keeping the first year in which an individual was observed.

Correlates of family break-up

Brood size

If families break up gradually, parents with large broods should be associated with at least some young for longer than parents with small broods. We used logistic regression (GENMOD procedure, SAS Institute 1996) to investigate the relationship between brood size of marked females in fall and the probability of being still associated with at least one offspring in winter and spring. We used the highest brood size recorded for a given female as her original fall brood size. Mean brood sizes of typical families (2 adults) from group counts in fall 1997-98 and 1998-99 were also compared with a t-test to assess annual differences in brood size.

Age of females

The ability to provide parental care for extended periods may be dependent on a female's age and previous breeding experience. We tested whether mean age of neck-banded females accompanied by young differed from that of females without young using an ANOVA for unbalanced designs. Because we had too few marked females of known age, we used minimum age as a surrogate. Minimum age was defined as the number of years elapsed since marking as a breeding adult plus 2 years because Snow Goose females do not breed before age 2 (Cooch et al. 1999a, Reed et al. 2003b). We used only females that had been marked in 1997 or earlier (at least 3 years old).

Hatch date of juveniles

The amount of parental care that a female invests may depend on the quality and recruitment prospects of her offspring. In geese, hatch date is negatively correlated with growth and survival to breeding age (Cooch et al. 1991, Sedinger et al. 1995, Lepage et al. 2000). Hatch date can be calculated by the difference between capture date and age at capture. Age was estimated from a linear model of age as a function of the length of the 9th primary wing feather established in a sample of known-age goslings in 1998 (see Lepage et al. 1998 and Cooch et al 1999a for details). The relationship used was:

$$\text{Age} = 0.085 \cdot 9^{\text{th}} \text{ primary length (mm)} + 25.17$$

$$(n = 78, R^2 = 0.77, \text{Reed et al. 2003b})$$

Observations of juveniles with tarsal leg bands associated with a marked female in fall, winter and spring 1998-1999 were used. We tested for differences in mean hatch date of broods among seasons with an ANOVA for unbalanced designs.

Unless otherwise mentioned, mean ± 1SE are presented and all statistical tests are two-tailed.

Results

Analysis of family break-up

Intra-annual family break-up

We observed and determined the family status of 2008 marked females (fall: 883, winter: 371, spring: 754) and collected 564 resightings in 1998 - 1999 (winter: 140, spring: 363, summer: 61). Goodness of fit tests indicated that our general model fitted well the data (global test: $\chi^2_4 = 4.45$, $P = 0.35$).

Uncertainty in model selection (our top 6 models had $\Delta\text{AICc} \leq 2$, Table 1) was largely due to survival and sighting probabilities. Survival of adult females was constant over time and did not differ between parental and non-parental birds in 4 of these 6 models (cumulative $\omega\text{AICc} = 0.56$), whereas sighting rates varied over time and differed between the 2 groups. In all models, transition probabilities varied over time and differed between non-parental ($\Psi^{\text{NY-Y}}$, i.e. adoption) and parental birds ($\Psi^{\text{Y-NY}}$, i.e. total brood loss). Since our main interest was on estimation of transition probabilities rather than on testing specific hypotheses, we averaged parameter estimates across all candidate models.

The rate of family break-up was highest between spring and early summer, intermediate between fall and winter and, lowest between winter and spring (Fig. 2). Adoptions were rare and followed the same pattern (Fig. 2). Survival of adults was estimated at 0.929 ± 0.031 per 56-day period. Sighting probabilities were lowest in early summer and highest in spring, with parents having lower sighting probabilities (range: 0.032 ± 0.009 to 0.299 ± 0.060) than non-parents (0.055 ± 0.009 to 0.426 ± 0.046).

Inter-annual differences in family break up

We observed and determined the family status of 646 marked females in 1997-98 (fall: 358, spring: 288), resulting in 177 resightings (spring: 66, summer: 111). In 1998-99, excluding the winter observations, we observed 1022 marked females (fall: 655, spring: 367), resulting in 237 resightings (spring: 200, summer: 37). It was not possible to conduct GOF tests on our general model with only 3 sighting occasions.

Our top 5 models (ΔAICc < 2.0) again provided little evidence that survival probabilities differed between parental and non-parental birds and season, and evidence for a year effect was weak (cumulative ωAICc for a year effect: 0.354). Sighting probabilities varied between seasons and years (Table 2). Three of our top 5 models indicated that probabilities of family break-up ($\Psi^{Y\text{-}NY}$) were similar between years but varied by season, whereas the other two indicated that they varied by year and season. Average family break-up was higher between spring and early summer than between fall and spring in both years (Fig. 3), a result consistent with the more detailed intra-annual analysis.

In contrast, adoption probabilities ($\Psi^{NY\text{-}Y}$) varied between years and seasons (both effects present in the five top models, Table 2). Adoption probabilities were very low but tended to be higher between fall and spring than between spring and early summer in 1997-98, a trend opposite the one found in 1998-99 (Fig. 3).

Correlates of family break-up

Brood size

Mean brood size in fall was slightly higher in 1997 (2.69 ± 0.04, n = 1222 broods) than in 1998 (2.52 ± 0.03, n = 1440; t = 3.24, P = 0.001). However, there was no effect of fall brood size on the probability for a female to be still associated with offspring in winter (χ^2_1 = 0.16, P = 0.69, n = 24) or spring (χ^2_1 = 0.08, P = 0.78, n = 63). Mean brood size in fall for families still intact in winter was 1.71 ± 0.29 (n = 7) compared to 1.94 ± 0.21 (n = 17) for broken up families (similar values for fall to spring were 1.94 ± 0.26, n = 23, and 1.93 ± 0.15, n = 40, respectively). Thus, there was no evidence that fall brood size was related to the duration of parent-offspring association.

Age of mothers

We observed 1577 females which were 3 years old or more in 1998 - 99 (range: 3 to 16 years of age, mean: 4.88 ± 0.06). Age of females did not vary between parental and non-parental geese or by season (season: $F_{3,\,1569} = 0.03$, $P = 0.99$; family status: $F_{1,\,1569} = 0.72$, $P = 0.40$; interaction: $F_{3,\,1569} = 0.27$, $P = 0.85$). Therefore, it appears that females of all ages were as likely to remain with at least part of their brood throughout winter and spring.

Hatch date of broods

We observed 87 leg-banded goslings (from 41 broods) associated with a neck-banded female and for which hatch date could be estimated. Mean hatch date of broods (in Julian days) still associated with parents decreased by 1.5 d between fall and spring (fall: 185.9 ± 0.4; winter: 185.3 ± 1.0; spring: 184.4 ± 0.5) but this decline was not significant ($F_{2,\,38} = 2.75$, $P = 0.08$). Thus, there was no evidence that the length of association between parents and offspring differed between early and late-hatched broods.

Group counts

The proportion of paired adults accompanied by young decreased more than 3-fold from fall to spring in our group counts (Table 3). Seasonal differences were marginally significant (χ_2^2 = 6.00, P = 0.0497). Mean brood size (n = 2044) decreased steadily between fall and early summer (fall: 2.52 ± 0.03, winter: 1.93 ± 0.09, spring: 1.51 ± 0.06, summer: 1.34 ± 0.22; season effect: $F_{3,\ 2040}$ = 85.4, P < 0.001). The proportion of orphaned young followed an opposite trend during that period (Table 2), but this increase was not significant (χ_2^2 = 3.30, P = 0.19). Mean proportion of orphans in the counts was 0.14 ± 0.02. Thus, both the proportion of pairs with young and brood size declined from fall to spring, but the proportion of orphans in the flock remained stable during that period.

Discussion

We showed that the probability of family break-up was moderate between fall and winter, low between winter and spring and highest between spring and early summer. Thus family break-up peaked just prior to breeding. Our results are consistent with other studies that concluded that the rate of family break-up was highest either during the last stages of spring migration (Black and Owen 1989a), or just prior to or during egg laying on the breeding grounds (Prevett and MacInnes 1980).

The multistate mark-recapture approach that we used allowed us to circumvent many of the potential biases associated with the follow up of marked individuals in time. We were able to correct our estimates of family break-up for differences in survival and sighting probabilities between parental and non-parental females, as well as for seasonal variation. This was important, as sighting probabilities differed across seasons and between parental and non-parental geese.

The pattern of family break-up that we described was also consistent across years even though conditions were quite different. Mean brood size in fall was higher in 1997 than in 1998, there was a spring conservation hunt on Greater Snow geese in 1998-99 but not in 1997-98, and breeding effort was high in summer 1998 but very low in 1999. Nevertheless, it appears that the process of family disintegration was not very sensitive to increased harvest of young in 1998-99, or to different probabilities of upcoming reproduction. Our results also showed that, within a year, fall brood size did not have a significant influence on a female's probability to remain with offspring.

Seasonal differences in estimated family break-up confound mortality of offspring and accidental or voluntary separation. To quantify the importance of each, we would need to estimate juvenile survival for the same periods as family break-up. However, we were unable to observe a sufficient number of plastic leg-banded goslings to provide accurate estimates of seasonal survival of young. High densities of geese on refuges during fall increase the likelihood of accidental separation (Prevett and MacInnes 1980) and the frantic searches of lone juveniles for their parents make them highly vulnerable to hunters (Prevett and MacInnes 1980). There is some evidence that hunting vulnerability of juveniles relative to adults declines steadily from fall to spring (Lemoine 2003). In non-hunted populations of geese, natural mortality rates of juveniles also decrease throughout their first year of life (van der Jeugd and Larsson 1998). This indirect evidence suggests that variations in mortality of juveniles can explain the decline in probability of family break-up between fall and spring. We showed that the proportion of pairs accompanied by young declined during that period but that the proportion of orphans in the flock remained stable, indicating that the rate of family separation remained relatively stable from arrival on fall staging areas to departure from spring staging areas.

In contrast, the large increase in the probability of family break-up between spring and early summer cannot be explained by mortality of the young alone. Family break-ups during that period are likely due to actual separation of adults and young rather than death of offspring. A measurable conflict between parents and offspring appears in spring when parents begin showing aggression towards their young (Turcotte and Bédard 1989b, Black and Owen 1989a). According to Trivers (1974), conflict arises whenever parents should not invest so much in current offspring as to jeopardize their ability to invest in future offspring. Evidence for the occurrence of parent - offspring conflict comes from the fact that lone juveniles in spring spend less time foraging than family juveniles because they are more often attacked by conspecifics (Turcotte and Bédard 1989a), and females associated with offspring in spring suffer increased mortality in the following year than females without young (Chapitre 2, but see Black and Owen 1989a). Thus, we believe that increased family break-up from spring to early summer is the result of parent-offspring conflicts becoming particularly acute during the period immediately preceding breeding rather than through accidental separation of the family.

We could not determine whether break-up was a decision of parents or of offspring. In some species, offspring leave the family group voluntarily (e.g. Bustamante 1994), but in most cases, parents terminate the association by chasing away their young (Prevett and MacInnes 1980, Black and Owen 1989a). Greater Snow Geese have molting areas that are located away from the breeding and brood rearing areas so yearlings do not molt in great numbers on Bylot Island (Reed et al. 2003a). Since geese do not breed as yearlings (Cooch et al. 1999a), it is possible that some choose to fly directly to molting areas during the spring migration rather than follow their parents to the breeding area, thus causing the separation. However, given the advantages of parental care for offspring (e.g. Scott 1980, Black and Owen 1989a, Gregoire and Ankney 1990) and the associated costs for mothers, it seems more likely that parents are responsible for break-ups in Greater Snow Geese.

If families break-up gradually, one offspring at a time, pairs with initial large broods should be associated with at least one of their offspring for longer than those with small broods. In the Barnacle Goose (*Branta leucopsis*), length of parent-offspring association increased with brood size (Black and Owen 1989a), but this was not the case in Greater Snow Geese. Black and Owen's (1989a) study was carried on a population that was not subject to hunting whereas hunting occurred from fall arrival to spring departure in our study. If hunting induces mortality that is not independent among brood members (i.e. if hunting mortality within a brood is dependent on whether a brood mate has already been shot) then this may mask an effect of brood size on the duration of association between parents and offspring.

Younger, inexperienced females may also be less efficient in providing parental care than older, more experienced females (Black and Owen 1989a). Our results indicate that younger females were as likely to be associated with their offspring for long periods than older ones. This result should be viewed with caution though, because we used minimum age as a surrogate for true age and thus there are variations in true age of birds assigned to the same minimum age class. Parental abilities of first-time breeders could also be reduced but we could not investigate this. More data on known age females would provide much insight on this point.

Parents should benefit by associating for longer periods with offspring of better quality. However, it is not clear whether parents provide less parental care to offspring with low survival prospect (Pöysä 1992, 1995) or if abandoning the brood is a salvage strategy in which energetic stress limits the parents' ability to care for their young and results in lower survival of offspring (Bustnes and Erikstad 1991, Kilpi et al. 2001). In arctic nesting geese, hatch date is a good indicator of offspring quality because early-hatched young grow faster (Larsson and Forslund 1991, Lepage et al. 1998), become larger adults (Sedinger et al. 1995), and have enhanced first-year survival (Owen and Black 1989, Lepage et al. 2000). We found no evidence that the duration of parent-offspring association was related to 'quality' of the offspring, as indexed by hatch date.

Adoption of goslings by adults has been described for a few species (Eadie 1988, Choudury et al. 1993, Williams 1994). In our study, the probability of apparent adoption was consistently low and estimates were relatively imprecise. Our classification of family status for an observed female was also prone to errors (between 3.8 and 5.9% within a season, Chapitre 2), thus increasing the probability of detecting apparent adoptions. The fall - winter and winter - spring estimates (0.04 and 0.03) are within our family status determination error rate, suggesting that few, if any, genuine adoptions occurred. The estimate of apparent adoption for the spring – early summer period (0.12) suggests that either misidentification of family status occurred more frequently in spring or that true adoptions occurred between the staging and breeding grounds. We believe that the high probability of apparent adoption between spring and early summer may be mediated by increased errors on family status identification, likely due to looser social bonds between parents and offspring.

Some studies have shown the importance of post-fledging parental care for offspring fitness. Increased first year survival has been related to the length of parent-offspring association in Brown Thornbills (*Acanthiza pusilla*), Siberian Jays (*Perisoreus infaustus*) and Mute Swans (*Cygnus olor*) (Conover et al. 2000, Ekman et al. 2000, Green and Cockburn 2001). The benefits of long-term parent-offspring association may be long lasting and result in early recruitment of offspring in the breeding population (Raveling et al. 2000). However, long-term association may also be costly for the parents if their efforts reduces their survival or future reproductive success. We have evidence, in our study population, that prolonging the period of association with offspring until the following spring entails a survival cost for mothers (Chapitre 2). Thus, parents may adjust their parental effort in order to attain optimal fitness. We have provided evidence that voluntary family break-up is most pronounced between spring staging and arrival on the breeding grounds, and that a large proportion of surviving juveniles are still associated with their parents during spring staging, 10 months or more after hatch. However, heterogeneity in offspring and/or parent quality may still result in different optimum values of parental care among individuals.

Table 1. Model selection of seasonal family break-up in Greater Snow Geese for the year 1998-99. Models include survival (*S*), resighting (*p*) and transition (Ψ) probabilities and are ranked by their AICc value with only the most relevant models being presented. For each model, we give the difference in corrected Akaike's Information Criterion relative to the most parsimonious model (ΔAICc), the model's AICc weight (ωAICc) and the number of estimable parameters (np).

MODEL	ΔAICc	ωAICc	np
S, p_{g+t}, Ψ_{g+t}	0.00	0.182	9
S, p_{g*t}, Ψ_{g+t}	0.11	0.172	11
S, p_{g+t}, Ψ_{g*t}	0.59	0.136	11
S_g, p_{g+t}, Ψ_{g+t}	1.65	0.080	10
S, p_t, Ψ_{g+t}	1.99	0.067	8
S_g, p_{g*t}, Ψ_{g+t}	2.00	0.067	12
S_g, p_{g+t}, Ψ_{g*t}	2.07	0.065	12
S, p_{g*t}, Ψ_{g*t}	2.25	0.059	13
S_t, p_{g+t}, Ψ_{g*t}	2.60	0.049	12
S, p_t, Ψ_{g*t}	2.78	0.045	10
S_g, p_{g*t}, Ψ_{g*t}	4.14	0.023	14
S_t, p_{g*t}, Ψ_{g*t}	4.28	0.021	14
S_{g*t}, p_{g+t}, Ψ_{g*t}	5.00	0.015	14
S_{g*t}, p_{g*t}, Ψ_{g*t}	5.72	0.010	16

Subscript (*g*) distinguishes females accompanied or not by young, and (*t*) represents the time periods (fall, winter, spring, and summer). Interactions between terms in the model are denoted with an (*), additivity with a (+).

Table 2. Model selection of inter-annual family break-up in Greater Snow Geese for the years 1997-98 and 1998-99. Models include survival (*S*), resighting (*p*) and transition (Ψ) probabilities and are ranked by their AICc value with only the most relevant models being presented. Probabilities of family break-up ($\Psi^{\text{Y-NY}}$) and adoption ($\Psi^{\text{NY-Y}}$) are split when required. For each model we give the difference in corrected Akaike's Information Criterion relative to the most parsimonious model (ΔAICc), the model's AICc weight (ωAICc) and the number of estimable parameters (np).

MODEL	ΔAICc	ωAICc	np
S, p_{y*t}, $\Psi^{\text{Y-NY}}{}_{t}$, $\Psi^{\text{NY-Y}}{}_{y*t}$	0.00	0.302	11
S_y, p_{y*t}, $\Psi^{\text{Y-NY}}{}_{t}$, $\Psi^{\text{NY-Y}}{}_{y*t}$	0.67	0.216	12
S, p_{y*t}, Ψ_{y*g*t}	1.30	0.158	13
S_y, p_{y*t}, Ψ_{y*g*t}	1.97	0.113	14
S_g, p_{y*t}, $\Psi^{\text{Y-NY}}{}_{t}$, $\Psi^{\text{NY-Y}}{}_{y*t}$	1.99	0.112	12
S_g, p_{y*t}, Ψ_{y*g*t}	3.29	0.058	14
S_{y*g}, p_{y*t}, Ψ_{y*g*t}	5.81	0.017	16
S_{y*g*t}, p_{y*g*t}, Ψ_{y*g*t}	10.76	0.001	20

Model notation is as in Table 1, except for (*y*) which represents the year.

Table 3. Proportions of juveniles alone or with adults and proportion of paired adults with or without young. Data from group counts conducted in fall, winter and spring 1998-99. Sample sizes represent the number of counts in a season. Mean ± SE of counts by season are presented.

	Juveniles[a]		Adult pairs[b]
	n	Lone	With young
Fall	15	0.11 ± 0.02	0.63 ± 0.04
Winter	6	0.17 ± 0.02	0.41 ± 0.04
Spring	9	0.19 ± 0.04	0.19 ± 0.03

[a] Only juveniles that could be assigned to a social group are considered.

[b] Only groups of 2 adults are considered.

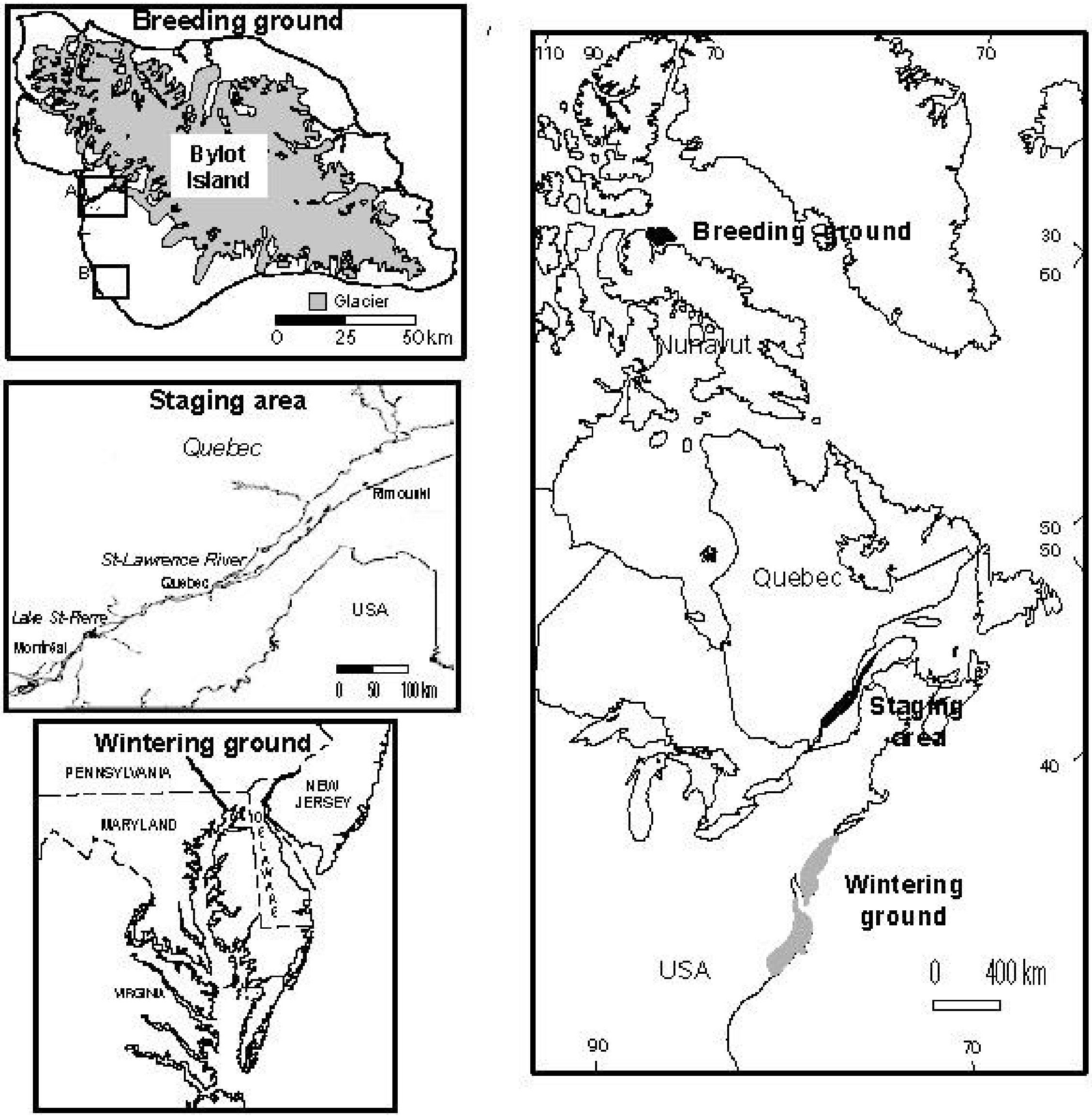

Figure 1. Range of the Greater Snow Goose and study areas. Observations of marked females and captures occurred on the breeding grounds at Bylot Island, Nunavut Territory, Canada. Observations were also conducted during fall and spring staging along the St-Lawrence River estuary, Quebec, Canada, and in winter in Delaware, Maryland, New Jersey and Virginia, USA.

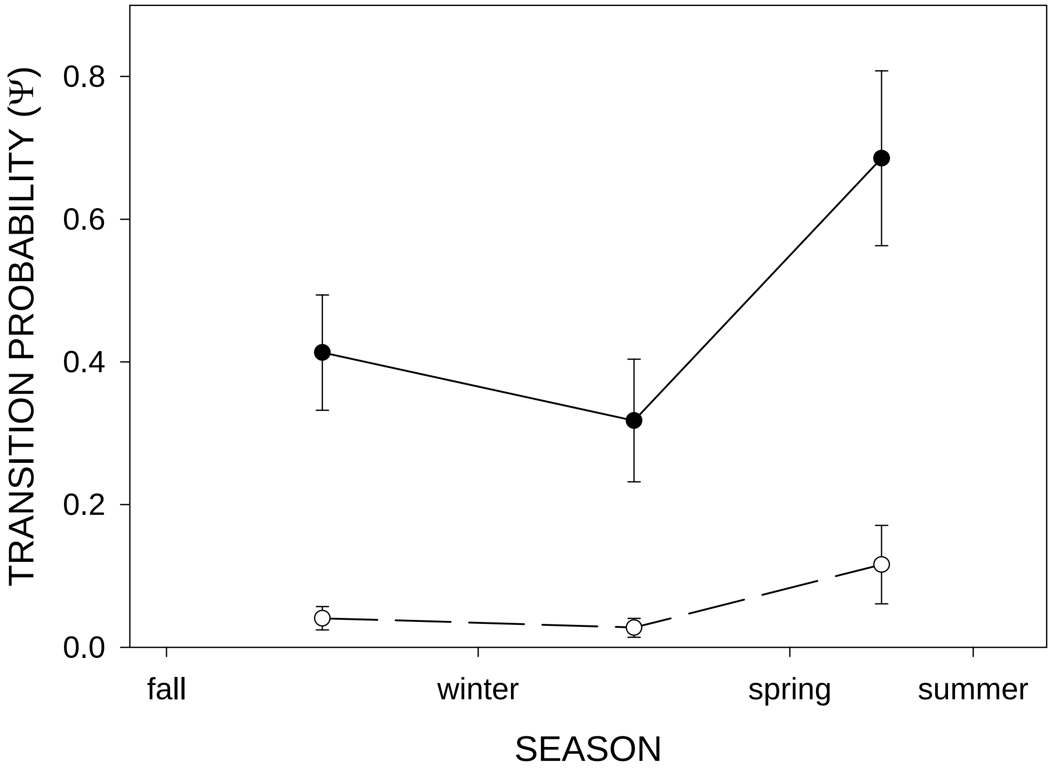

Figure 2. Probability of total family break-up (black dots, transition $\Psi^{Y\text{-}NY}$) and adoption (white dots, transition $\Psi^{NY\text{-}Y}$) of neck-banded female Greater Snow Geese from fall 1998 to summer 1999. Transition probabilities (± SE) are averaged across models.

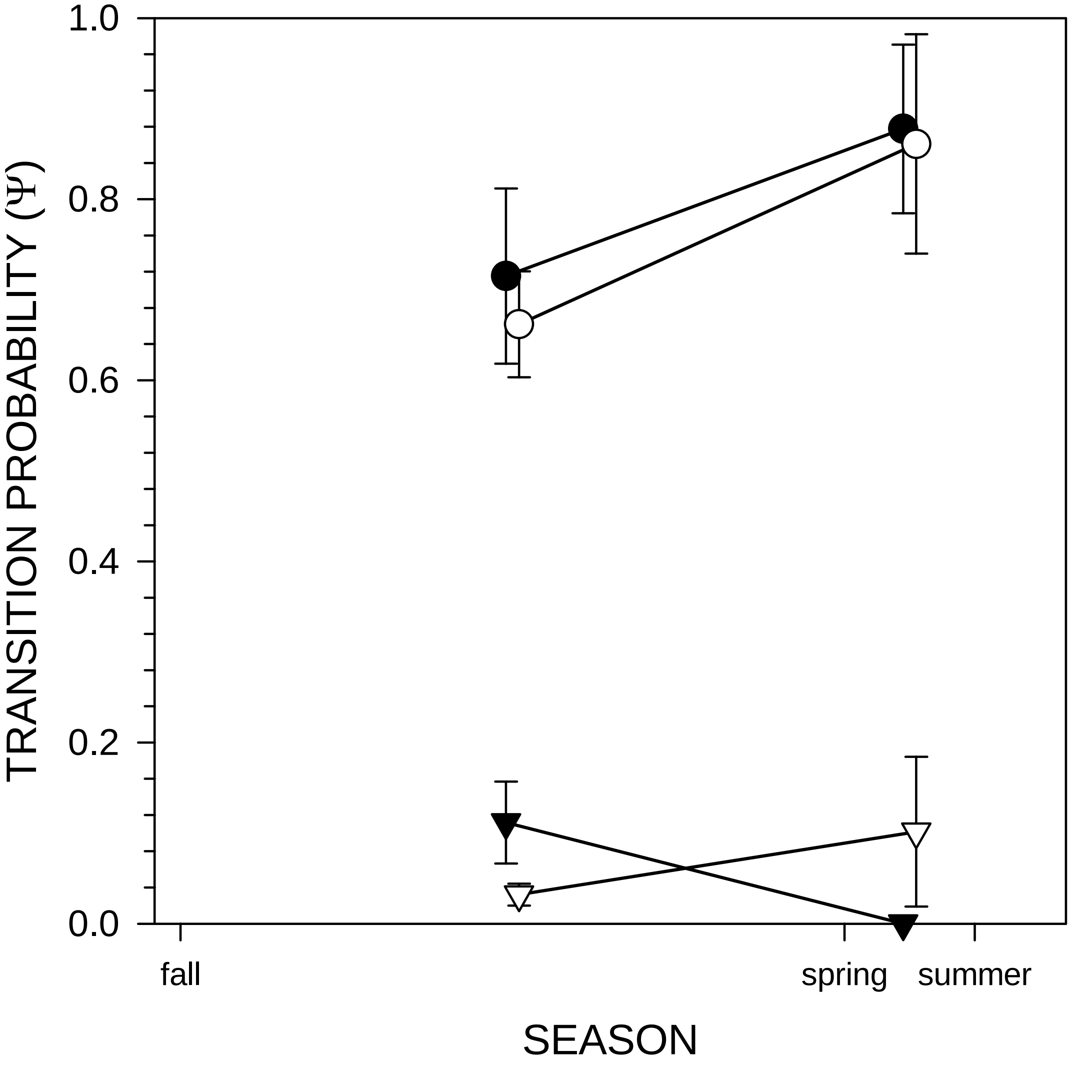

Figure 3. Inter-annual variation in total family break-up (dots, transition $\Psi^{Y\text{-}NY}$) and adoption (triangles, transition $\Psi^{NY\text{-}Y}$) of neck-banded female Greater Snow Geese. Data from fall 1997 to summer 1998 (black symbols) and from fall 1998 to summer 1999 (white symbols) are compared. Transition probabilities (± SE) are averaged across models.

CHAPITRE 2

COSTS OF EXTENDED PARENTAL CARE IN A PRECOCIAL BIRD: THE GREATER SNOW GOOSE

Eric T. Reed et Gilles Gauthier

Résumé

Chez les oiseaux nidifuges, les coûts des soins parentaux sont peu connus mais sont souvent considérés comme faibles. Les oies sont une exception chez ces espèces car elles prodiguent des soins de longue durée à leurs jeunes, et ce jusqu'à un an après la naissance. Nous avons donc étudié les coûts, en terme de survie ou fécondité future réduite des mères, des soins parentaux prolongés chez la Grande Oie des neiges (*Chen caerulescens atlantica*). Nos données proviennent d'une étude de marquage-observation à long-terme (1993 – 2000) menée sur les principales aires de reproduction et haltes migratoires. La survie des femelles accompagnées de jeunes à l'automne ne différait pas de celles non-accompagnées de jeunes. Par contre, les femelles encore accompagnées de jeunes au printemps avaient une survie réduite de 9 à 15 % par rapport à celles non-accompagnées de jeunes. Les taux de retours à la colonie reproductrice ne différaient pas entre les femelles accompagnées de jeunes ou non-accompagnées de jeunes, et ce autant à l'automne qu'au printemps. Nos résultats indiquent que le prolongement des soins parentaux peut entraîner un coût en terme de survie future chez cette espèce nidifuge et que la durée de l'association entre parents et jeunes serait déterminante dans ce coût.

Abstract

In precocial birds, costs of post-hatch parental care, although often thought to be low, are poorly understood. Geese are exceptional in providing care to their offspring for an extended period, with young accompanying parents for up to one year. We examined whether prolonged parent-offspring association entailed costs for parental female greater snow geese (*Chen caerulescens atlantica*) in terms of reduced future survival or fecundity. We used data from a long-term (1993 – 2000) mark-resight study conducted on the breeding and staging areas. Survival to the next year of females accompanied by young in the fall was similar to those not accompanied by young. However, females that were accompanied by young in the spring experienced a 9 to 15% reduction in survival to the next year compared to those not accompanied by young. Return rates of females to the breeding colony did not differ between those accompanied by young and those that were not in the previous spring or fall. Our results indicate that extended parental care may entail a survival cost in this precocial species and that the length of the parent-offspring association may be an important determinant of this cost.

Introduction

The notion of a fitness cost associated with reproduction is a central assumption in theories of life-history evolution (Clutton-Brock 1991; Stearns 1992). Parental care has seemingly evolved to enhance offspring phenotypic quality but this behaviour presumably entails some costs to the parents. If parental care is costly, the optimum effort by parents should be a compromise between increased quality of present offspring on one hand, and survival and future reproduction of parents on the other hand (Trivers 1972; Lazarus and Inglis 1986).

Estimating fitness costs of parental care from empirical data is difficult because of possible interactions with environmental factors, and variations in individual quality (Williams 1966; Stearns 1992; Cam et al. 1998, Cooch et al. 2002). Studies of phenotypic correlations between reproductive effort and fitness costs sometimes are criticized because genetic and environmental effects are confounded (Reznick 1985, 1992; van Noordwijk and de Jong 1986). Despite their limitations, phenotypic correlation studies can provide a useful assessment of costs of parental care and allow the study within an evolutionary framework, of behaviours that are not easily manipulated (Linden and Møller 1989; Partridge 1992).

Parental care in geese typically lasts for up to one year following hatching (Prevett and MacInnes 1980; Turcotte and Bédard 1989; Reed 1993), and sometimes can be maintained for several years (Ely 1993; Warren et al. 1993), which is unusual in birds. Geese thus provide a good model to examine the potential costs associated with extended parental care. They are migratory birds that must acquire large nutrient reserves in spring in order to meet the energetic demands of migration, egg formation and incubation, and thus breed successfully (Ankney and MacInnes 1978; Gauthier et al. 1992; Choinière and Gauthier 1995; Ebbinge and Spaans 1995; Bêty 2001). Therefore, any factor that reduces body condition or nutrient acquisition in spring may have negative impacts on their upcoming reproduction (e.g. Mainguy et al. 2002). Precocial birds such as geese provide mostly unshared parental care (i.e. independent of brood size, Lazarus and Inglis 1978) in the form of brood defence, vigilant behaviour and teaching of feeding techniques. Although these types of parental care may not represent a large energetic investment for parents, their extension into the following pre-breeding period may represent a significant cost on future reproduction or survival. Because unshared parental care in precocial birds is predicted to be independent of brood size (Lazarus and Inglis 1986), we hypothesized that duration of care would be a good correlate of parental investment.

In greater snow geese (*Chen caerulescens atlantica*), Gauthier and Tardif (1991) reported that the proportion of paired adults accompanied by young declined from 65% in fall to 23% in spring and less than 10% upon arrival on the breeding grounds. Family break up in fall mostly is a consequence of offspring mortality but in the spring more family break ups may be due to parent-offspring conflicts (Chapitre 1, Black and Owen 1989a). Length of association between parents and their offspring is one aspect of reproductive effort that is difficult to experimentally manipulate in birds. However, natural variation in length of parental care among individuals provides an opportunity to test for costs or benefits associated with extended parental care.

Recent developments in mark-recapture (or resight) modelling provide robust tools for addressing questions of interest to evolutionary ecology (Nichols and Kendall 1995). In particular, multistate capture – recapture models can be used to estimate survival and transition probabilities in populations stratified by state variables (Arnason 1973; Brownie et al. 1993). We used this approach to evaluate the consequences of providing parental care in the fall and spring (3 and 10 months following hatch, respectively) on survival and subsequent reproduction of female greater snow geese. We also examined return rates of parental and non-parental geese to their breeding colony to assess the impact of parental care on breeding propensity. We hypothesized that costs were additive such that females that extend parental care in the spring should have lower survival and/or lower breeding propensity than females that provide care for a shorter period of time.

Methods

Field methods

The greater snow goose (hereafter GSG) breeds in the eastern Canadian high arctic and western Greenland, and winters along the US Atlantic coast. During both spring and fall migration, the population stages along the St-Lawrence River in Québec, Canada (Reed et al. 1998). We conducted our study at two different geographic locations.

Our breeding ground work was conducted on Bylot Island, Nunavut Territory, site of the largest GSG colony (Reed et al. 1998). At the end of the summer, flightless GSG families were rounded up and driven into net traps. Every individual captured was marked with an individually coded USFWS metal leg band and approximately 80% of adult females (but not males) were fitted with individually coded plastic neck bands (see Menu et al. 2000 for details). A total of 4 595 adult females were fitted with neck bands from 1990 to 1999. Because non-breeders or failed-nesters leave Bylot Island before moult or have regained flight capacity early, they escape capture at the end of the summer (Reed et al. 2003a). Therefore, only successful nesters were caught and fitted with neck bands, and all previously marked females recaptured at banding were considered to be successful nesters in that year. Visual observations of neck-banded females were also conducted on Bylot Island.

We conducted observations in all major areas used by GSG along the St-Lawrence river estuary during fall and spring staging. A fraction of the population (c.a. 20%) overflies the area in fall, but the entire population is believed to stage there in spring (Reed et al. 1998). Observers used spotting scopes (20-60X) to find neck-banded females in goose flocks located in fields and tidal marshes (Gauthier et al. 2001); they also attempted to determine whether females were paired and/or accompanied by young of the year (Menu 1998). Only observations of neck-banded females for which we determined family status were used in subsequent analyses.

Accuracy of pair and family status data

Errors can occur when determining the status of a marked bird in the field. This may arise from the inability of the observer to detect subtle behaviours bonding individuals or a temporary break up between family members (Prevett and MacInnes 1980; Ely 1993). Because pair (presence of a mate) and family (presence of young) status were not always recorded simultaneously for a given individual, we analysed accuracy of pair and family status independently.

We used data from fall 1998 to calculate error rates on status identification because that season had the largest sample size. We used data from females that had their pair and/or family status determined twice or more within that season, assuming that each observation was independent. For each individual, we computed the number of observations for which the status differed from the one determined for the majority of observations (or the other observation when n = 2). The proportion of observations where the status differed among all observations was defined as the maximal error rate. Because hunting occurred during our observations, status changes (e.g. loss of young or mate) could be due to mortality. We thus defined the minimal error rate as the proportion of observations where the status differed but which could not be attributed to mortality. For instance, a female observed with young but reobserved without young is considered an erroneous status in the calculation of maximal error rates but not minimal error rates as the change could be due to mortality; in contrast, a female observed without young but reobserved with young is included in the calculation of both error rates. We assumed re-pairing following loss of a mate and adoption were rare within a season (Demers 2003; Chapitre 1).

Survival in relation to family status: Multistate modeling

To determine if prolonged parental care was costly to adult females in terms of probabilities of survival and of having young in the following year, and if these costs were additive, we analysed fall and spring data separately. Since adoption of young is rare in GSG, adult females accompanied by young in spring will have, on average, provided parental care for a longer period than females that lost their young between fall and spring.

We used multistate models (Brownie et al. 1993; Nichols et al. 1994) to estimate survival, sighting and transition probabilities between states of marked females. Here, state refers to the family status of an individual (accompanied by young of the year or not). These probabilities were defined as:

S_t^r = probability that a bird in state r in year t survives until year $t + 1$,

p_t^r = probability that a bird alive and present in state r in year t is observed during that period,

Ψ_t^{rs} = probability that a bird in state r in year t is in state s in year t + 1, given that it survived from year t to year t + 1,

Ψ_t^{rr} = 1 - Ψ_t^{rs}, probability that a bird alive and in state r in year t remains in state r in year t + 1, given that it survived from year t to year t + 1.

We started by fitting a general model that had time and state effects on survival, transition and sighting probabilities. There are no reliable goodness-of-fit tests (GOF) available for multistate models. As an alternative, we tested each state separately with GOF tests developed for the Cormack-Jolly-Seber model with program U-Care (Choquet et al. 2002). This test provides information on structural problems or overdispersion of the data within state but ignores potential interaction effects.

Modelling was conducted with program MARK v1.9 (White and Burnham 1999) and we used the Akaike's Information Criterion corrected for small sample size (AICc, Burnham and Anderson 1998) to assess parsimony of the various models fitted. For each model, we computed its difference in AICc (ΔAICc) relative to the most parsimonious model, and its AICc weight (ωAICc). ωAICc represents the weight of evidence in favour of a model as being the actual most parsimonious one among the set of candidate models (Burnham and Anderson 1998). When more than one model appeared to fit the data, we averaged parameter values, weighted by their model's ωAICc, across candidate models. Model averaging takes into account both sampling variance and model selection uncertainty (Burnham and Anderson 1998).

Model notation followed Lebreton et al. (1992). Our starting model (S_{g*t}, Ψ_{g*t}, p_{g*t}) included a parental care (g) and year (t) effect and their interaction on survival, transition and sighting probabilities. All biologically interesting reduced models were examined. By default, transitions $\Psi^{Y\text{-}NY}$ (Y = young, NY = no young) and $\Psi^{NY\text{-}Y}$ are modelled, which prevented us from testing within the model selection process whether the presence of young influenced the probability of being accompanied by young in the following year (i.e. $\Psi^{Y\text{-}Y}$ vs. $\Psi^{NY\text{-}Y}$). We addressed this question using a posteriori comparisons between parameter estimates using a chi-square test with program CONTRAST (Hines and Sauer 1989).

Because sparse data in early years resulted in non-estimable sighting probabilities, we could not fit models that constrained sighting probabilities to be additive between parents and non-parents in the spring analysis. Sighting probabilities of females with young were fixed at 1.0 (none missed) from fall 1998 to 1999, and transition to a state with young ($\Psi^{Y\text{-}Y}$ or $\Psi^{NY\text{-}Y}$) at 0.0 because GSG reproduction was a near complete bust in 1999 (Mainguy et al. 2002) and no neck-banded females were observed with young that fall.

Breeding in relation to parental care

All females seen at the colony during or after the incubation period or on brood rearing areas were considered successful nesters (Reed et al. 2003a). To reduce biases associated with unpaired individuals, we only used data from birds that had been observed with a mate twice or more in fall or spring in a given year. Breeders, as determined by observation or capture on the breeding grounds, also were considered paired. We used contingency tables to test for differences in return rates to the breeding grounds between females that did or did not provide care in the previous fall or spring. We analysed each year separately because large yearly variations in breeding conditions may impose different constraints on females and influence our ability to detect costs of parental care on reproduction. We used chi-square and, when one or more expected cell counts was less than 5, Fisher's exact tests to assess significance of differences between groups (SAS institute 1996). Only data from 1997 to 1999 were used due to insufficient data prior to that date.

Results

Precision of pair and family status data

We determined the pair status of 409 females at least twice (mean: 3.3 observations/female; range: 2 – 14). We had 148 observations (out of 1344) that were likely to be misidentifications (i.e. that could not be attributed to mortality), for a minimum error rate of 11.0% on pair status. When including cases where mortality of the mate could be involved, 224 observations of status diverged from the majority, for a maximum error rate of 16.7%. The probability of misidentifying a pair status twice (error rate^2) was thus between 1.2 and

2.8%. To minimize error rates, we only used individuals for which the same pair status was independently assigned at least twice in the same season.

We determined the family status of 545 females at least twice (mean: 3.8 observations/female; range: 2 – 14). We had only 78 observations (out of 2066) that were likely misidentifications of family status, for a minimum error rate of 3.8%. When cases where mortality could be involved were included, 121 observations were potentially erroneous (maximum error rate: 5.9%). Because the probability of assigning a wrong family status was fairly low, we retained single determinations of family status in our analyses. When a female was sighted twice and was assigned a different family status each time (3% of females), we assumed that it was accompanied by young.

Survival, transition and sighting probabilities - fall

We observed 2727 neck-banded females and cumulated 1062 resightings of them between fall 1993 and 1999. The GOF test for each state, of our general model indicated good fit (no young χ^2_{15} = 15.59, P = 0.41; young χ^2_{9} = 2.64, P = 0.98).

The most parsimonious model had time dependence on survival but no effect of association with young (Table 1). Transition probabilities were constant through time but differed between states. Finally, sighting probabilities were time dependent and were slightly higher in females with young than in those without. ωAICc for this model (0.420, Table 1a) indicated that it was almost twice as likely to be the best model compared to model 2.

Model 2, 3, and 4 also represented our data fairly well (Table 1a). All three models retained the same effects on transition and sighting probabilities as our most parsimonious model. Models 2 and 3 provided evidence that survival probabilities were lower in females with young than in those without, but the sum of ωAICc for models that included a parental care effect on survival was weak (0.41). Survival probabilities of parents with young in fall averaged across all models was only 1 to 2% lower than those of parents without young (Fig. 1a).

The probability of being associated with young in the fall did not differ between females that were accompanied by young and those that were not in the previous fall ($\chi_1^2 = 0.04$, P = 0.85). Transition probabilities averaged across all models were consistent with this result (Fig. 2a).

Survival, transition and sighting probabilities - spring

We observed 853 neck-banded females and cumulated 270 resightings of them between spring 1994 and 1999. The GOF test, by state, of our general model indicated a good fit for females not accompanied by young ($\chi_{11}^2 = 14.95$, P = 0.18) but we did not have sufficient data to assess GOF for females with young.

The most parsimonious model included an effect of the presence of young on survival, transition and sighting probabilities, and an effect of time on sighting probabilities (model 1, Table 1b). Based on ωAICc (0.407), this model was more than twice as likely as model 2 to be the best model. Although model 2 did not include an effect of presence of young on survival, the sum of ωAICc of all models that included this effect was high (0.70, Table 1b). This suggests an important effect of parental care provided in spring on subsequent survival. Survival probabilities of parents with young in spring averaged across all models was 9 to 15% lower than those of parents without young (Fig. 1b).

The probability of being associated with young in spring did not differ between females that were accompanied or not by young in the previous spring ($\chi_1^2 = 0.04$, P = 0.85). Transition probabilities averaged across all models were consistent with this result (Fig. 2b).

Breeding in relation to parental care

We determined the family status in the fall of 994 paired females but only 77 were seen or recaptured the following summer on Bylot Island (1996-97:14 out of 325; 1997-98: 49 out of 160; 1998-99: 14 out of 509). Return rates to the breeding site did not differ between females that were accompanied by young in the fall and those that were not (1997: Fisher's exact test P = 1.00; 1998: $\chi_1^2 = 0.51$, P = 0.48; 1999: Fisher's exact test P = 0.15) (Fig. 3a).

We determined the family status in the spring of 802 paired females and we recaptured or sighted 141 of them the following summer on Bylot Island (1997: 11 out of 99; 1998: 104 out of 232; 1999: 26 out of 471). Return rates to the breeding site did not differ between females that were accompanied by young in the spring and those that were not (1997: Fisher's exact test P = 1.00; 1998: $\chi_1^2 = 0.61$, P = 0.44; 1999: $\chi_1^2 = 0.33$, P = 0.60), although they tended to be higher in the latter group in all 3 years (Fig. 3b).

Discussion

Our results indicate that survival of females still associated with offspring in spring was reduced compared to those without young, but not in fall. We thus found some evidence of a negative phenotypic correlation between current reproductive investment (duration of parent-offspring association) and future survival of parental females. However, parental care provided in fall or spring had no effect on return rates to the breeding colony, suggesting that subsequent reproduction was independent of length of post-fledging parental care.

In an experiment where parental investment was modified by manipulating the length of the incubation period in barnacle geese (*Branta leucopsis*), Tombre and Erikstad (1996) did not detect any costs of increased parental investment on future survival or return rates to the breeding colony in the following year. Other studies conducted on geese during the brood rearing period also have largely failed at detecting a cost of parental care on adult survival (Black and Owen 1989a; Loonen et al. 1999). The latter studies have investigated the relationship between brood size and costs to the parents. However, given that parental care in geese is mostly unshared (i.e. independent of brood size, Lazarus and Inglis 1978), we might expect duration of care to be a better correlate of parental investment than brood size. Our results are in agreement with this as only females that extended parental care into the subsequent pre-breeding season (i.e. spring) suffered an apparent cost.

Differences in previous interpretations of costs of parental care may also be explained by the methodological approaches used. Few studies have used robust capture-mark-recapture (or resight) methods to quantify fitness costs of parental care (but see Yoccoz et al. 2002). The methods usually used assume that the probability of being caught or seen is the same regardless of parental status but in many field sampling situations this assumption is unlikely to be met, resulting in biased estimations of demographic parameters (Clobert 1995; Boulinier et al. 1997). Our estimation of survival probabilities based on a long-term data set allowed us to detect differences that may have a significant impact on an individual's life history.

Since observations were conducted on spring staging grounds used by all individuals in the population, permanent emigration did not bias our spring survival estimates. Survival estimates are biased low due to neck band loss (estimated at 3 – 5% per year, Gauthier et al. 2001). However, there were no reasons to believe that neck band loss differed between parents and non-parents, and thus comparisons between these two groups remain valid. Survival estimates were lower but nevertheless comparable to estimates of true survival for this population ($S = 0.78 \pm 0.05$ without adjusting for neck band loss, Gauthier et al., 2001) for the fall (S between 0.50 ± 0.08 and 0.77 ± 0.05) and the spring data sets (S between 0.54 ± 0.08 and 0.71 ± 0.03). Menu et al. (2000) also showed that neck bands did not impair survival in GSG, contrary to some other species of geese. Therefore, we think that our multistate modelling results were robust enough to provide valuable insights on the effects of prolonged parental care on survival.

There is a debate about the relevance of phenotypic correlationnal studies and the methods that should be used to detect reproductive costs (Reznick 1985, 1992; van Noordwijk and de Jong 1986; Partridge 1992; Viallefont et al. 1995b). Our study does not address the genetic basis of trade-offs nor is it a formal test of the occurrence of physiological trade-offs. However, reproductive cost and individual quality hypotheses still provide a useful framework for the interpretation of correlations between reproductive effort and demographic parameters observed in the wild (Curio 1983; Forslund and Pärt 1995).

A negative phenotypic correlation between current reproductive investment and future survival of parental females may be due to variation in individual quality and/or represent true reproductive costs. It has been suggested that individuals should increase their reproductive effort in response to decreasing residual reproductive value (e.g. Williams 1966; Forslund and Pärt 1995). Thus, females that were associated with offspring for the longest may have been of poor quality (e.g. senescing or in poor condition). However, this explanation appears unlikely. We found no difference in minimum age between females accompanied by young in spring and those without (Chapitre 1), such that senescence is unlikely to be the cause of the phenotypic correlation observed in our study. Furthermore, there is no evidence of a senescent decline in survival of geese before at least 15 years of age (Owen 1984; Francis et al. 1992a) whereas signs of reproductive senescence appear in ≥8 year-old females (Ratcliffe et al. 1988; Black and Owen 1995). Thus, if females still associated with offspring in spring were senescent, we should expect a stronger negative correlation between length of parental care and reproduction than with survival, contrary to our results. Similarly, if body condition was negatively correlated to parental care, we should detect sublethal effects on reproduction before survival in a long-lived species. Empirical studies in birds also suggest that the intensity or duration of parental care that females are able to provide is often condition dependent, with a tendency for females in poor condition to abandon their brood sooner (Monaghan et al. 1992; Kilpi et al. 2001).

The aim of our study was to detect possible costs of parental care rather than determining the proximate factors affecting vital rates. However, we can offer some hypotheses to explain the decrease in survival of parental females that extend care into spring. In geese, families tend to be more exploratory and use more risky locations for feeding (Owen 1972; Giroux and Bédard 1986; Lambeck 1990), and thus are more vulnerable to hunting mortality (Prevett and MacInnes 1980). Giroux and Bédard (1986) even proposed that the persistence of females to follow their young outside refuges increased their probability of being shot by hunters. If females with young are exposed to increased hunting compared to those without young, they may have a lower survival because hunting mortality is mostly additive in adult geese (Francis et al. 1992b, Gauthier et al. 2001). However, females still with young in spring had survived the hunting season (which extends from October to late January) and thus direct hunting mortality cannot account for their subsequent decrease in survival. A possible explanation is that many parental females were injured rather than directly killed by hunters. Several studies have revealed high frequencies (28% to 62% of individuals examined) of adult geese carrying shotgun pellets (Ankney 1975; Grieb 1970; Noer and Madsen 1996). Madsen and Noer (1996) estimated that pink-footed geese (*Anser brachyrhynchus)* carrying embedded shotgun pellets in muscles suffered a 10% decrease in survival compared to non-carriers. If the probability of injuries by shotgun pellets is dependent upon hunting exposure, then we might expect parents to have decreased future survival.

In our population, natural mortality also is important (half of annual adult mortality is due to factors other than hunting, Gauthier et al. 2001), such that the survival cost associated with extended parental care also may be due to natural factors. Decreased resistance to parasitic infections as a consequence of parental investment has been reported in many species (e.g. Festa-Bianchet 1989; Møller 1993; Norris et al. 1994), and waterfowl are host to a large number of endoparasites (Gajadhar et al. 1983; Mclaughlin and Burt 1979). Parasitic infections have been linked with reduced winter survival and breeding in red grouse (*Lagopus lagopus scoticus*) through morbidity and increased vulnerability to predation (Hudson et al. 1992; Dobson and Hudson 1994). Parental effort and increased energetic demands lead to immunodepression in some birds (Deerenburgh et al. 1997), and susceptibility to haematozoan parasitic infection is correlated to parental effort in some altricial birds (Ilmonen et al. 1999). Haematozoan infections potentially have important fitness consequences on their host since they are positively correlated with mortality rates in waterfowl (Sorci and Møller 1997). Vigilance also makes up a substantially greater proportion of parents' than non-parents' time budgets, thus reducing feeding opportunities (Lazarus and Inglis 1978; Scott 1980; Lessells 1987; Forslund 1993). Parents engage more often in aggressive interactions for defence of resources or space (Scott 1980, Black and Owen 1989b, Turcotte and Bédard 1989), possibly increasing their energetic expenditure and exposure to injuries.

We did not find evidence that post-fledging parental care reduced breeding propensity of female GSG. If parental care interferes with accumulation of nutrient reserve in spring, it is possible that reproductive parameters other than breeding propensity, such as timing of nest initiation (Drent and Daan 1980; Rowe et al. 1994, Bêty 2001), may be affected. Delays in nest initiation may have important fitness consequences for the parents since clutch size, nesting success, and survival and recruitment of offspring follow a steep seasonal decline (Cooke et al. 1984; Dawson and Clark 2000; Lepage et al. 2000). Unfortunately, we could not assess this question due to lack of information on nesting parameters of individuals for which we could estimate duration of parental care.

Several benefits for the parents have been associated with prolonged parental care such as increased survival or fecundity of the offspring and social dominance of families (Conover et al., 2000; Raveling et al., 2000). However, few studies have detected costs of long-term parental care in a precocial species (Scott 1980). We showed that providing parental care for extended periods of time was correlated with reduced survival probabilities in GSG, and thus may entail some costs as well.

Table 1. Multistate models of the effect of time (t) and parental care (g; presence or absence of young with female) on probabilities of survival (S), transition between states (female accompanied by young or not) (Ψ), and sighting (p) of female greater snow geese during a) fall 1993 to 1999, and b) spring 1994 to 1999. For each model we give the number of estimable parameters (np), the difference in corrected AIC value compared to the most parsimonious model (ΔAICc), and the AICc weight (ωAICc). Only the 6 most parsimonious models and the general model (#7) are shown.

Model	np	ΔAICc	ωAICc
A) Fall			
(1) $S_t\ \Psi_g\ p_{g+t}$	14	0.00	0.420
(2) $S_{g+t}\ \Psi_g\ p_{g+t}$	15	1.05	0.248
(3) $S_g\ \Psi_g\ p_{g+t}$	11	2.20	0.140
(4) $S\ \Psi_g\ p_{g+t}$	10	2.27	0.135
(5) $S_t\ \Psi_{g*t}\ p_{g+t}$	22	6.37	0.017
(6) $S_t\ \Psi_{g+t}\ p_{g+t}$	18	8.11	0.007
(7) $S_{g*t}\ \Psi_{g*t}\ p_{g*t}$	*32*	*18.75*	*0.000*
B) Spring			
(1) $S_g\ \Psi_g\ p_{g*t}$	14	0.00	0.407
(2) $S\ \Psi_g\ p_{g*t}$	13	1.73	0.171
(3) $S_g\ \Psi_g\ p_t$	9	3.38	0.075
(4) $S_g\ \Psi_{g+t}\ p_{g*t}$	18	3.39	0.075
(5) $S_g\ \Psi_{g+t}\ p_t$	13	3.50	0.071
(6) $S\ \Psi_{g*t}\ p_t$	14	3.72	0.063
(7) $S_{g*t}\ \Psi_{g*t}\ p_{g*t}$	*28*	*20.52*	*0.000*

Interactions between terms in the model are denoted with an (*) whereas (+) represents additivity.

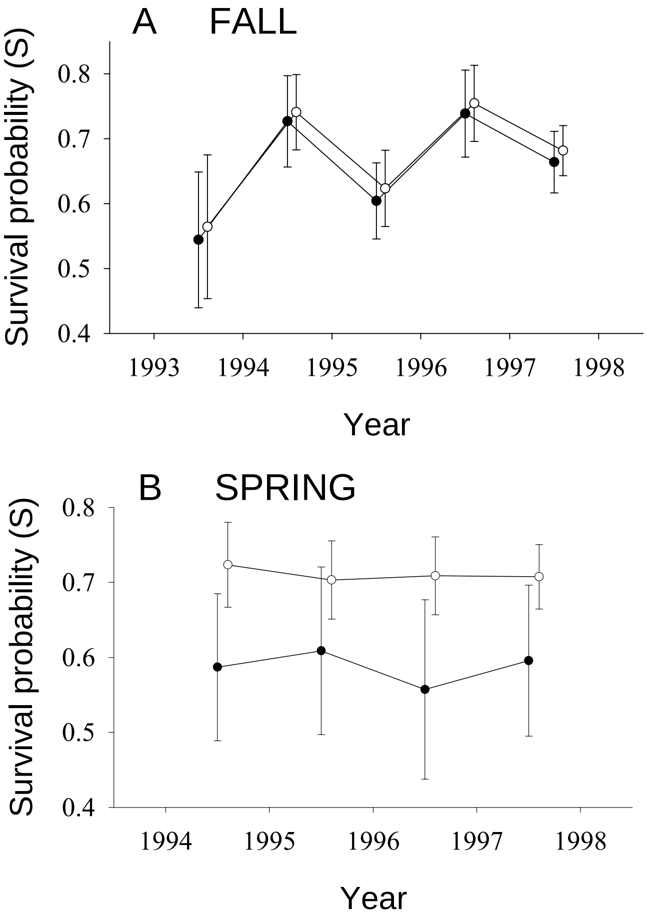

Figure 1. Annual survival probabilities (± SE) of female GSG averaged across all models based on A) the fall observations, 1993-1999, and B) the spring observations, 1994-1999. Survival probabilities are separated between females accompanied by young in the previous year (black dots) and those not accompanied by young (white dots). The last survival estimate is not shown because it is confounded with the last sighting probability in several models.

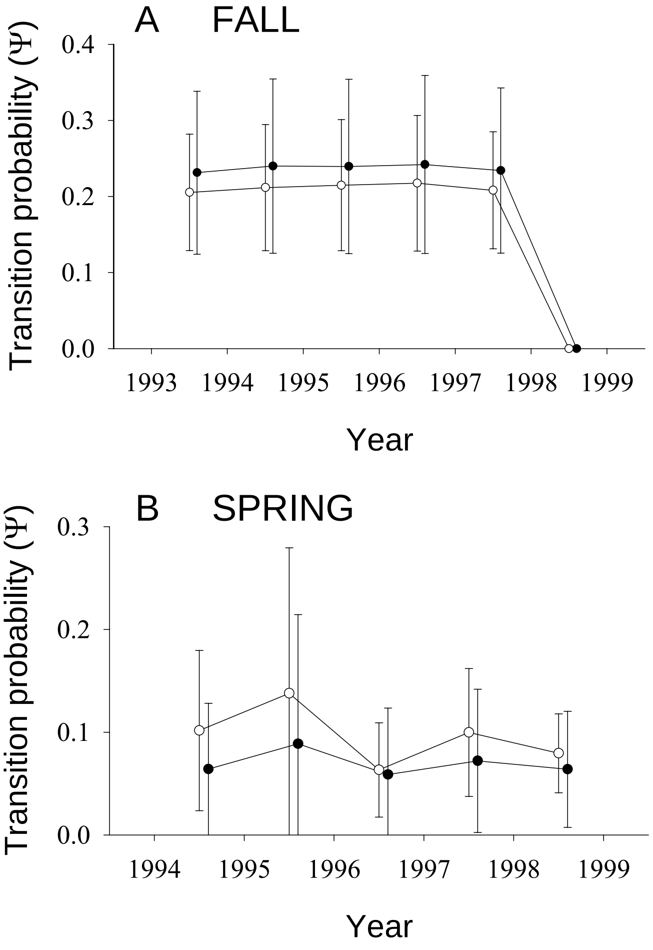

Figure 2. Annual transition probabilities between state (± SE) of female GSG averaged across all models based on A) the fall observations, 1993-1999, and B) the spring observations, 1994-1999. Probabilities that females accompanied by young will again be accompanied by young next year ($\Psi^{Y\text{-}Y}$, black dots) and that females not accompanied by young will be accompanied by young ($\Psi^{NY\text{-}Y}$, white dots), given they survive. The last fall probability was fixed at 0 due to a near complete reproductive failure in 1999.

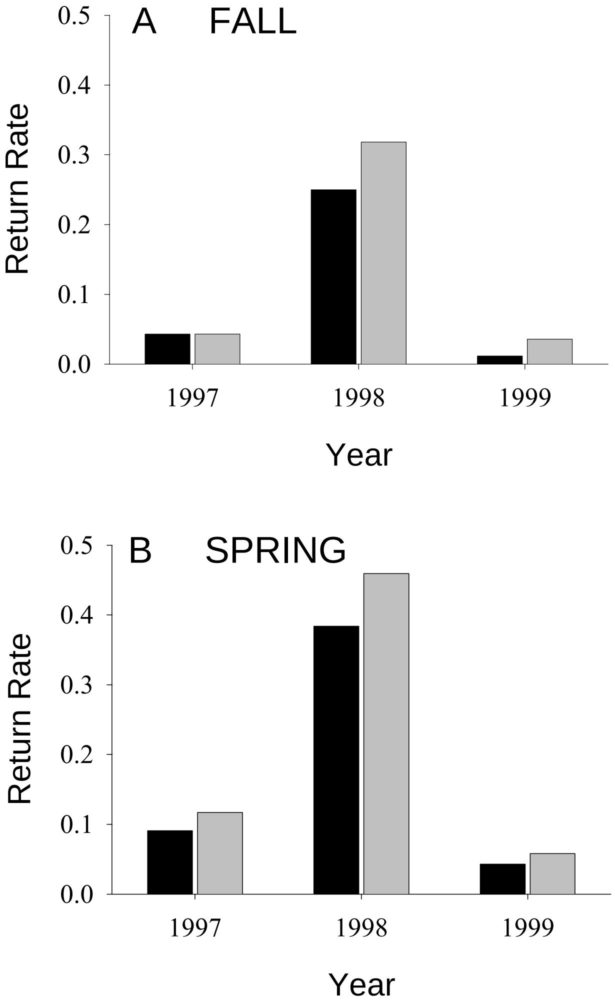

Figure 3. Return rates of female GSG to the breeding site in relation to their parental status in the previous fall (A) or spring (B) for summers 1997 - 1999. Females accompanied by young in the previous fall or spring (black) vs. those not accompanied by young (grey).

CHAPITRE 3

MOLT MIGRATION IN RELATION TO BREEDING SUCCESS IN GREATER SNOW GEESE

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Reproduit avec la permission du Arctic Institute of North America, Reed, E. T., J. Bêty, J. Mainguy, J.-F. Giroux, and G. Gauthier. 2003. Molt migration in relation to breeding success in Greater Snow Geese. Arctic 56: *in press*.

Résumé

Nous décrivons les mouvements migratoires estivaux de la grande oie des neiges (*Chen caerulescens atlantica*) nichant à l'Île Bylot, Nunavut. De 1997 à 2001, 121 femelles munies de radio-émetteurs ont été suivies afin de déterminer la fréquence et la chronologie de leur départ de la colonie pour la migration de mue en relation avec leur statut reproducteur et leur succès de nidification. Nous avons trouvé que 90% (n=51) des non-reproducteurs (pas de nid trouvé) et 97% (n=29) des femelles dont le nid a été détruit avant l'éclosion ont entrepris une migration de mue au cours des deux premières semaines de juillet. Les quelques non-reproducteurs ayant demeuré à l'Île Bylot tout l'été ont mué plus tôt et ont apparemment aussi entrepris la migration automnale plus tôt que les adultes accompagnés de jeunes. Une seule femelle ayant nichées avec succès (2%, n=41) a migré pour la mue, présumément après avoir perdu ses jeunes au début de l'élevage des jeunes. La migration de mue chez des adultes matures semble donc fortement dépendante du statut reproducteur et du succès de nidification. Nous ne connaissons pas les sites utilisés ni les conditions requises pour la mue de ces individus. Nous suggérons que la rareté de certains types de refuges contre les prédateurs telles que de grandes étendues d'eau à l'Île Bylot puisse être un facteur important, incitant les oies à muer ailleurs.

Abstract

We describe summer migratory movements by female greater snow geese (*Chen caerulescens atlantica*) breeding on Bylot Island, Nunavut. We followed 121 radio-collared females between 1997 and 2001 to determine the frequency and timing of departure from the colony in relation to breeding status, nesting success, and molting chronology. We found that 90% (n = 51) of non-breeders (no nest found) and 97% (n = 29) of failed nesters (nest destroyed or abandoned before hatch) departed the island before molting. The few non-breeders that remained on Bylot Island all summer molted earlier than adults with young, and appeared to initiate the fall migration before breeding geese. In contrast, only 2% of successful nesters (n = 41) left Bylot Island to molt, and those that did presumably had lost their offspring in the early stages of brood-rearing. Thus, the occurrence of a molt migration in greater snow geese appears to be strongly dependent on reproductive status and nesting success. The area used by molt migrants and their habitat requirements during molt remain unknown. We suggest that the paucity of predator-safe areas such as large water bodies on Bylot Island may be an important factor that drives the geese to molt elsewhere.

Introduction

Migratory behavior of animals is believed to have evolved in seasonal environments to take advantage of ephemeral resources and conditions optimal for the different stages of the life cycle (Gauthreaux, 1982). In many species of water birds, the flight and tail feathers are shed simultaneously once a year, thus rendering the birds flightless during the molting period (Bellrose, 1980). If feeding conditions or refuges from predators are not optimal for molting on the breeding areas, failed and non-breeders may undertake a pre-molt migration to distant and more favorable areas (Salomonsen, 1968).

Most goose populations of the Palearctic and Nearctic regions undertake long migrations from their wintering to their breeding grounds in temperate or Arctic regions. These long distance migrations are well documented (e.g. Bellrose, 1980) but movements on and around the breeding grounds are poorly known. Salomonsen (1968) described different types of migratory movements once on the breeding areas, such as dispersal to other breeding areas, molt migration and the return fall migration. In North America, molt migrations have been described for Canada geese (*Branta canadensis*), emperor geese (*Chen canagica*), black brant (*Branta bernicla nigricans*), and lesser snow geese (*Chen caerulescens caerulescens*) (Blurton Jones, 1972; Krohn and Bizeau, 1979; Abraham, 1980; Bollinger and Derksen, 1996; Abraham et al., 1999). Field studies on molting areas indicate that flocks are mostly composed of non-breeders and failed nesters of both sexes (Bollinger and Derksen, 1996). However, the frequency or the timing of departure from the breeding grounds for a molt migration in relation to the breeding status or nesting success of individuals is poorly documented.

In this study, we describe the summer migratory movements by adult female greater snow geese (*C. c. atlantica*) from a large breeding colony in the Canadian Arctic. We used radio-marked birds to determine the frequency and timing of departure from the colony for the molt migration in relation to breeding status and success.

Methods

The breeding ecology of greater snow geese has been studied since 1988 at a colony located on the south plain of Bylot Island, Nunavut (73°08'N, 80°00'W; see Lepage et al., 1996 for details of the study area). This colony is the largest known concentration of breeding greater snow geese and accounts for approximately 15% of the world population (Reed et al., 1998). Geese typically arrive on the Island in early June (Bêty, 2001) and the peak in nest initiation is generally around 12 June (range: 6 to 20 June; Lepage et al., 1996; 2000). Like other goose species, flight feathers are shed simultaneously once a year in greater snow geese, thus rendering the birds flightless for some time.

We captured and marked 305 adult female greater snow geese during the molting period in August 1996 to 1999 with radio-transmitters affixed to neck bands (see Demers, 2003 and Menu et al., 2001 for details). In addition, we also affixed radio-transmitters on another 32 adult females that were captured on their nest in June 2000 and 2001. The radios had a minimum life expectancy of 16 months but many were still functioning after 24 months. This allowed us to track individuals returning to Bylot Island to breed during the summer following their initial marking and, in 2000 - 2001, to track birds marked at the end of incubation for the rest of the summer.

Several times each summer from 1997 to 2001, geese were radio-tracked using two four-element Yagi antennas fixed on each side of a helicopter. Most aerial surveys covered all areas used by geese on Bylot Island's south plain (ca. 1600 km^2). We also conducted ground-based tracking every one to two days during the pre-laying, laying and incubation periods, using antennas mounted on a snowmobile or from fixed-location towers located near the two main nesting areas (Mainguy et al., 2002). Detection range of radios was approximately 5-10 km from the ground and 10-20 km from the air (Bêty, 2001).

We performed 3 to 8 tracking flights per year at various intervals throughout the breeding cycle of geese, and these were grouped into four main periods: laying/early incubation, incubation, early brood-rearing, and molt. The dates of these four periods varied among years due to differences in nesting phenology and aircraft availability (Table 1). The egg laying/early incubation period began when the first radio-marked female was detected on Bylot Island. Coverage was most extensive during this early period, in part due to the additional ground tracking. Despite this extensive coverage, some females were missed in this early period, either because they were not yet present on the Island when we conducted our tracking flights or they staged there for only a short period of time. In the subsequent periods, we are confident that we did not miss any previously-detected females since their movements were reduced to small nesting or molting territories, allowing us to concentrate our searches in areas where birds were known to be previously. We considered a female present in the first period if she was detected during that period or on a later date on the Island. Thus, the first period always included all females subsequently detected in a given year.

To determine breeding status of radio-marked females, we conducted extensive nest searches at all locations where females were detected more than once either during the aerial survey or from the ground during incubation. Females were either categorized as breeders (nest found) or non-breeders (no nest found). We are confident that we did not miss nests of incubating radio-marked females although some females categorized as non-breeders could have initiated a nest but lost it very early (e.g. during laying). Successful nests were defined as those from which at least one egg hatched (Bêty et al., 2001). In 2000 and 2001, an emphasis was placed on observing or capturing radio-marked females still present during the molt period to determine if they were still accompanied by young.

Some females were followed in more than one season. To avoid pseudoreplication (Hurlbert, 1984), we used only the first summer in which a female was detected on Bylot Island in all analyses. Radio failures occurring during the summer would appear as emigration. Thus, we computed the proportion of females that were detected in at least one season subsequent to the summer in which they were followed on Bylot Island. We then tested, using a two-tailed Fisher's exact test, whether radio failure (i.e. lack of detection in any subsequent season) was similar for (1) females that were detected on Bylot Island for the whole summer and (2) those for which we lost the signal during the summer. This was possible for the summers 1997-1999 because intensive radio-tracking was conducted in those years during the subsequent fall and spring on the staging grounds in southern Quebec (Demers, 2003). Two females known to have died during the summer were excluded from the analyses.

There was a high incidence of non-breeding in 1999 (Mainguy et al., 2002) so we conducted an extensive aerial survey at the end of the hatching period (15 July) to determine the number of non-breeders and failed nesters that were molting on Bylot Island. We covered all significant water bodies where molting geese might occur. We landed and made total counts and age ratios (goslings, yearlings, and >1 year-old birds could be identified based on plumage coloration) for all molting flocks with $\geq$ 50 individuals, whereas total counts were made from the helicopter for smaller groups.

Results

We followed 121 radio-marked females during the nesting season from 1997 to 2001; 89 of these females had been marked during the molting period prior to the summer that they were followed, and the remaining 32 females were captured and marked on their nests during the summer that they were followed. Seventy of the 121 females were categorized as nesting birds whereas 51 of them were categorized as non-breeding birds. We did not find any nests of radio-marked females in 1999, which was a year with a very low proportion of geese attempting to breed (Mainguy et al., 2002). Forty-one of the females that were classified as nesting birds successfully hatched at least one young whereas the remaining 29 females were failed nesters (Table 2).

Eighty-six percent of the 51 radio-marked females that were categorized as non-breeders were present on the Island during incubation, but only 10 % of these birds were still present shortly after hatch (Table 2). Thus, most non-breeding females (90%) left Bylot Island during the late nesting period to molt elsewhere. Of the 29 females that lost their nest before hatch (failed nesters), 27 (93%) had disappeared shortly after hatch (Table 2). Thus, these females also left the island to molt elsewhere. In contrast, 98% of the 41 successful nesters were detected during the early brood rearing period, and 83% were still present on Bylot Island during molt (Table 2). Two of the seven successful nesters that emigrated before the molt period were last detected on 14 and 20 July (i.e. before wing molt of parents), whereas the other five nesting females were last detected between 4 and 6 August (during wing molt). No goslings were capable of flight at any of these dates (E.T. Reed, personal observation). All nine successful nesters that were present during the molt period in 2000 were still accompanied by their goslings, whereas 5 of the 13 successful nesters present during the molt period in 2001 had lost their offspring by then.

Although most non-breeders and failed nesters left the breeding colony to molt, small flocks of molting adults and sub-adults without young were seen on Bylot Island every year. In 1999 we observed 704 molting geese distributed in 15 flocks (group size range: 10-138) during the 15 July survey. We estimated that 18.5% of these molting geese were yearlings and we found no goslings in these groups (n = 504 individuals aged). As no females with young had started to shed their flight feathers at that time (E. T. Reed, personal observation), the molting pattern of these birds strongly suggests that the five non-breeding females that were detected on Bylot Island after hatch molted on the island as they were last detected between 31 July and 8 August.

The proportion of females that were never detected again after the summer in which they were followed was low and did not differ significantly between those that disappeared before the molt period and those that did not (Fisher's exact test P = 0.33). Only 5 of the 60 (8.3%) females for which we lost the radio signal from Bylot Island before the molt period in 1997 to 1999 were never detected after the summer, compared to 2 of the 12 (16.7%) females that were still present during the molt period. This illustrates that radio failure was low during the summer and that very few females still present on the island were misclassified as having departed because of that.

Discussion

This study showed that breeding performance of greater snow geese nesting on Bylot Island had a strong influence on migratory patterns of this population; the majority of successful nesters molted on the island whereas most non-breeding and failed-nesting birds left the island to molt elsewhere. Non-breeding and failed-nesting female greater snow geese departed Bylot Island and initiated a molt migration after a 4 to 6-week residency period in early summer. Although only adult females were marked in this study, molt migration patterns are likely to be identical in males because greater snow geese, like other geese, form long-lasting pair bonds (Demers, 2003).

The timing of departure for molting areas is similar to that of lesser snow geese at La Pérouse Bay, a sub-Arctic colony (Abraham, 1980). The disappearance of some non-breeders in early August may represent an early departure for the southward fall migration, which normally starts during the last days of August in parental birds (Blouin, 1996; for similar evidence in Brant see O'Briain et al., 1998). The few non-breeders that stayed on Bylot Island during the summer molted earlier than parental birds and thus regained flight capabilities earlier. In contrast, molt migration was largely absent in successful nesters as only one (2%) of them disappeared in mid July, presumably after having lost her goslings, to molt elsewhere. Although six other successful nesters disappeared in early August when parental birds were still molting, it is highly unlikely that this was a molt migration so late in the summer. These birds probably molted on Bylot Island but at an earlier date, presumably after having lost their goslings after hatch, and, like some non-breeders, they initiated their fall migration early.

The occurrence of a molt migration in adult greater snow geese appears to be strongly dependent on reproductive status and nesting success. The number of molt migrants may therefore be highly variable among years and should be especially high in years with high incidence of non-breeding or failed-nesting (McLaren and Alliston, 1985), which occurs periodically in arctic-nesting geese (Reed et al., 1998). For instance, 1999 was the year with the highest incidence of non-breeding and failed nesting in 30 years on Bylot Island (Bêty et al., 2002; Mainguy et al., 2002), and the number of geese molting on the south plain was estimated at less than 2000 non-breeding, failed- and successful-nesting adults (G. Gauthier, unpublished data). In contrast, colony surveys conducted every 5 years showed that the number of adults present on Bylot Island during molt in good breeding years ranged from 25 500 to 69 475 adults between 1983 and 1998, of which 62% to 83% were successful nesters (Reed et al., 1992; Reed et al., 1998; A. Reed, Canadian Wildlife

Service, unpublished data). Thus, the number of adult geese molting on the breeding colony or elsewhere may vary dramatically among years according to overall breeding success of colonies.

This is the first study that shows a major molt migration in mature adult greater snow geese, a species breeding in the High Arctic. The direction of molt migrations of ducks and geese breeding in temperate and sub-arctic areas is often a northward migration (Salomonson, 1968; Abraham, 1980; Abraham et al., 1999) even though molt migrations in other directions have been documented as well (Bollinger and Derksen, 1996, Nilsson et al., 2001). Few concentrations of molting greater snow geese are known but we suspect that a major destination may have been an area approximately 200 km to the south on Baffin Island where surveys conducted in 1993, a year of very good breeding success, revealed the presence of 20 280 adults, including 19 127 (94.3%) non-breeders or failed nesters (A. Reed, Canadian Wildlife Service, unpublished data). The 7200 km^2 surveyed area covered several large lakes, including Erichsen and Quartz Lake (approximately 70°40'N, 80°41'W and 70°57'N, 80°42'W respectively). However, it remains unknown whether geese from Bylot Island and other colonies molt together in a few restricted areas such as this one, or in several flocks scattered over a broad expanse.

Because wing molt does not represent a severe nutritional stress in geese (Ankney, 1979; 1984), it is likely that food supply is not the only factor involved in the selection of molting areas by adults without young. Since non-parental geese almost entirely avoid dry upland habitats on Bylot Island (Hughes et al., 1994), the presence of predator-safe areas such as large bodies of water, which are generally rare on Bylot Island, may be an important factor that drives the geese to molt elsewhere. In contrast, the abundance of small ponds on the island may provide more adequate predator refugia for small goslings unable to swim in presence of large waves (Hughes et al., 1994).

Molting areas are potentially of great importance in the dynamics and structure of populations as mixing of breeding populations on molting areas have been described for other species of geese (Abraham, 1980; Bollinger and Derksen, 1996; Abraham et al., 1999). Mixing of birds from different breeding populations increases the likelihood of genetic exchange among populations. Geese are also known to be faithful to specific molting areas (Bollinger and Derksen, 1996).

Although greater snow geese have been intensively studied in the past 20 years, resulting in a comprehensive knowledge of their ecology and habitat use during breeding, wintering, and fall and spring staging (summarized in Batt, 1998), the area used by molt migrants and their precise habitat requirements remain unknown. With the dramatic increase in the greater snow goose population over the past 30 years (Reed et al., 1998), molting areas have either seen an increase in the number of geese using them and/or there has been an increase in the number of sites used. A shift in molting area of greylag geese (*Anser anser*) in Southern Sweden was linked to an increase in population size, possibly because the carrying capacity of the traditional molting site had been reached (Nilsson et al., 2001). Therefore, increase in goose use in some molting areas may have important ecological implications. Our findings of a large segment of molt migrants in greater snow geese and the lack of information about the molting areas underscore the need for further studies of this question.

Table 1. Dates and periods of radio-tracking in relation to the breeding cycle of greater snow geese on Bylot Island's south plain in 1997 – 2001.

Year	Egg Laying/early incubation	Incubation	Early brood Rearing	Molt
1997	28 May - 14 June	30 June	15 July	9 – 15 August
1998	30 May - 13 June	28 June	13 -16 July	8 August
1999	10 - 25 June	28 June	15 July	-[a]
2000	9 – 26 June	3 July	16 July	7 August
2001	11 – 19 June	1 – 9 July	17 July	8 August

[a] No surveys were conducted during molt in 1999 because no radio-marked geese had been detected in the study area during early brood-rearing.

Table 2. Number of radio-marked greater snow goose females detected during egg laying, incubation, brood rearing, and molting periods on Bylot Island's south plain in 1997-2001. Birds are split according to breeding status. Females that were detected, but for which no nest was found, were considered non-breeders. Failed nesters were females for which a nest was found, but where no eggs hatched. A female was considered present in a period if she was detected during that period or any subsequent period.

Year	Egg Laying / early incubation	Incubation	Early brood-rearing	Molt
		Non-breeders		
1997	14	13	2	0
1998	15	15	0	0
1999	7	4	0	-[a]
2000	15	12	3	3
2001	0	0	0	0
Total	51	44	5	3
		Failed nesters		
1997	10	10	0	0
1998	9	9	0	0
1999[b]	0	0	0	-[a]
2000	3	3	0	0
2001	7	6	2	1

Total	29	28	2	1
		Successful nesters		
1997	9	9	9	7
1998	8	8	8	5
1999[b]	0	0	0	-[a]
2000	10	10	10	9
2001	14	14	13	13
Total	41	41	40	34

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[a] No aerial surveys were conducted during molt in 1999 because no radio-marked geese had been detected in the study area during the brood rearing period.

[b] No nests of radio-marked females were found in 1999.

CHAPITRE 4

EFFECTS OF NECK BANDS ON REPRODUCTION AND SURVIVAL OF ADULT FEMALE GREATER SNOW GEESE

Eric T. Reed, Gilles Gauthier, Roger Pradel

Résumé

Une des prémisses de base des études de marquage-recapture est que le marqueur utilisé n'a pas d'effet sur l'animal. L'utilisation de colliers pour l'étude des oies est très répandue mais il y a des inquiétudes grandissantes sur le fait que ces colliers pourraient avoir des effets négatifs sur les oies. Des études récentes ont produit des résultats divergents à propos de tels effets négatifs chez les oies. Nous avons étudié la question chez la Grande Oie des neiges (*Chen caerulescens*) en contrastant la probabilité de reproduction et de survie apparente d'oies portant un collier avec celles portant une bague de métal seulement, sur une période de 11 ans à l'Île Bylot, Nunavut. Nous avons aussi testé l'effet du collier sur d'autres paramètres de la reproduction (date de ponte, taille de ponte et succès de nidification) sur une période de 3 ans. Les femelles munies de colliers avaient une taille de ponte et une probabilité de capture réduite par rapport aux autres femelles, mais leur survie apparente, date de ponte et d'éclosion, et succès de nidification n'étaient pas affectés. La probabilité de reproduction, représentée par les probabilités de capture, était réduite en moyenne de 48% chez les femelles munies de collier par rapport aux femelles simplement baguées et la taille de ponte était réduite de 10%. L'utilisation de modèles multi-états nous a permis d'estimer le taux de perte de collier (3% par année) et d'obtenir des probabilités de capture et de survie qui n'étaient pas biaisées par cette perte. Nous recommandons la prudence dans l'utilisation de colliers dans un but d'estimation de paramètres démographiques, et que l'effet négatif potentiel des marqueurs utilisés soit quantifié.

Abstract

A requirement of mark-recapture studies is that the marker has no effect on the animal. Neck bands have been used extensively for goose research but there is growing concern that they may have negative effects on birds. Recent studies have yielded contradictory results regarding such negative effects in geese. We therefore evaluated the effects of neck bands on adult female Greater Snow Geese (*Chen caerulescens atlantica*) by contrasting breeding propensity and apparent survival of geese marked with both a plastic neck band and a metal leg band and those marked solely with metal leg bands over an 11 year period on Bylot Island, Nunavut Territory. We also tested the effects of neck bands on other reproductive parameters (laying date, clutch size and nest success) over a 3-year period. Neck-banded females had decreased clutch size and capture probabilities but their apparent survival rate, nest initiation and hatching dates, and nest survival were not affected compared to other females. Breeding propensity, indexed by capture probabilities of neck-banded females was, on average, 48% lower that that of leg-banded only females and clutch size was 10% lower. The use of multistate mark-recapture models allowed us to estimate neck band loss (3% per year) and to obtain survival and capture probabilities that were not biased by such loss. We urge researchers to be cautious in the use of neck bands for estimation of population parameters, and that the potential negative effects of neck bands be assessed.

Introduction

A requirement of studies based on the recapture or follow up of marked individuals is that the marker has no negative effect on the animal. In geese, plastic neck bands have been used extensively to study population dynamics, distribution and movement patterns, to determine population size and to conduct behavioral observations (Ballou and Martin 1964, Fjetland 1973, Hestbeck et al. 1991, Gauthier et al. 2001). Neck bands provide a wealth of information from resightings of marked individuals, leading to increased precision in estimation of vital rates (Hestbeck et al. 1990).

There is growing concern that neck bands may have negative effects on birds, resulting in biased parameter estimates. However, studies that have examined the effects of neck bands on behavior and fitness components, such as survival and reproduction, have often yielded contradictory results. Neck bands have been shown to reduce survival in some species of geese (Ballou and Martin 1964, Castelli and Trost 1996, Schmutz and Morse 2000) but not in others (Menu et al. 2000). There is also evidence that neck bands reduce breeding propensity in Black Brant (*Branta bernicla nigricans*) and White-Fronted Geese (*Anser albifrons*) (Lensink 1968, MacInnes and Dunn 1988), and clutch size in Emperor Geese (*Chen canagica*) (Schmutz and Morse 2000).

In Greater Snow Geese (*Chen caerulescens atlantica*), Menu et al. (2000) recently found that survival of adult females was not affected by neck bands but their capture rates at the breeding site were lower than those of females marked with metal leg bands alone. These low capture rates may be due to several factors: (1) breeding propensity or nesting success may be reduced due to a decrease in body condition (MacInnes and Dunn 1988, Schmutz and Morse 2000); (2) neck bands may interfere with social signaling, resulting in decreased potential to form pair bonds or increased divorce rates among pairs (Frankel and Baskett 1961, Goforth and Baskett 1965, Demers 2003); (3) individuals that are handled for a long period of time at marking (usual with neck bands) may show trap “shyness” in the following years or be prone to permanent emigration (Pradel et al. 1995). Distinguishing among these possibilities requires the simultaneous marking of individuals with and without neck bands and a detailed follow up afterwards. Capture-mark-recapture methods provide tools to distinguish between permanent and temporary emigration and make it possible to evaluate the effects of neck bands on breeding propensity (Pradel et al. 1995, Kendall et al. 1997).

We used multistate mark-recapture models (Brownie et al. 1993, Nichols et al. 1994) to estimate and compare apparent survival (confounds true survival and fidelity) and capture probabilities of adult female Greater Snow Geese fitted with neck bands or leg bands at their breeding site over an 11-year period. Neck band loss is a recurrent source of bias in mark-recapture studies (Nichols et al. 1992, Nichols and Hines 1993, Gauthier et al. 2001, Samuel et al. 2001) and the use of multistate models allowed us to directly correct our estimates for such losses. We also tested the effects of neck bands on other reproductive parameters (laying date, clutch size and nest success) over a 3-year period.

Methods

Collection of Mark-Recapture Data

Data were collected at the Bylot Island breeding colony, Sirmilik National Park, Nunavut Territory, between 1990 and 2000 (see Hughes et al. 1994 for description of the study area). During the molting period (7-day period in early August), geese were rounded up with the help of a helicopter and personnel on foot, and driven into coral traps (see Menu et al. 2001 for details). Captured birds are mostly successful nesters and their young of the year, since non-breeders and failed-nesters leave the island to molt elsewhere or have regained flight capacity at the time of banding (Reed et al. 2003a).

All birds captured for the first time were fitted with a metal U.S. Fish and Wildlife Service leg band, and a number of adult females, chosen haphazardly within a catch, were fitted with individually coded plastic neck bands. Recaptures were systematically noted. Neck bands (height: 57mm, thickness: 1.5mm, weight: 20g) were made of rigid single-wrap, 2-plex gravoply (New Hermes Inc., Duluth, GA) and rims were folded at both ends. Two types of UV-resistant surface plastic were used: a matte surface was used from 1990-94 and 1998-99 and a textured surface between 1995 and 1997. There was some evidence that neck band loss was slightly higher for the latter type (Gauthier et al. 2001).

Analysis of Mark-Recapture Data

Mark-recapture data were analyzed with mulistate models. In this study, state refers to the presence or absence of a neck band (i.e. leg-banded only or neck band and a leg band). Apparent survival (Φ), capture (p) and transition (Ψ) probabilities were defined as:

Φ_t^r = probability that a bird in state r in year t survives and does not permanently emigrate from the study area until year t + 1,

p_t^r= probability that a bird alive and present in state r in year t is captured during that period,

Ψ_t^{rs} = probability that a bird in state r in year t is in state s in year t + 1, given that it survived from year t to year t + 1,

Because a bird had to be captured to receive a neck band, we fixed transition probabilities from “leg-banded only” to “neck-banded” at 0. This procedure de facto constrained the transition probabilities from “leg band only” to “leg band only” to 1. This assumption is reasonable because leg band retention rate is extremely high (Gauthier et al. 2001). We thus had only one transition probability to estimate, the probability of neck band loss.

Only adult females were used in this analysis. We considered the first capture as an adult as the initial marking of females that were originally marked as goslings. Because radio-collars may affect breeding performance (Demers 2003), we censored the capture history of females that were fitted with radio-collars upon recapture (analogous to losses on capture). For a few leg-banded females that were later fitted with a neck band, the initial capture history was also censored when the neck band was fitted and a new capture history was started. We applied the same procedure when old neck bands were occasionally replaced by a new one upon recapture, to account for differences in probability of neck band loss as a function of its age.

We started by fitting a general model that had time and state effects. Although there are no adequate goodness-of-fit tests (GOF) for multistate models, an indirect way is to partition states into independent groups and test each group with the GOF tests developed for the Cormack-Jolly-Seber model (Burnham et al. 1987). However, this approach cannot test for heterogeneity in transitions between states. We used program U-Care (Choquet et al. 2000) to carry these tests. We calculated a variance inflation factor (ĉ) to account for overdispersion in our data as:

$$\hat{c} = \chi^2 / df$$

where χ^2 is the sum of the GOF statistics and df the sum of the degrees of freedom.

Model notation followed Nichols et al. (1994). The factorial structure of a model was represented by subscripting survival, capture and transition. Our general model (Φ_{g*t}, p_{g*t}, $\Psi_{age*type}$) included group (g, neck band or leg band only) and year (t) effects and their interaction on apparent survival (Φ) and capture (p) probabilities. Transition probabilities (Ψ) were constrained to differ depending upon the type (matte or textured) and age of the neck band.

We assessed the effects of variables on survival, capture, and transition probabilities by deleting these variables from the general model. We used the Akaike's Information Criterion modified for overdispersed count data and small sample size (QAICc) to select the best approximating model (lowest QAICc value, Burnham and Anderson 1998). Other models were ranked relative to deviations from the best model (ΔQAICc). We also used QAICc weights (ωQAICc), which represent the weight of evidence in support of each model in the candidate set given the data (Burnham and Anderson 1998). We used program MARK v2.1 (White and Burnham 1999) for these analyses. When the only difference between two models is a single covariate, the confidence intervals around the beta (β) estimates (slope of the linear relation between the parameter and the covariate) provide more useful evidence of an effect than the ΔQAICc. We used this approach and concluded that covariates had an effect when their 95% confidence intervals did not include 0.

Collection of Nesting Data

Nests were found by systematic searches during egg laying or early incubation during the summers 1999 - 2001. Nests were revisited in the first half of incubation, during hatching and after the goslings had left the nest in order to determine their fate (Bêty et al. 2001). Nesting parameters are generally not biased by our visits (Bêty and Gauthier 2001). As part of a long-term monitoring program, a pre-defined area of ca. 8 km^2 in the center of the colony (main nesting area - MNA) is searched for nests every year (Lepage et al. 1996) and this provided a sample of nests of mostly unmarked females. Because these nests were not a random sample, we set up 40-ha plots randomly positioned over most of the breeding colony (25 km^2 study area). We searched as many plots as possible to get a sufficient sample of nests, and all nests located within our plots were recorded. We also searched for as many nests of neck-banded females as possible within the colony. The latter were usually found a few days later than the two first samples (early to mid-incubation).

Among the 999 nests found, 3.3% occurred in 2 groups (18 nests of neck-banded females located in the MNA and 5 in random plots; 10 nests located in both the MNA and random plots). To insure independence, nests of neck-banded females were excluded from random plots or MNA and nests in random plots were excluded from the MNA. Random plots were used to assess whether the MNA was a representative sample of the entire breeding colony.

In each nest, we recorded the number of eggs and marked them with a permanent felt pen for individual recognition. Nests were classified as found during laying if new eggs appeared later. For nests found during incubation, the mass, length and width of each egg was recorded.

Analysis of Nesting Data

Nest initiation date (date at which the first egg was laid) was estimated assuming a laying interval of 1.5 days (Schubert and Cooke 1993). For nests found during incubation, we estimated initiation date using a retrocalculation based on hatch date (assuming 23 days of incubation), or using a linear relationship between egg density and stage of incubation (Lepage et al. 1999).

Nest hatch date was measured directly if goslings were found in or just leaving the nest. When eggs hatched between visits, we estimated hatching date as the most likely date if the eggs were showing signs of hatching when visited last, or by adding the length of the laying and incubation periods to the initiation date.

Because initiation and hatch dates were not normally distributed, we rank transformed the data and tested treatment and year effects with a two-way ANOVA for unbalanced design (SAS Institute 1996). This method, although robust for the analysis of additive factors, has low power for testing interactions (Seaman et al. 1994). We tested interactions of rank transformed data with the aligned rank test (ART) procedure as recommended by Salter and Fawcett (1993). We computed pairwise comparisons among treatments using a Tukey - Kramer adjustment for multiple comparisons of Least Square Means (PROC GLM, SAS Institute 1996).

Total clutch size was estimated as the maximum number of eggs found in a nest. Nests with clutch sizes of one were rare (2 %) and were removed from the analysis as suggested by Lepage et al. (2000). We compared total clutch size among treatments and years with a two-way ANOVA for unbalanced design (PROC GLM, SAS Institute 1996).

Successful nests were defined as those where at least 1 gosling hatched. We estimated daily nest survival with the nest survival procedure of program MARK v2.1. This approach is analogous to a Known Fate analysis with the difference that in the case of unsuccessful nests, we do not know the exact day the nest was destroyed. With this method we define:

i = first day a nest was found.

j = last day a nest was visited and seen alive.

k = last day a nest was visited ($j = k$ for successful nests, i.e. the day that eggs hatched).

Nest survival probability (S) was estimated for each day separately. A nest was not considered at risk of failure the day it hatched. The cell probability was modeled as the product of the survival rates (S) from day i to day j-1. For successful nests, day k was ignored. When hatch date was not known exactly, k was the estimated date of hatch. For unsuccessful nests, the cell probability for the nest was taken as the product of the survival rates from day *i* to day *j*-1, times 1 minus the product of survival from *j* to *k*-1.

An advantage of using this method is the possibility to include individual covariates in model selection and nest survival estimation. We fitted models assuming a constant nest survival throughout the nesting period. However, because nests of neck-banded females are most easily found during incubation, when nest attendance increases and egg predation is possibly reduced, we used the 'age' of the nest when found (date found minus estimated laying date) as an individual covariate in our models. There was no reason to believe that this age effect varied among treatments so we only modeled year specific relationships between 'age' and nest survival. AICc was used for model selection.

Results

Breeding Propensity and Survival

Between 1990 and 2000 a total of 7235 adult females were marked (5256 neck-banded and 1979 leg-banded only), producing 323 and 276 recaptures of neck-banded and leg-banded females, respectively.

The goodness of fit test of our general model indicated some lack of fit (leg-banded birds: $\chi^2_{32} = 52.8$, P = 0.01, neck-banded birds: $\chi^2_{29} = 57.5$, P = 0.001). There was a slight transient effect (TEST3.SR for leg-banded birds: z = 3.23, P = 0.001; neck-banded birds: z = 2.05, P = 0.04) and the presence of trap dependence in the form of trap-shyness for both groups (TEST2.CT: z = 2.08, P = 0.04 and z = 2.70, P = 0.01, respectively). Lack of fit was driven by a few cells and was not always consistant (e.g. there was trap-happiness in some time periods). These results and the relatively small value of the variance inflation factor from the global test ($\hat{c} = 1.81$) were compatible with overdispersed count data so this correction factor was used in subsequent analyses. Since the two groups behaved in the same manner regarding possible transient or trap dependence effects, our comparison between them should not be affected by these effects.

Our 4 most parsimonious models had time dependent apparent survival [estimate range: 0.52 ± 0.09 to 1.00 ± 0.12], with no difference between leg-banded and neck-banded birds, but additive effects of marker and time on capture probabilities (Table 1). The 5th model, which also represented well the data, had an additive effect of neck bands on apparent survival. Overall, models without a neck band effect on survival had a sum ωQAICc = 0.85 (Table 1), indicating that neck bands had little effect on survival. In contrast, capture probabilities of leg-banded females were on average 48.2% [range: 47.3% - 48.9%] higher than those of neck-banded females (Fig. 1).

The 5 top models differed in the constraints imposed on transition probabilities, i.e. on the rate of neck band loss. Our best model indicated that neck band loss was constant over time and did not differ between matte and textured neck bands. Although the other 4 best models were close in terms of ΔQAICc, the beta estimates did not provide strong support for an effect of the covariates (neck band type: $\beta = 0.62$ [-0.20 to 1.44] model 2, and 0.25 [-0.50 to 0.99] model 4; age of neck band: $\beta = 0.26$ [-0.03 to 0.55] model 2, and 0.18 [-0.10 to 0.46] model 3). Annual loss of neck bands was estimated at 3.03% [95% CI: 2.05% – 4.45%] under our most parsimonious model.

Nesting Components

There was a significant interaction between year and treatment effects on nest initiation date ($F = 3.69$, df = 4, 884, $P < 0.01$). Pairwise comparisons indicated that nest initiation date was later for neck-banded females than those in the MNA in 2000 ($P < 0.01$), but did not differ between any other treatments within a given year. Overall, there was no clear evidence that nest initiation date was later for neck-banded females (Fig. 2). For hatch date, there was no interaction between year and treatment ($F = 1.70$, df = 4, 538, $P = 0.15$), and no significant differences among our treatments (MNA vs. random plots: $P = 0.06$; MNA vs. neck bands: $P = 0.99$; random plots vs. MNA: $P = 0.41$) (Fig 3).

Both year and treatment had a significant effect on total clutch size (year: $F = 9.79$, df = 2, 785, $P < 0.001$; treatment: $F = 4.37$, df = 2, 785, $P = 0.03$; interaction: $F = 1.05$, df = 4, 785, $P = 0.38$). There was no difference in total clutch size between nests in random plots and in the MNA (LS MEANS random plots: 3.56 ± 0.07; MNA: 3.44 ± 0.05; $P = 0.37$) or between nests of neck-banded females and those in the MNA (LS MEANS neck-banded: 3.20 ± 0.10; $P = 0.08$). However, neck-banded females had lower clutch size than females nesting in random plots ($P < 0.01$).

For nest survival, our 2 best models fitted the data equally well and both indicated that survival varied among treatments and years, but also that the age of a nest when found was positively related to its survival probability (Table 2). There was some uncertainty whether differences among treatments were constant through time (model 2) or varied annually (model 1). Daily nest survival averaged across all models varied considerably among years, with nest success being lowest in 1999 and highest in 2000 (Fig. 4). There were no systematic differences in nest survival between neck-banded females and those in random plots while nest in the MNA generally had higher survival probabilities (Fig. 4)

Discussion

Our results indicate that neck bands affected some components of reproduction but not apparent survival of female Greater Snow Geese. Neck-banded females had decreased clutch size and capture probabilities but their nest initiation and hatch dates and nest survival were not affected compared to other females.

Capture probabilities of neck-banded females were the parameters that differed the most compared to leg-banded females (almost 50%). Capture probabilities confound temporary emigration from the study area and true capture probability given presence in the study area (Kendall et al. 1997). It is unlikely that one group is more apt at escaping capture than the other because neck-banded and leg-banded birds are intermixed on the study area, goose flocks are selected randomly for capture and geese rarely escape before entering the traps (G. Gauthier, personal observation). Therefore, we believe that our results are indicative of a higher temporary emigration of neck-banded females compared to other females. Temporary emigration from our study area results mainly from non-breeders and failed-nesters migrating to distant molting areas (Reed et al. 2003a). Since we did not detect increased nest failure in neck-banded females, we suggest that differences in capture probabilities between groups is indicative of a difference in breeding propensity. Therefore, our results provide evidence that neck-banded females skipped breeding at a higher rate than leg-banded females, a phenomenon also suggested for other species of geese (Lensink 1968, MacInnes and Dunn 1988).

We suggest that the negative effect of neck bands on breeding propensity and other reproductive parameters may result from sublethal effects of neck bands on body condition of females. The accumulation of fat reserves during spring migration is an important determinant of reproductive success in geese (Ebbinge 1989, Ebbinge and Spaans 1995). These reserves are used to sustain long migratory flights (Gauthier et al. 1992) and for egg formation and incubation (Ankney and MacInnes 1978, Choinière and Gauthier 1995). It is possible that neck bands slightly increase aerodynamic drag during flying as this has been shown with backpack radio-transmitters (Gessaman and Nagy 1988, Obrecht et al. 1988). This could increase flight cost during the 3000 km-long spring migration to the arctic breeding ground (Gauthier al. 1992), and thus reduce the condition of arriving females. Reduced spring body condition due to a spring hunt has been shown to reduce breeding propensity in this population (Mainguy et al. 2002). Demers (2003) showed that radio-transmitters mounted on neck bands also had a negative effect on all breeding parameters of adult female Greater Snow Geese (breeding propensity, nest initiation date, clutch size and nest success). This was due to a bulkier and heavier package than neck bands alone and this could have decreased pre-breeding body condition even further. Increased thermoregulatory costs due to feather wear under neck bands may also reduce condition but this is unlikely because recaptured neck-banded birds showed negligible feather wear (G. Gauthier, personal observation). Neck bands may also interfere with behavior and the pair bond (Lensink 1968) but Demers (2003) found that spring time budgets of neck-banded females did not differ from unmarked ones and divorce rate was negligible in neck-banded Greater Snow Geese.

Total clutch size of neck-banded females was slightly reduced in comparison to nests located in random plots (up to 0.36 eggs or 10%) but there was no clear trend for nest initiation dates between neck-banded females and those in our 2 other treatment groups.

Schmutz and Morse (2000) noted a decline of about 1 egg laid after Emperor Goose (*Chen canagica*) females were fitted with a neck band but no marker effect on nest hatching date was detected, as in our study (they did not test for differences in initiation date).

Current theories of avian clutch size determination suggest that individuals in good condition typically nest earlier and produce larger clutches (Newton et al. 1983, Dijkstra et al. 1988, Rowe et al. 1994). The timing and number of eggs laid represent a trade-off between advantages of early breeding (greater offspring value) and the advantages of delay (greater accumulated condition, hence increased potential clutch size) (Drent and Daan 1980, Bêty 2001). Advantages of early breeding in geese include enhanced reproductive success for adults as well as improved growth and first-year survival for goslings (Owen and Black 1989, Cooch et al. 1991, Lepage et al. 1998, Lepage et al. 2000). We detected a reduction of clutch size for neck-banded females compared other females but not in nest initiation date. Radio collared female Greater Snow Geese also had a greater reduction in clutch size than expected from the delay in nest initiation caused by the radio collar (Demers 2003), suggesting that neck bands or radio collars have an additional effect on clutch size independent of nest initiation date. If females cannot reach a minimal condition threshold required for successful breeding early enough (Bêty 2001), skipping a breeding season could be an adaptive strategy.

Because neck-banded females are handled for a longer period of time at banding, they may be more likely to emigrate permanently from the study area than leg-banded females (Pradel et al. 1995). Although our estimates of apparent survival confound both true survival and permanent emigration from the study area, it has been shown that neck bands do not affect true survival of female Greater Snow Geese (Menu et al. 2000) and permanent emigration of leg-banded adult females from our study area is negligible (Reed et al. 2003b). Therefore, the absence of difference in apparent survival between the two groups suggests that neck-banded females were not more prone to permanent emigration than leg-banded females.

Our estimates of apparent survival and capture probabilities are particularly robust because we were able to directly estimate and take into account neck band loss in our models. Neck band loss, estimated at 3.03% per year, would have otherwise negatively biased survival estimates and obscured interpretation of the results.

Research Implications

The magnitude of negative effects of neck bands appears to differ among goose species but in most instances where it has been studied, some effects on survival or breeding potential have been detected (e.g. Samuel et al. 1990, Castelli and Trost 1996, Schmutz and Morse 2000, our study). Based on these considerations, Schmutz and Morse (2000) questioned the use of neck bands for future studies of goose demographics. While we agree that demographic studies should be based on individuals marked with non-disruptive markers to provide unbiased results applicable to the entire study population, we believe that neck bands may still be useful for behavioral studies (e.g. Prevett and MacInnes 1980, Hestbeck et al. 1991, Ely 1993) or in situations where it is impractical to recapture birds repeatedly (e.g. when estimating seasonal survival rate, Gauthier et al. 2001). However, whenever neck bands are used, their effects on the parameters of interest should be assessed with a control group representative of the study population. In any banding study, we recommend marking a large sample of birds with metal leg bands only for estimation of vital rates pertaining to the whole population and as a control group for assessing the effects of alternative markers.

The multistate mark-recapture approach that we used is well suited for determining effects of markers like neck bands on vital rates as well as for unbiased parameter estimation when conducting recapture studies of doubly-marked animals (see also Alisauskas and Lindberg 2002). First, this method allows the integration of marker loss rate into the modeling procedure, allowing vital rate probabilities to be directly adjusted as a function of neck band loss probability. Thus, estimation of vital rates for neck-banded birds is not biased by wrongly assigning a bird that has lost its marker to the marked group. Second, this approach can handle marker loss rates dependent on the age of markers more easily than ad hoc methods that require annual correction of parameter estimates for the marked sample, resulting in reduced precision (Pollock 1981, Nichols et al. 1992, Nichols and Hines 1993). Third, groups can be pooled when no marker effects are detected (e.g. survival in our analysis), resulting in increased sample size and hence precision for the parameter estimated. Finally, the multistate model used here could be extended to include data from band recoveries (see Lebreton et al. 1999 for details) and allow the joint estimation of marker effect on true survival and permanent emigration.

Table 1. Model selection of the effects of neck bands and year on apparent survival (Φ) and capture (p) probabilities, and neck band loss rate (Ψ) of adult female Greater Snow Geese, 1990-2000. Models are ranked by their QAICc value with only the most relevant models being presented, and the general model (Φ_{g*t}, p_{g*t}, $\Psi_{type*age}$). For each model, we give its ΔQAICc value (difference in QAICc between model i and the model with the lowest value), QAICc weight (ω_i) and the number of estimable parameters (#par).

Model	ΔQAICc	ωQAICc	#par
1) Φ_t, p_{g+t}, Ψ	0.00	0.25	21
2) Φ_t, p_{g+t}, $\Psi_{type+age(lin)}$	0.54	0.19	23
3) Φ_t, p_{g+t}, $\Psi_{age(lin)}$	0.72	0.18	22
4) Φ_t, p_{g+t}, Ψ_{type}	1.59	0.11	22
5) Φ_{g+t}, p_{g+t}, Ψ	1.90	0.10	22
6) Φ_t, p_{g+t}, $\Psi_{type*age(lin)}$	2.20	0.08	24
7) Φ_{g+t}, p_{g+t}, Ψ_{type}	3.56	0.04	23
8) Φ_{g*t}, p_{g*t}, $\Psi_{type*age}$	35.69	0.00	53

Subscripts: g = groups (neck band or leg band only), t = year, type = neck band type (matte and textured plastic), age = age (in years) of neck band, age(lin) = linear function (logit scale) between age of neck band and rate of loss, + = additive model, * = model with interaction.

Table 2. Model selection of the effects of treatment and year on daily nest survival (S) in female Greater Snow Geese, 1999-2001. Models are ranked by their AICc value. For each model, we give its ΔAICc value (difference in AICc between model *i* and the model with the lowest value), AICc weight (ω_i) and the number of estimable parameters (#par).

Model	ΔAICc	ωAICc	#par
1) $S_{(g*t)+age}$	0.00	0.44	12
2) $S_{g+t+age}$	0.01	0.44	8
3) S_{g+t}	3.31	0.08	5
4) S_{g*t}	6.28	0.02	9
5) S_{t+age}	8.16	0.01	6
6) S_t	8.54	0.00	3
7) S_g	342.18	0.00	3

Subscripts g = treatment (unmarked females [main nesting area [MNA] and random plots] or neck-banded), t = year, age = age of the nest when found (date found minus estimated nest initiation date), + = additive model, * = model with interaction.

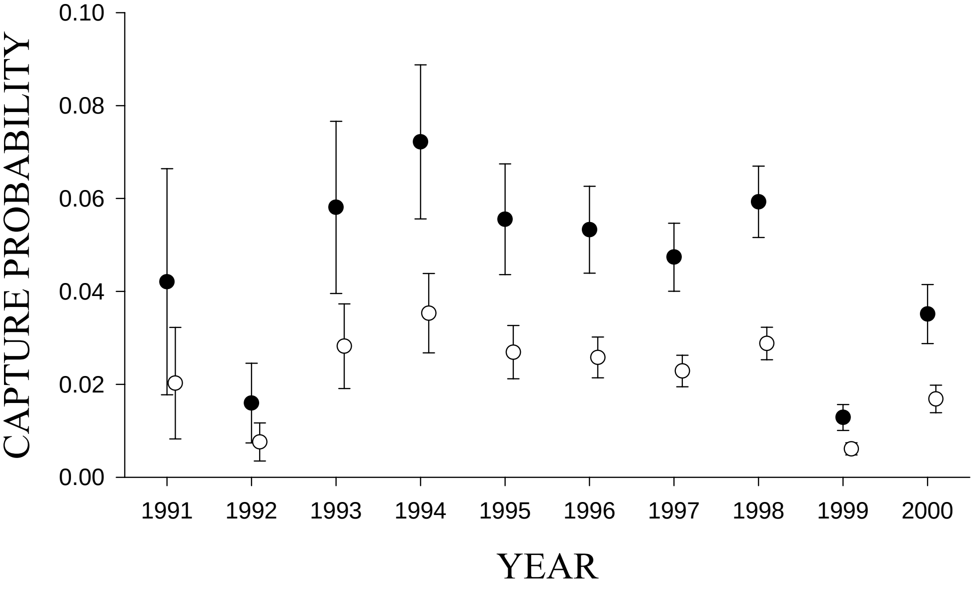

Figure 1. Annual capture probabilities of neck-banded (white dots) and leg-banded only (solid dots) female Greater Snow Geese on Bylot Island, NU. Estimates are derived from our most parsimonious model (Φ_t, p_{g+t}, Ψ). Mean ± 1 SE (SE adjusted for extra-binomial variation, $\hat{c} = 1.81$).

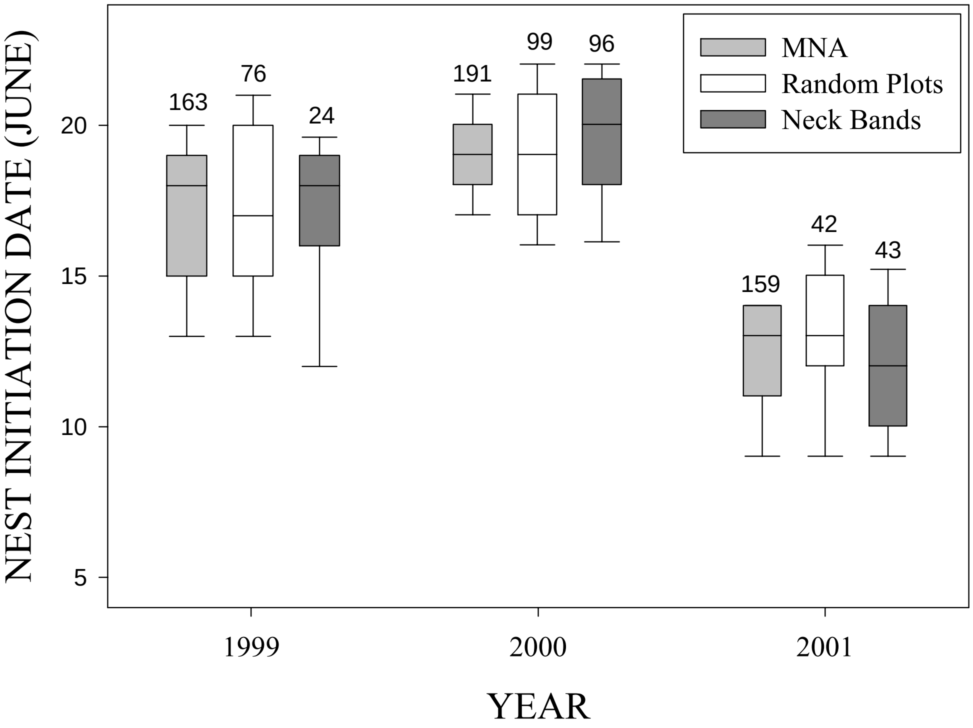

Figure 2. Nest initiation dates of unmarked females (main nesting area [MNA] and random plots) and neck-banded females from 1999 to 2001. The middle bar represents the median, the lower and upper bound of the box the 25th and 75th percentiles and the whiskers the 10th and 90th percentile. Numbers above boxes are sample sizes.

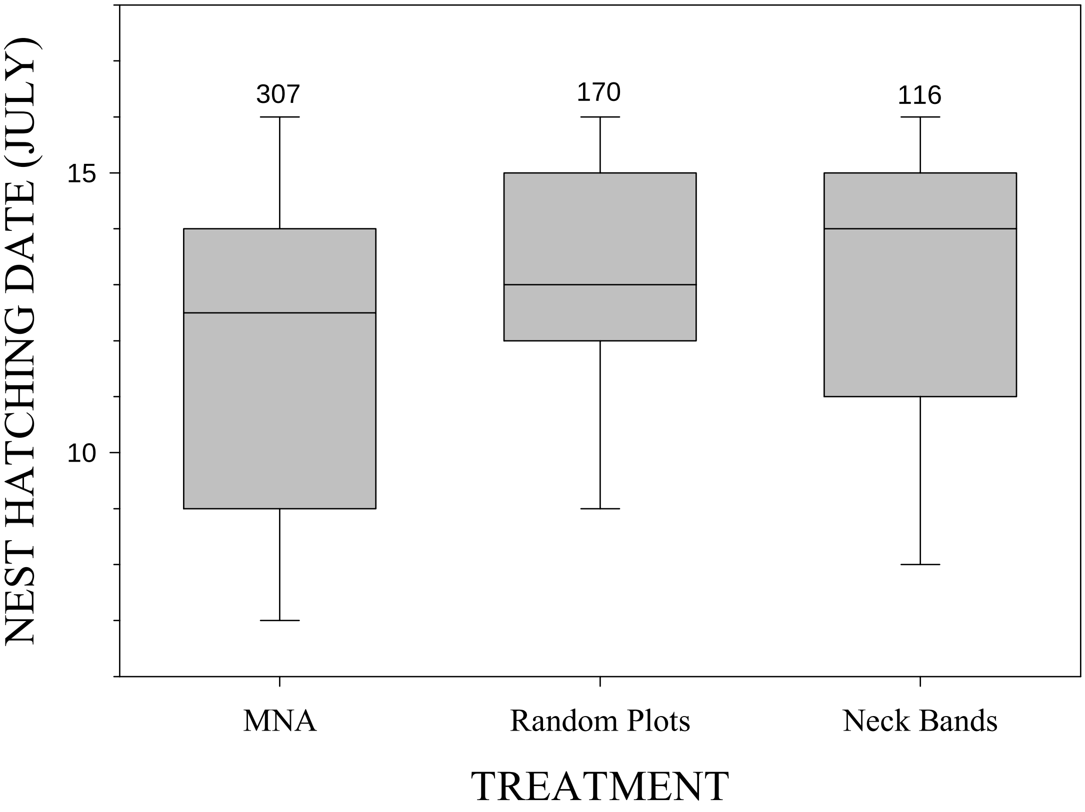

Figure 3. Nest hatching dates of unmarked females (main nesting area [MNA] and random plots) and neck-banded females from 1999 to 2001. The middle bar represents the median, the lower and upper bound of the box the 25th and 75th percentiles and the whiskers the 10th and 90th percentile. Numbers above boxes are sample sizes. The year by treatment interaction was not significant so we show nest hatching dates by treatment only.

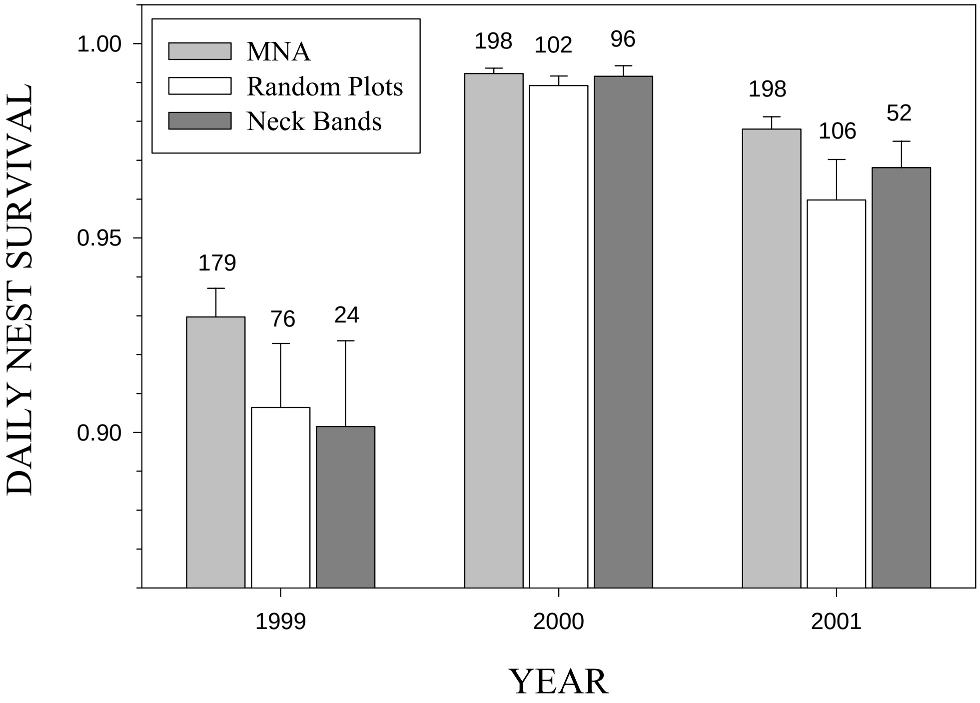

Figure 4. Annual fluctuations in daily nest survival among nests of unmarked females (main nesting area [MNA] and random plots) and those of neck-banded females. Daily nest survival estimates are averaged across all models. Means ± 1 SE are presented. Numbers above bars are sample sizes.

CHAPITRE 5

AGE AND ENVIRONMENTAL CONDITIONS AFFECT RECRUITMENT IN GREATER SNOW GEESE

Eric T. Reed, Gilles Gauthier, Roger Pradel, Jean-Dominique Lebreton[1]

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Résumé

Le recrutement est une composante importante du fitness individuel et de la croissance d'une population mais peu d'études ont examiné l'effet de la stochasticité environnementale sur ce trait d'histoire de vie. De plus, la majorité des études ont été incapables de séparer la contribution de la survie juvénile et des probabilités de reproduction spécifiques à l'âge sur le recrutement. Nous avons utilisé une nouvelle approche, où le recrutement est analysé par un modèle multi-états avec un état 'non-reproducteur' non-observable. Les données proviennent d'une étude à long-terme de la Grande Oie des neiges, une espèce longévive nichant dans l'Arctique. Ces données incluent le marquage d'oisons femelles et d'adultes reproducteurs d'âge inconnu et leur recaptures entre 1990 et 2000. Le modèle considère 4 paramètres: la probabilité qu'un individu d'âge i sans expérience commence à se reproduire (a_i), la survie apparente juvénile et adulte (Φ) et la probabilité de capture de reproducteurs (p). La flexibilité de ce modèle nous permet d'évaluer l'influence des conditions ontogéniques et au moment de la première reproduction sur la survie juvénile et la probabilité de recrutement spécifique à l'âge. Nos résultats indiquent que le recrutement est un processus graduel, commençant à 2 ans (a_2 = 0.25 [IC à 95%: 0.12 – 0.45], a_3 = 0.57 [0.20 – 0.87]) et complété à 4 ans. La survie juvénile était plus élevée chez les femelles nées tôt en saison que chez celles nées plus tardivement. La survie juvénile variait considérablement entre les cohortes mais les variables environnementales à l'étude ne pouvaient expliquer ces différences. La probabilité qu'un individu d'âge i sans expérience commence à se reproduire était moins variable mais réduite lors d'années de faible abondance de lemmings. Ces résultats suggèrent que les conditions environnementales peuvent avoir un impact significatif sur les traits d'histoire de vie des oiseaux évoluant dans des environnements saisonniers. Par contre, la proportion d'individus d'une cohorte qui vont recruter dans la population reproductrice est expliquée majoritairement par la survie juvénile. L'utilisation de modèles multi-états augmente la précision de l'estimation des paramètres avec l'addition de données d'adultes d'âge inconnu. Par contre, nous sommes encore restreints par certaines prémisses, notamment celle d'absence d'émigration temporaire.

Abstract

Recruitment is an important determinant of fitness and population growth rates but few studies have examined the effect of environmental stochasticity on this life-history trait. Furthermore, most studies have been unable to separate the influence of juvenile survival and age-specific breeding proportions on recruitment. We used a recently developed approach, based on capture-mark-recapture methods, in which local recruitment is analyzed in a multistate model with an unobservable "non-breeder" state. The data are drawn from a long-term study of a long-lived arctic-nesting bird, the Greater Snow Goose, and include marking of female goslings and breeding adult females of unknown age and their recaptures between 1990 and 2000. The model considers four parameters: the probability that an individual aged i with no breeding experience starts breeding (a_i), juvenile and adult apparent survival (Φ), and capture probability of breeders (p). The flexibility achieved allows us to assess the influence of environmental conditions encountered during early life and at breeding on juvenile survival and probabilities to start breeding at a given age. Recruitment was a gradual process (probability to start breeding at age 2: 0.25 [95% CI: 0.12 to 0.45]; at age 3: 0.57 [0.20 to 0.87]) and was completed by age 4 (i.e. all remaining immature females started to breed at that age). Juvenile survival was higher in early-hatched than late-hatched females. Juvenile survival varied considerably among cohorts but our environmental covariates could not explain these differences. Probabilities to start breeding were less variable, except in lemming crash years when they were considerably reduced. Snow cover at breeding or hatch date did not affect probabilities to start breeding. These results suggest that environmental conditions can have an impact on life history traits of birds in seasonal environments but that variations in juvenile survival probably account for most of the fluctuation in the proportion of birds from a cohort that recruit into the breeding population. Use of multistate models to estimate recruitment increases precision in parameter estimates with the addition of data from adults of unknown age. However, we are still restricted by some assumptions, most notable the one of an absence of temporary emigration.

Introduction

Recruitment, defined as the establishment of new individuals into the breeding segment of populations, is an essential component of population dynamics. The probability of recruitment into the population is a three-stage process: survival from hatching to fledging (or weaning in mammals), survival from fledging to age of sexual maturity, and age of first breeding (age at maturity). At the individual level, age at first breeding may be an important determinant of fitness (Gadgil and Bossert 1970), whereas at the population level it may have a major impact on population growth rates (Porter and Coulson 1987, Gaillard et al. 1998). Delayed accession to reproduction is common in long-lived species, often exceeding the age at which reproduction is physiologically possible (Bell 1980).

Poor environmental conditions at birth or at breeding may restrain or constrain early reproduction by reducing potential benefits of an early breeding attempt (Curio 1983, Cam et al. 1998). While numerous studies have addressed the influence of environmental stochasticity on different life-history traits (e.g. Boyce and Perrins 1987, Sedinger et al. 1995), very few have studied the impact of environmental conditions encountered at birth or at breeding on recruitment.

In seasonal environments, hatch date may be an important determinant of fitness. Even though accession to reproduction may not occur for several years, the date that an individual hatches from its egg may still influence the circumstances that determine recruitment. Individual hatch date influences survival and age of first breeding across a variety of bird species (e.g. Spear and Nur 1994, Verboven and Visser 1998, Prévot-Julliard et al. 2001). Hatch date is negatively related to recruitment in geese (Cooke et al. 1984, Sedinger et al. 1995) and ducks (Dawson and Clark 2000), but it is not clear whether this is an effect of hatch date on juvenile survival (Owen and Black 1989, Cooch et al. 1993, Schmutz 1993, Lepage et al. 2000) or on age of first breeding. Environmental conditions at the start of the breeding season may affect recruitment if they result in delayed nest initiation (Prop and de Vries 1993, Lepage et al. 1996), restricted access to feeding (Gauthier and Tardif 1991, Choinière and Gauthier 1995, Ganter and Cooke 1996) or generally reduce breeding effort and success (Barry 1962, Skinner et al. 1998). Predator abundance and activity at the colonies during the pre-breeding period can also induce birds to forego breeding (Spaans et al. 1998).

Environmental influence on recruitment has rarely been studied in long-lived species due to the difficulty of estimating this life history trait from field data. Most previous studies of recruitment have relied on estimation methods that may suffer from some biases, such as measuring the age distribution of first-time breeders without correcting for variations in survival or capture probabilities among cohorts or time (e.g. MacInnes and Dunn 1988, Moser and Rusch 1989, Thompson et al. 1994, Schmutz 2000). Therefore, an individual observed breeding for the first time may have bred previously. Recently, robust mark-recapture methods have been developed to obtain unbiased estimates of age at first breeding (Clobert et al. 1994, Pradel 1996, Pradel and Lebreton 1999, Schwarz and Arnason 2000), but only a few studies have made use of these new methods (Pradel et al. 1997, Cooch et al. 1999a, Prévot-Julliard et al. 2001, Sedinger et al. 2001, Tavecchia et al. 2001).

We used a method that has been developed only recently and that, to our knowledge, has never been applied to field data. This method, described in Pradel and Lebreton (1999), is a particular case of a multistate mark-recapture model (Brownie et al. 1993, Nichols et al. 1994) with two states, including one that is non-observable (e.g. when non-breeders cannot be captured on the breeding grounds; see also Lebreton et al. 1999). With this method, data from individuals of known age (i.e. marked as young) are used to estimate juvenile survival and age-specific probabilities of becoming a breeder, while data from individuals marked as adults (i.e. of unknown age) are used to estimate adult (breeder) survival and capture probabilities. Including data from the latter group increases precision of adult parameter estimates. When following only one cohort, age and time are confounded but by treating many cohorts simultaneously, we can separate age and time effects on recruitment probabilities. This method also has the advantage of allowing the separate estimation of juvenile survival and proportion of individuals alive entering the breeding population at a given age. An additional advantage of the multistate method includes the possibility to assess the effects of external and individual covariates on recruitment parameters pertaining to different cohorts.

We examined the influence of environmental conditions in early life (cohort median hatch date and within cohort relative hatch date) and at breeding (snow cover at the onset of laying and lemming abundance) on recruitment in Greater Snow Geese (*Chen caerulescens atlantica*), hereafter GSG. This species is a good model to test this multistate approach because it is relatively long-lived, it shows delayed maturity (females start reproducing at age 2 or later) and it breeds in a stochastic environment where variations in weather and predation risk may lead to occasional breeding skips. The multistate approach is especially well suited for sampling schemes where non-breeding individuals elude capture while many captured birds are of unknown age every year, a situation found in many field situations such as ours. In geese, females exhibit a high degree of natal philopatry whereas males have high dispersal rates (Rohwer and Anderson 1988), so we analyzed data from females only.

Methods

Study location and data set

The study was conducted on the southwest plain of Bylot Island ($73^0$08’N, $80^0$00’W), Sirmilik National Park, Nunavut Territory, Canada. This area supports the largest nesting colony of GSG (55 000 breeders in 1993), representing ca. 15% of the world breeding population (Reed et al. 1998). From 1990 to 2000, extensive nest searches were conducted during the egg laying and early incubation period. Nests were revisited at hatch and goslings were marked with individually coded web-tags before they left the nest (see Lepage et al. 2000 for details).

Molting adult geese and their offspring were captured shortly before fledging in mass banding drives (Menu et al. 2001). Because non- or failed-breeders leave the Island to molt or have regained flight capacity when banding occurs, only adults that have bred successfully are caught (Reed et al. 2003a). Upon capture, goslings and adults were sexed by cloacal examination and marked with individually coded metal USFWS leg bands. A random sample of adult females was also fitted with individually coded plastic neck bands (Menu et al. 2000). Most goslings were measured and weighed (see Lepage et al. 1998 for details). Goslings were checked for the presence of web-tags and adults were checked for neck bands, bands and web-tags.

Our data set thus consisted of the initial capture and all subsequent recaptures of females of known age (i.e. marked as goslings in banding drives) for which we had 9th primary wing feather measurements on initial capture. These females were classified as non-breeders (NB) from initial capture until they recruited into the breeding population. We also used data from females caught initially as adult breeders (B) (i.e. of unknown age). Because there is evidence that breeding propensity of adult females fitted with a neck band is reduced (Menu et al. 2000, Chapitre 4), we excluded these females from the data set. If a neck band was fitted to a female that had previously been marked with a metal leg band only, all subsequent recaptures were deleted by considering this individual as lost on capture. In a similar way, females that lost their neck bands were included in the data set of breeders, by considering their first capture without a neck band as their initial capture event. In this way, a maximum amount of information was kept while avoiding the biases due to heterogeneity in capture rates.

Environmental covariates

We examined four covariates representing environmental conditions encountered in early life and at time of breeding (three group and one individual).

Median nest hatching date-- Nest hatching date was directly recorded or estimated for every nest that hatched at least one young in the sample of nests followed by field crews. Hatch date was defined as the date at which at least half the brood had hatched. Hatching was synchronized within a clutch (usually <24 h). Annual median hatch date was calculated to obtain a population estimate for a given year.

Individual hatch date of marked goslings -- Individual hatch date of goslings web-tagged in the nest and captured during banding (ca 4 % of captured goslings) was known. For the other goslings, we estimated their age from the annual linear relationships between age of web-tagged goslings and length of their 9th primary. Because there is little sexual dimorphism at that age, males and females were combined in these relationships. Primary length is a good predictor of age before fledging as its growth is less sensitive to environmental conditions than other morphometrics (Lepage et al. 1998, Cooch et al. 1999b). Individual hatch dates were transformed into relative values with respect to median annual hatch date.

Snow cover-- A qualitative assessment of total snow cover in the main valley of the Island was made during the snowmelt period every year from a vantage point near the base camp. We used snow cover estimated on 5 June, which is just before the peak of nest initiation (average across years: 11 June, annual range: 6 to 20 June), as an annual index of spring phenology. Preliminary analyses showed that snow cover on 5 June was highly correlated to mean air temperature during the pre-laying and laying periods (25 May to 15 June). We chose snow cover over air temperature in our analyses because it is more representative of nest site and food availability at the onset of egg laying.

Lemming abundance-- We used a categorical variable to describe annual lemming abundance on Bylot Island. Each year since 1993 intensive trapping of lemmings or winter nest surveys have been conducted at our study site (Bêty et al. 2001). Presence of Snowy Owl (*Nyctea scandiaca*) nests is another index of lemming abundance because they only occur during peak lemming years in our study area. We categorized lemming abundance as high when abundance reached a peak (every 3 to 4 years in our area) and Snowy Owls were breeding, moderate when lemming abundance was intermediate, and low when lemming populations crashed.

Statistical method

Data were analyzed using a particular case of multistate model with 2 states (NB and B) of which one (NB) was non-observable except at birth (Lebreton et al 1999, Pradel and Lebreton 1999). Three kinds of parameters can be estimated with these models: apparent survival probability Φ_t^r, conditional transition probability Ψ_t^{rs}, and capture probability p_t^r (Brownie et al. 1993, Nichols et al. 1994).

Φ_t^r = probability that an individual in state r at time t survives until time t + 1. This is an apparent survival probability because we cannot differentiate between mortality and permanent emigration from the study area.

Ψ_t^{rs} = probability that an individual in state r at time t is in state s at time t +1, given that it survived from time t to t + 1.

p_t^r = probability that an individual is recaptured at time t in state r, given that it is alive and present in the study area at time t.

These parameters can be conveniently summarized in matrices of transition, survival and capture probabilities:

$$\begin{pmatrix} \Psi_i^{NB-NB} & \Psi_i^{B-NB} \\ \Psi_i^{NB-B} & \Psi_i^{B-B} \end{pmatrix}, \begin{pmatrix} \Phi_i^{NB} \\ \Phi_i^{B} \end{pmatrix} \text{ and } \begin{pmatrix} p_i^{NB} \\ p_i^{B} \end{pmatrix}$$

In the special case of recruitment analyses, transition probabilities are unidirectional, i.e. once an individual starts breeding, it remains a “breeder” for the rest of its life, thus transition probabilities from B to NB are fixed at 0. With the “non-breeder” state being unobservable, capture probabilities of NB are also fixed at 0. For this particular case, the matrices indexed by age i (for a given cohort, age and time are confounded) thus become:

$$\begin{pmatrix} 1-a_i & 0 \\ a_i & 1 \end{pmatrix}, \begin{pmatrix} \Phi_i \\ \Phi_i \end{pmatrix} \text{ and } \begin{pmatrix} 0 \\ p_i \end{pmatrix}$$

where a_i is the probability that an individual of age i that has not yet reproduced starts to breed (Pradel and Lebreton 1999; hereafter referred as probability to start breeding).

Starting assumptions -- A few assumptions need to be made with this model, some of which may be relaxed without leading to severe biases. The minimal assumptions under which this multistate model is valid are:

- Adult breeders (B) and non-breeders (NB) of the same age i share the same survival probabilities (no survival costs of reproduction).

- Experienced breeders do not emigrate temporarily from the study area. In many field situations, this assumption is synonymous with adult breeding propensity of 1. If breeding propensity < 1, then the parameter a_i will be relative to adult breeding propensity (as indexed by adult capture probabilities).

- Age at which all individuals have recruited into the breeding segment of the population (hereafter age of full breeding) must be determined and the parameter a_i fixed to 1 at that age. Non-breeders have a zero capture probability so individuals that never recruit into the local breeding population cannot be separated from individuals that die or emigrate permanently before recruiting locally. The age at which full breeding is attained can be tested formally in the model selection procedure.

Other assumptions, based on the biology of GSG and field considerations, were made. These assumptions reduced the number of parameters in our starting model, thus reducing parameter identifiability problems and the number of potential candidate models, allowing us to concentrate on models that address hypotheses relevant to the study of recruitment.

- Probability of capture at age 1 is 0, since only breeders are caught. Studies in other species of geese have shown that minimum age to reproduce is 2 (Cooch et al. 1999a). In the 11 years of our study, only 2 females out of 7541 marked as young were caught at age 1. They were likely still associated with their parents, as some families remain intact for more than a year (E. T. Reed and G. Gauthier, *unpublished data*). These recaptures were deleted from the capture history record.

- Juvenile survival is estimated over the age interval 0 (i.e. fledging) – 2 and survival after age 2 is equal to adult survival.

- There are no age effects on adult survival such that young adults (age 2 or more) are as likely to survive as older ones.

- There are no age or experience effects on capture probabilities. Because a breeding failure or skipping breeding in geese often leads to temporary emigration, we must assume that age or experience does not influence breeding success or breeding effort.

We discuss later the consequences on parameter estimates when some of these assumptions are violated.

Model selection

Model notation followed Nichols et al. (1994). The factorial structure of a model was represented by subscripting probabilities of apparent survival, capture and to start breeding at age *i* (a_i). Relations among factors were indicated via standard linear models notation (McCullagh and Nelder 1989). We started by fitting model $\Phi^J{}_c\ \Phi^A{}_t\ p^B{}_t\ a_{age\ (full\ a5)*c}$. In this model, apparent survival of juveniles (*J,* age 0-2) varies among cohorts (*c*) (here cohort is used for clarity as cohort and time are confounded). We fixed survival probability between age 0 and 1 at 1 such that survival for age 1 – 2 was the product of survival probabilities for the first 2 years of life. Apparent survival and capture probabilities of adults (*A*, breeders [B] or non-breeders, age 2 or more) varied over time (*t*). Probability to start breeding at age *i* (a_i) varied among cohorts and age (*age*) between age 2 and age of full breeding (but fixed to 0 between age 0 and 1, i.e. no female reproduces at age 1), with an interaction term (*). Age of full breeding ($a_i = 1$) was fixed at 5 (*full a5*).

There are no formal goodness-of-fit tests available for multistate mark-recapture models. However, one way of verifying whether our general model reasonably fits the data is to partition each state into independent groups and test each group separately with the goodness-of-fit (GOF) tests for developed the Cormack-Jolly-Seber model. Our study design allowed testing the GOF of our general model on the breeders' data only since non-breeders are never captured. We used program U-Care (Choquet et al. 2001) to assess the fit of our general model. GOF tests in U-Care are the same as those of program RELEASE (Burnham et al. 1987) but they further provide directional *z*-tests for possible structural problem in the data (e.g. transient or trap effects). We calculated a variance inflation factor ($\hat{c}$) to account for overdispersion in our data as:

$$\hat{c} = {}^{\chi^2}\!\Big/_{df}$$

where χ^2 is the goodness-of-fit statistic for our global model and *df* the model's degrees of freedom. We then used a modification of Akaike's Information Criterion (QAICc) for overdispersed count data (see Burnham and Anderson 1998 for details).

We used program MARK v1.9 (White and Burnham 1999) for model selection. Group and individual covariates were tested through ultrastructural models, and directly included into the iterative process through the design matrix option in MARK. Covariates were fitted to the model by linear constraints (on a logit scale). To ensure proper parameter estimation, all covariates, excluding lemming abundance, were standardized as:

$$(\mathrm{X} - \overline{\mathrm{X}}) \big/ SD$$

We tried to explain cohort effects on juvenile apparent survival and probability to start breeding with cohort specific median hatch dates. We also considered the influence of relative hatch date on these 2 parameters. We examined the consequences of snow cover and lemming abundance on probability to start breeding, but not survival, because these variables were most likely to affect breeding probability. Cohort median hatch date and individual relative hatch date referred to conditions encountered at birth whereas snow cover and lemming abundance referred to conditions encountered at breeding. When the only difference between two models is a single covariate, a small value of ΔQAICc between these two models is not good evidence of an effect of the covariate. Rather, the confidence intervals around the beta estimates (β: slope of the linear relation between the parameter and the covariate or difference among levels of a categorical covariate) provide useful evidence of an effect. We used this approach and concluded that covariates had an effect when their 95% confidence intervals did not include 0. Main effects and biologically relevant interactions between parameters and covariates were fitted.

Results

Environmental covariates

Snow cover on 5 June varied greatly from year to year, ranging from 10 to 95 % (Fig. 1a). Mean snow cover over the period 1992 – 2000 was 62% (SD = 30). Peaks in the lemming cycle occurred in 1993, 1996 and 2000, and lows in 1995 and 1999; other years had a moderate abundance (Bêty et al. 2001). There was no lemming trapping in 1992 but we categorized that year as having moderate abundance based on field observations of Lepage et al. (1996).

A total of 3173 nests were monitored between 1990 and 1998 (range: 168 – 846). During this period, median hatch date ranged from 3 to 15 July (Fig. 1b). We captured a total of 557 goslings of known age between 1990 and 1998 (range: 9 to 102), from which we calculated regression coefficients between age and length of 9th primary feather (Table 1). The difference in age at capture between known-age goslings and those for which it was estimated was slight for most cohorts (<1.6 d for 7 of the 9 cohorts, Table 1). Individual relative hatch dates varied from 10 d before the median to 14 d after (Fig. 2).

Goodness of fit of the general model

Between 1990 and 1998, we marked 6395 female goslings, of which 206 were recaptured as known age breeders between 1992 and 2000. In addition, 1979 adult females of unknown age were initially captured as breeders between 1990 and 1999, and 276 were recaptured between 1991 and 2000.

The GOF test of our general model, applied only to the breeder state, indicated lack of fit ($\chi^2_{45} = 75.42$, $P < 0.01$). There was evidence of a transient effect (TEST3.SR: $\chi^2_9 = 22.26$, $P < 0.01$) and trap dependence in the form of trap-shyness (TEST2.CT: $\chi^2_8 = 18.02$, $P = 0.02$). This lack of fit was driven by a few cells that had high χ^2 values and biological interpretation was not consistent among time periods (e.g. there was trap-happiness in some time periods). The results from our GOF tests and the relatively small value of the variance inflation factor from the global test ($\hat{c} = 1.66$) were compatible with overdispersed count data. We therefore applied this value of the variance inflation factor for all subsequent model fitting.

Adult survival and capture probabilities

There was no detectable yearly variation in apparent survival of adults over the course of our study (Table 2). Apparent survival of adults was estimated at 0.84 [95% CI: 0.77 to 0.90]. Capture probabilities of breeders varied across years, but this variation could not be explained by environmental conditions (snow cover or lemming abundance) (Table 2). Annual capture rates ranged from 0.02 [0.00 to 0.18] to 0.08 [0.06 to 0.12].

Environmental and cohort effects on juvenile survival

Juvenile apparent survival varied considerably among cohorts, but this variability could not be simply explained by a cohort's median hatch date (Table 2). In contrast, relative hatch date of individual females had a strong effect on their survival probabilities (this effect was present in the 9 top models in Table 2), with early hatched females surviving to age 2 in greater proportion than late hatched ones (β = -1.09 [-1.65 to -0.52], model 1, Table 2). The absence of interaction between cohort and relative hatch date suggested that this effect was consistent across all cohorts, survival probabilities declining rapidly in late-hatched goslings (Fig. 3). Average cohort apparent survival of juveniles ranged from 0.76 [0.25 to 0.97] to 0.09 [0.04 to 0.19] (Fig. 4). This parameter could not be estimated for the 1998 cohort since we only had one recapture occasion to assess it.

Age of full breeding

There was strong evidence for an age effect on recruitment (Table 2). We could reduce age of full breeding (i.e. age at which all females have started breeding) to age 4 but not further. Thus, some adult females had not started to breed at age 2 and 3 but all of them had started by age 4. The probability that a female with no breeding experience started to breed at age 2 was consistently lower than at age 3 (Fig. 5). Average probabilities that surviving females started to breed at age 2 were estimated at 0.25 [0.12 to 0.45], 0.57 [0.20 to 0.87] at age 3, and 1.00 at age 4 (derived from model 3, Table 2).

Environmental and cohort effects on age at first breeding

The probability that a female with no breeding experience started to breed was affected by lemming density. The cumulative QAICc weight for models with a lemming effect was 0.62 (Table 2). Results from our best model indicated that a_i was highly reduced in lemming crash years (β = -14.96 [-17.33 to -12.59]) but similar at medium (β = 0.30 [-1.70 to 2.29]) and high lemming densities (Fig. 5). We had little evidence that probability to start breeding was affected by snow cover (β = -0.18 [-1.43 to 1.07], model 2), relative hatch date (β = -0.93 [-3.03 to 1.16], model 4), or cohort median hatch date (β = 0.63 [-0.65 to 1.92], model 5, Table 2).

Discussion

We showed that accession to reproduction was a gradual process in GSG, with the first females starting to breed at 2 years and the last ones at 4 years. Among the environmental conditions studied, only lemming density had an effect on the probability that an individual started to breed. Juvenile apparent survival was highly variable among cohorts, and was much more influenced by environmental conditions during early development than probabilities to start breeding at a given age. Thus, juvenile survival seems to be the major factor responsible for variability in recruitment into the breeding population among different cohorts.

Effect of age on local recruitment

Delayed accession to reproduction is common among long-lived birds (Wooler and Coulson 1977, Pradel et al. 1997, Cooch et al. 1999a, Sedinger et al. 2001). Delayed reproduction has been linked to differences in individual quality (Forslund and Pärt 1995) and improved foraging or breeding skills (Recher and Recher 1969, Desrochers 1992). In geese, the high energetic demands of long migrations and reproduction (Ankney and MacInnes 1978, Gauthier et al. 1992, Choinière and Gauthier 1995) may constrain young, inexperienced individuals to delay reproduction. Lack of experience between young mates may also delay first reproduction because pairing in geese occurs in the second or third year of life and breeding success increases with time since pairing (Owen et al. 1988, Black and Owen 1995).

Few studies have quantified age-specific breeding probability in birds with robust mark-recapture methods (Cooch et al. 1999a, Anderson et al. 2001, Sedinger et al. 2001). It appears that probabilities to start breeding in GSG are reduced at age 2 and 3 compared to Black Brant (*Branta bernicla nigricans*) and Lesser Snow Geese (*Chen c. caerulescens*), but in all three species most females have recruited at age 4 (Cooch et al. 1999a, Sedinger et al. 2001). High population density could result in delayed accession to reproduction, but even though the GSG population more than doubled during our study (Reed et al. 1998), we failed to detect a consistent trend in the age to start breeding (see also Sedinger et al. 2001 for similar evidence in Black Brant). It appears more likely that the great unpredictability and stochasticity of the high Arctic environment, where delays in snow-melt frequently deny access to nesting sites and prevent females of acquiring nutrients used for egg-formation (Choinière and Gauthier 1995, Ganter and Cooke 1996), may result in reduced breeding effort (Prop and de Vries 1993). The long and energetically costly migration of GSG (Gauthier et al. 1992) may also constrain young birds in their ability to acquire sufficient nutrient reserves for successful breeding.

Effect of conditions at time of breeding on recruitment

We found that probabilities to start breeding were considerably reduced when lemming densities were at their lowest during their 3 to 4-year cycle in comparison to years of high and medium lemming densities. Bêty et al. (2001) showed that annual nest failure of GSG on Bylot Island is negatively associated with lemming abundance and is generally highest in low lemming years. This high nest failure should mostly affect the probability of capture (p) because most failed nesters leave the island before banding (Reed et al. 2003a). However, if inexperienced birds suffer a higher nest predation rate than experienced breeders, this could negatively bias the probability to start breeding (a_i) in lemming crash years. Alternatively, disturbance by predators during the pre-laying and laying period may be sufficient to deter some females from breeding (e.g. Spaans et al. 1998). During lemming low years, predators such as Arctic Foxes (*Alopex lagopus*) switch to alternative preys and are more active at goose colonies (Bêty et al. 2002). Therefore, it is possible that lemming density indirectly influences a female's decision to delay reproduction until more favorable conditions are met.

We had no evidence that variable snow cover encountered at breeding, when females were 2 or 3 years of age, affected their probability to start breeding. This suggests that, although breeding propensity and nesting success of adults is often reduced in years of late snowmelt (Barry 1962, Prop and de Vries 1993, Skinner et al. 1998), birds at their first breeding attempt are not disproportionately affected by spring phenology.

Effect of conditions in early life on recruitment

Poor growth of late-hatched goslings has been reported in many goose species (Cooch et al. 1991, Larsson and Forslund 1991, Sedinger and Flint 1991), including GSG (Lepage et al. 1998). Manipulative experiments have demonstrated that variation in gosling growth is of environmental origin rather than a function of parental quality (Larsson and Forslund 1991, Lepage et al. 1999). These variations have fitness consequences since body size at fledging affects post fledging survival (Owen and Black 1989, Menu 1998, Dawson and Clark 2000). Our results are consistent with these studies and show that survival declines sharply in late-hatched goslings. Our juvenile apparent survival estimates are well correlated with first-year survival estimates obtained from band recovery data for the cohorts 1990 – 1995 (Menu et al. 2002), except in 1990 where our estimate was possibly biased high due to low sample sizes. Juvenile survival estimate for the 1997 cohort was also likely biased low because all females from that cohort had not recruited when our study ended (full breeding attained only in 2001). Therefore, the apparent linear decline in juvenile survival over the course of our study may be due to biased survival estimates in 1990 and 1997 rather than being indicative of a density-dependent effect. Furthermore, Menu et al. (2002) found no evidence of density-dependent effects on other demographic parameters despite the population increase.

In Black Brant, small body size negatively affects some reproductive parameters, possibly because small birds are less able to acquire sufficient body condition to breed (Sedinger et al. 1995). Because surviving late-hatched goslings become adults of small body size (Cooch et al. 1991, Larsson and Forslund 1991), we expected a negative association between hatch date and probability to start breeding. However, our failure to detect such a relationship suggests that adult body size may have little effect on this demographic parameter.

An important assumption in our study is that length of 9th primary is an unbiased estimator of gosling age during the summer. Age estimated from body size measurements may nonetheless suffer from a positive bias in early-hatched goslings and a negative bias in late-hatched goslings, thus weakening our ability to detect seasonal effects on survival or probabilities to start breeding (Cooch et al. 1999b). This bias is due to delays in the age of emergence of the 9th primary in late-hatched goslings (Lindohlm et al. 1994). By using year-specific models to estimate gosling age, we at least controlled for inter-annual differences in 9th primary growth.

Survival, age at maturity and population dynamics

Our results suggest that annual differences in accession to reproduction at 2 and especially 3 years of age are relatively small, except in low lemming years. This contrasts with juvenile survival, which varied considerably among cohorts. Prospective analyses of GSG population dynamics indicated that adult survival had the greatest influence on population growth rate, whereas juvenile survival and recruitment had lower elasticities, and were thus potentially less influential than adult survival (Gauthier and Brault 1998; see also Tombre et al. 1998). However, some vital rates may have a greater impact on population growth rates under natural conditions than estimated by their elasticities if they account for a larger proportion of variance in population growth rates (Gaillard et al. 1998, Caswell 2000, Cooch et al. 2001). Thus, juvenile survival may still play a dominant role in the population dynamics of this species because it varies considerably more, under natural conditions, than adult survival (Gauthier et al. 2001) and probability to start breeding at a given age.

Model assumptions and validity

The use of multistate mark-recapture models to study recruitment requires fixing the value of some parameters and some assumptions. Because the computation of a_i is based on the frequencies of first-time and non-breeders (i.e. individuals of age i that have not yet reproduced) in the population (a = first-time breeders / (non-breeders + first-time breeders); Pradel and Lebreton 1999), estimates will be biased when either estimated frequency is.

First, we had to postulate that breeders and non-breeders share the same survival probabilities, hence that there is no cost of reproduction. Early maturation can sometimes be costly in terms of reduced survival (Wooler and Coulson 1977, Pyle et al. 1997, Tavecchia et al. 2001) but other studies have found a positive correlation between breeding effort and survival (Cam et al. 1998, Annett and Pierotti 1999). Although Francis et al. (1992a) found a trend for higher survival in non-breeding geese compared to breeders, Gauthier et al. (2001) found no evidence for increased mortality of breeding females during the summer. Viallefont et al. (1995a) showed that apparent survival of Lesser Snow Geese did not differ between females recruiting at age 2 and 3. Tombre and Erikstad (1996) did not detect reduced survival in Barnacle Goose (*Branta leucopsis*) females that had their incubation period (and hence reproductive investment) extended. In GSG, survival of females that provide parental care to their offspring for 10 months or more is reduced (Chapitre 2, but see Black and Owen 1989a), although few females provide care for such long periods (Gauthier and Tardif 1991). Our estimate of apparent adult survival (0.84) is very similar to estimates of true adult survival of GSG (0.81 and 0.85, Menu et al. 2000; 0.83, Gauthier et al. 2001), suggesting that our estimate was unbiased and that breeding philopatry was very strong.

We also had to postulate that there were no age effects on adult survival (age 2 or more). There is no evidence for age effects on survival between 2 and 15 years in geese (Owen 1984, Francis et al. 1992a), such that not taking age in consideration likely did not bias our adult survival estimates. A negative bias in survival would affect the estimation of non-breeders of a given age and potentially lead to a positive bias in a_i.

Perhaps a more serious problem in our analysis is the assumption of no temporary emigration from the study area. Temporary emigration is confounded with true capture probabilities in most mark-recapture studies. In our particular case, temporary emigration can be explained by skipping (i.e. an experienced breeder does not attempt to breed in a given year) or by nest failure (unsuccessful females leaving the study site to molt or regaining flight capacity before capture time). Since temporary emigration is not an option for first time breeders (they have to breed successfully to recruit), the assumption that capture parameters are the same for first-time and experienced breeders may not hold.

In Lesser Snow Geese, females are more likely to skip breeding in the year following their first reproduction if they recruit at a young age (Viallefont et al. 1995a), and even experienced breeders may occasionally skip a breeding season. Nest failures, which also result in temporary emigration in our study, could lead to similar problems. If nest success also differs between first-time and experienced breeders (e.g. Rockwell et al. 1993), then this difference will be additive to the skipping bias on capture probabilities. Because estimation of the parameter a_i is conditional on adult capture probabilities, these effects may negatively bias age-specific probabilities to start breeding but reflect more precisely probabilities to start breeding with success.

Assuming no age or experience effects on capture probabilities may have thus introduced heterogeneity and led to some biases in our analysis. This may explain why our goodness-of-fit test detected the presence of transients and some heterogeneity in capture rates, although such effects are not unusual. The magnitude of these potential biases on parameter estimates and their effects on model selection are presently unknown. Unfortunately, all capture-recapture approaches available for the study of recruitment assume no temporary emigration. It may be possible to accommodate temporary emigration in these models by incorporating a breeding probability of less than 1 for experienced breeders. However, increasing the number of parameters in the models may lead to reduced precision on parameter estimates and to serious parameter identifiability problems due to overparametrization (Pradel and Lebreton 1999).

The impossibility to account for differences in capture probabilities between experienced and first-time breeders is still a weakness of all capture-recapture approaches for the study of recruitment. Nevertheless, these methods represent an important advance when an exhaustive census of all individuals present on the study area is not possible, leading to capture rates less than 1. The multistate method allowed us to include data on individuals marked as adults (i.e. of unknown age), leading to greater precision in parameter estimation. This method should be particularly useful when the number of known-age individuals recaptured as adults is small due to low juvenile survival and/or adult capture probabilities. Furthermore, extension of the multistate approach to include information from other sources, such as band recovery data and capture of non- or failed-breeders on molting sites, could potentially address most of the constraints and assumptions made in our study (see Lebreton et al. 1999 for details).

Table 1. Model for age estimation of Greater Snow Goose goslings captured at banding based on 9th primary length (mm), mean age (in days) of marked goslings and mean age of unmarked female goslings estimated by the model (± SE of the estimates).

Year	Marked young						Unmarked females	
	Intercept	Slope	MSE	R^2	*n*	Age at capture	*n*	Estimated age at capture
1990	16.73	0.076	0.87	0.82	9	41.7 ± 1.8	75	38.8 ± 3.0
1991[c]	18.98	0.111	1.80	0.73	17	39.4 ± 3.3	530	36.6 ± 3.1
1992[c]	19.52	0.099	1.15	0.84	47	29.6 ± 1.6	392	29.2 ± 2.4
1993[c]	22.81	0.099	1.75	0.63	102	40.2 ± 2.8	849	38.6 ± 2.7
1994[c]	27.62	0.071	1.69	0.72	62	36.1 ± 3.2	819	36.2 ± 2.4
1995[c]	22.50	0.098	1.19	0.75	74	36.0 ± 2.4	1072	35.7 ± 2.4
1996	23.15	0.080	1.49	0.75	96	31.3 ± 2.6	834	32.0 ± 3.2
1997	26.84	0.064	1.49	0.58	72	34.7 ± 1.7	1064	34.0 ± 1.8
1998	25.17	0.085	1.6	0.77	78	36.9 ± 2.9	631	37.1 ± 2.4

[c] Data from Lepage et al. 1998

Table 2. Selection among models of recruitment in female Greater Snow Geese. Models include probabilities of survival (Φ), capture (*p*) and to start breeding (*a*) and are ranked by their QAICc value with only the most relevant models being presented. For each model, we give its ΔQAICc value (difference in QAICc between the current model and the model with the lowest QAICc value), QAICc weight (w_i) and the number of estimable parameters.

Model name	ΔQAICc	w_i	# Par
1) $\Phi^{J}_{c+rel\_hatch}\ \Phi^{A}\ p^{B}_{t}\ a_{age\ (full\ a4)+Lem}$	0.00	0.43	25
2) $\Phi^{J}_{c+rel\_hatch}\ \Phi^{A}\ p^{B}_{t}\ a_{age\ (full\ a4)+snow+Lem}$	1.94	0.17	26
3) $\Phi^{J}_{c+rel\_hatch}\ \Phi^{A}\ p^{B}_{t}\ a_{age\ (full\ a4)}$	2.93	0.10	23
4) $\Phi^{J}_{c+rel\_hatch}\ \Phi^{A}\ p^{B}_{t}\ a_{age\ (full\ a4)+rel\_hatch}$	3.40	0.08	24
5) $\Phi^{J}_{c+rel\_hatch}\ \Phi^{A}\ p^{B}_{t}\ a_{age\ (full\ a4)+med\_hatch}$	3.65	0.07	24
6) $\Phi^{J}_{c+rel\_hatch}\ \Phi^{A}\ p^{B}_{t}\ a_{age\ (full\ a4)+snow}$	3.90	0.06	24
7) $\Phi^{J}_{c+rel\_hatch}\ \Phi^{A}\ p^{B}_{t}\ a_{age\ (full\ a4)+med\_hatch+rel\_hatch}$	4.53	0.04	25
8) $\Phi^{J}_{c+rel\_hatch}\ \Phi^{A}\ p^{B}_{t}\ a_{age\ (full\ a4)+med\_hatch+rel\_hatch+snow+Lem}$	5.92	0.02	28
9) $\Phi^{J}_{c+rel\_hatch}\ \Phi^{A}\ p^{B}_{t}\ a_{age\ (full\ a4)+med\_hatch+rel\_hatch+snow}$	6.53	0.02	26
10) $\Phi^{J}_{c}\ \Phi^{A}\ p^{B}_{t}\ a_{age\ (full\ a4)+med\_hatch+rel\_hatch}$	14.62	0.00	24
11) $\Phi^{J}_{c+rel\_hatch}\ \Phi^{A}\ p^{B}_{t}\ a_{age\ (full\ a4)+c}$	18.12	0.00	32
12) $\Phi^{J}_{c}\ \Phi^{A}\ p^{B}_{t}\ a_{age\ (full\ a4)}$	22.36	0.00	22
13) $\Phi^{J}_{med\_hatch+rel\_hatch}\ \Phi^{A}\ p^{B}_{t}\ a_{age\ (full\ a4)}$	24.60	0.00	16
14) $\Phi^{J}_{c}\ \Phi^{A}\ p^{B}_{t}\ a_{age\ (full\ a4)+c}$	34.15	0.00	30
15) $\Phi^{J}_{c}\ \Phi^{A}\ p^{B}_{t}\ a_{age\ (full\ a4)*c}$	42.99	0.00	37
16) $\Phi^{J}_{c}\ \Phi^{A}\ p^{B}_{t}\ a_{age\ (full\ a5)*c}$	53.97	0.00	44
17) $\Phi^{\mathrm{J}}_{\mathrm{c}}\ \Phi^{\mathrm{A}}_{\mathrm{t}}\ \mathrm{p}^{\mathrm{B}}_{\mathrm{t}}\ a_{age\ (full\ a5)*c}$	63.20	0.00	53
18) $\Phi^{J}_{c}\ \Phi^{A}\ p^{B}\ a_{age\ (full\ a5)*c}$	76.32	0.00	35

Φ^{J} = apparent survival of juvenile females between 0 and 2 years; Φ^{A} = apparent annual survival of adults; p^{B} = adult breeder capture rate; *a* = probability that an individual that has not yet reproduced starts to breed; *c* = cohort; *t* = time; *age* = age in years; *med_hatch* = cohort-specific median hatch date; *rel_hatch* = individual relative hatch date; *lem* = lemming density; *snow* = spring snow cover; *full ai* = full breeding at age *i* (i.e. age at which all individuals have recruited into the breeding segment of the population); + =

additive model, * = model with interaction. Variables *med_hatch* and *rel_hatch* refer to conditions encountered at birth whereas *lem* and *snow* refer to conditions in the year that birds first breed.

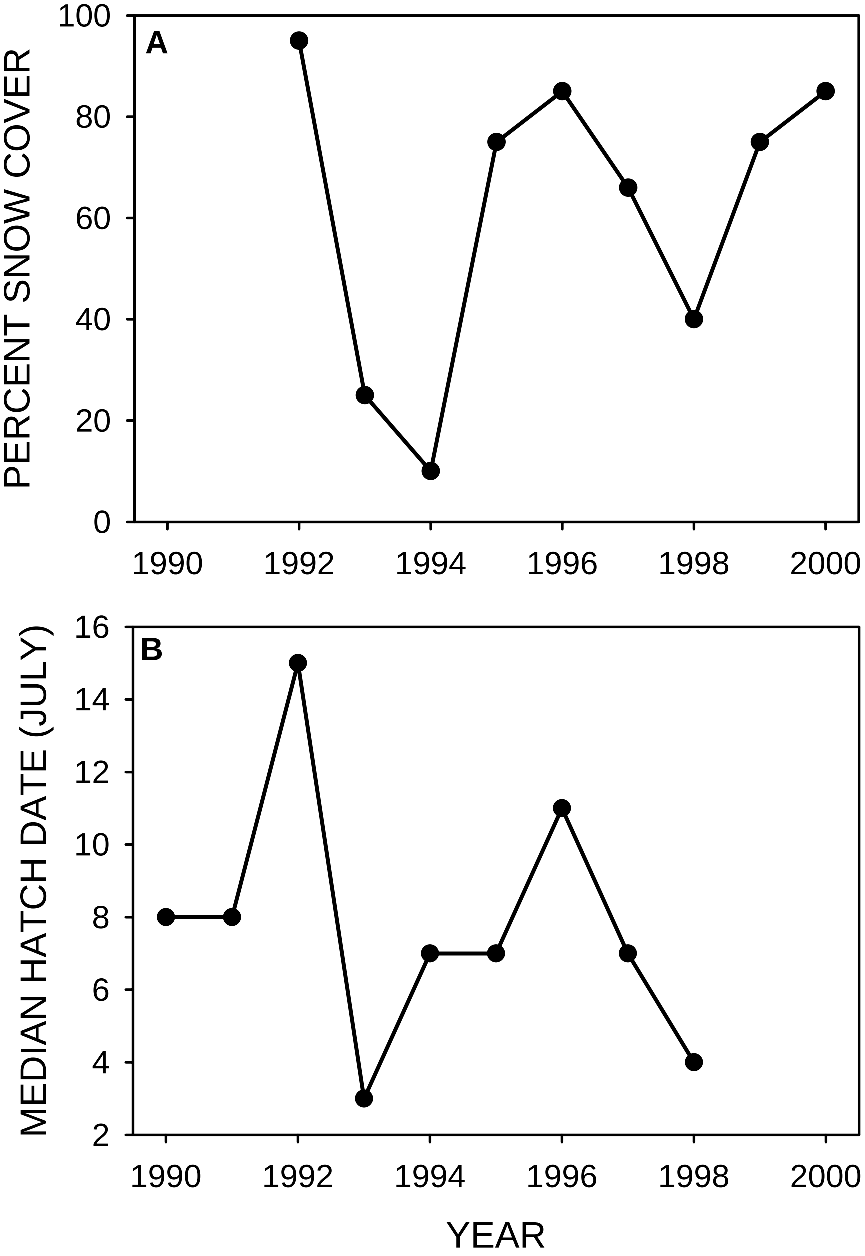

Figure 1. A) Percent snow cover on 5 June from 1992 to 2000 at our study site on Bylot Island, and B) year-specific median hatch dates from nests monitored between 1990 and 1998. Snow cover refers to conditions encountered in the year that birds first breed whereas median hatch date represents conditions encountered at birth.

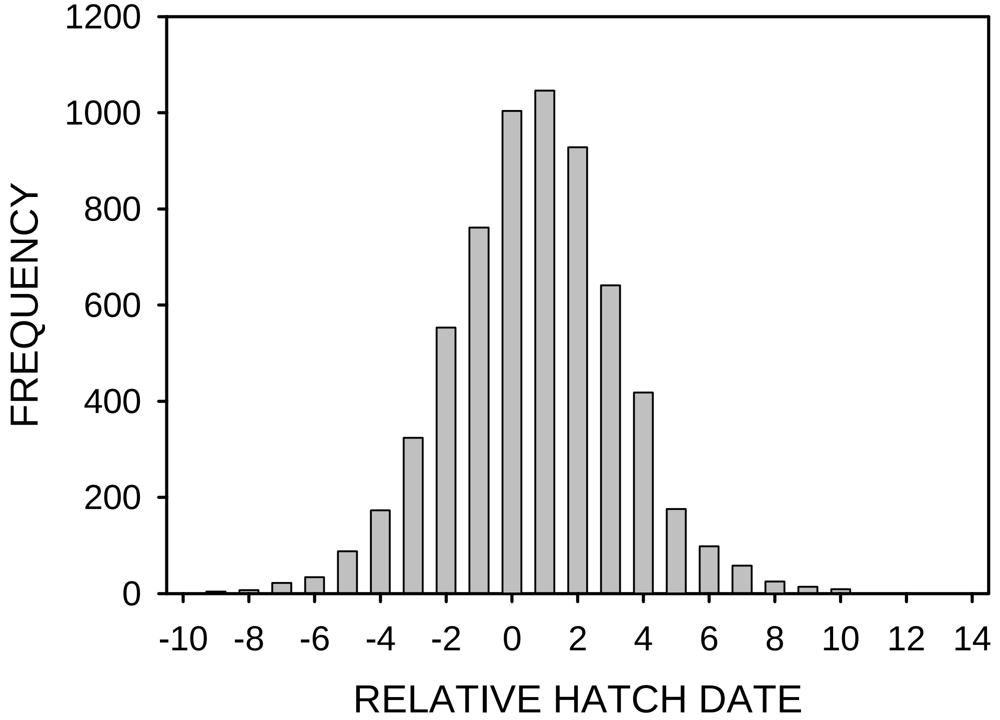

Figure 2. Frequency distribution of relative hatch dates of all female goslings marked on Bylot Island, 1990-1998. Individual hatch dates are relative to the median hatch date for a given cohort. Hatch dates were estimated from the length of the 9th primary feather (see Table 1).

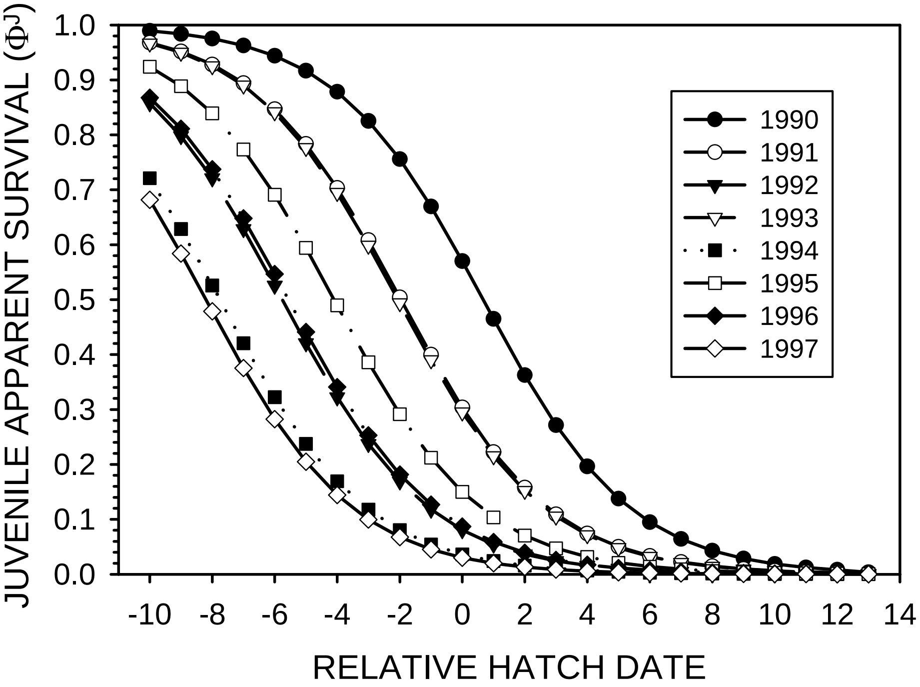

Figure 3. Relationship between juvenile apparent survival and relative hatch date of female Greater Snow Geese. Apparent survival is estimated from model 1 in Table 2 and covers the interval between age 0 (i.e. fledging) and 2. The relationship is additive among cohorts and linear on a logit scale (slope: ß = -1.09, SE = 0.29).

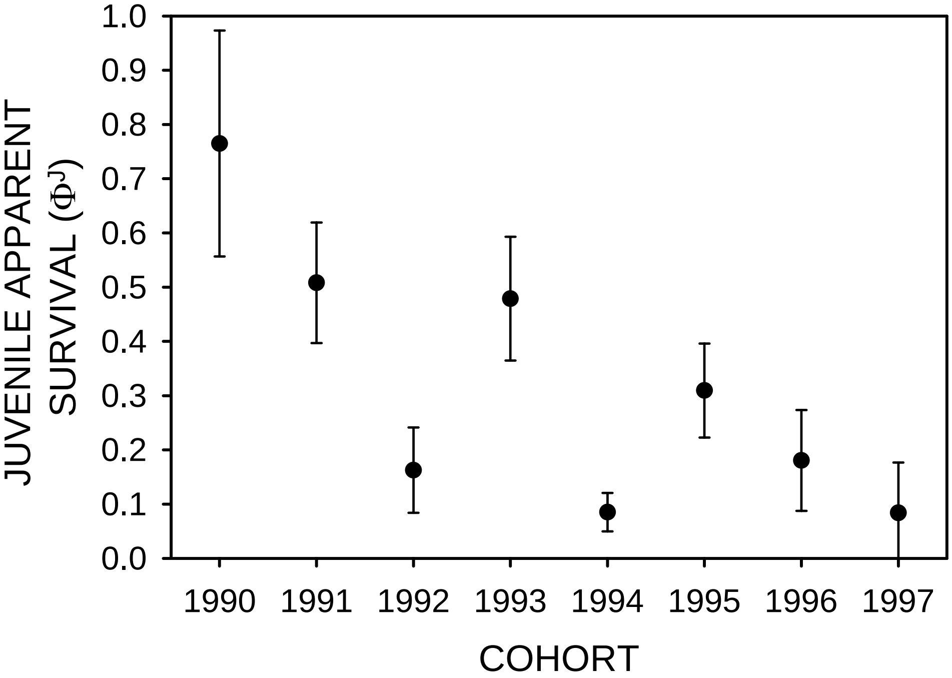

Figure 4. Variation in apparent survival probabilities (average across hatch date for each cohort) of juvenile female Greater Snow Geese. Apparent survival is estimated from model 1 in Table 2 and covers the interval between age 0 (i.e. fledging) and 2. Mean ± 1 SE (SE adjusted for extra-binomial variation, $\hat{c}$ = 1.66). Apparent survival for the 1998 cohort could not be estimated.

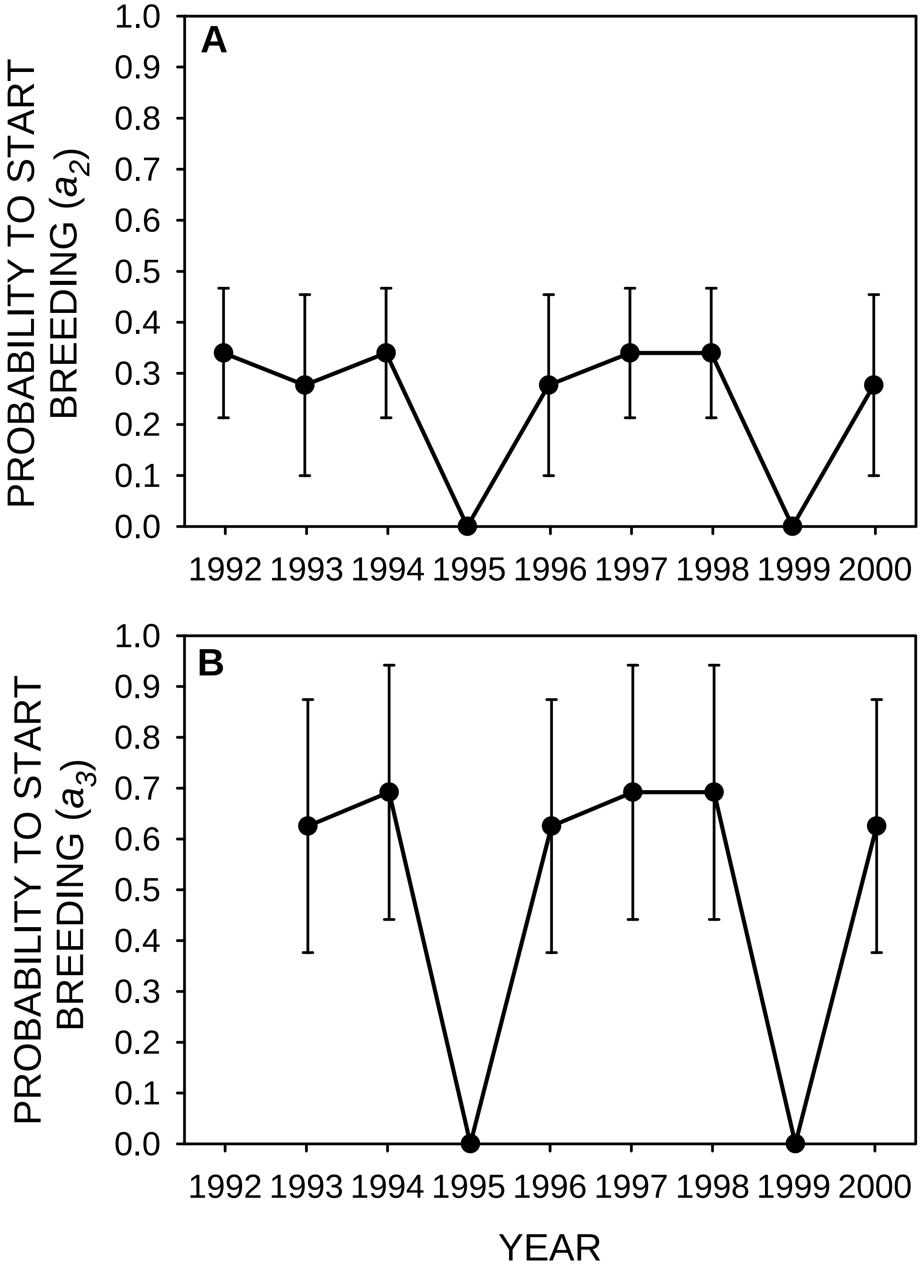

Figure 5. Variation, among cohorts, in the probability that a Greater Snow Goose female with no breeding experience starts breeding at: A) age 2, and B) age 3. Estimates are derived from model 1 in Table 2. Mean ± 1 SE (SE adjusted for extra-binomial variation, $\hat{c}$ = 1.66). Years 1995 and 1999 were lemming crash years.

CHAPITRE 6

EFFECTS OF SPRING CONDITIONS ON BREEDING PROPENSITY OF GREATER SNOW GOOSE FEMALES.

Eric T. Reed, Gilles Gauthier, Jean-François Giroux.

Résumé

La probabilité annuelle de reproduction d'un adulte sexuellement mature est un élément important de la productivité d'une population. C'est aussi un des paramètres démographiques les moins bien connus chez les vertébrés. Nous avons étudié la relation entre la probabilité de reproduction et les conditions rencontrées sur les haltes migratoires et les sites de reproduction chez la Grande Oie des neiges (*Chen caerulescens atlantica*), un migrateur de longue distance nichant dans le Haut Arctique. Nous avons combiné de l'information provenant de données de capture-recapture, de télémétrie et de suivi de la nidification récoltée sur une période de 7 ans afin d'estimer la probabilité de reproduction. Nous avons testé l'effet de la couverture de neige printanière et d'une chasse de conservation sur la probabilité de reproduction. La variation temporelle réelle était considérable (probabilité de reproduction moyenne: 0.574 [IC à 95% considérant uniquement la variation naturelle: 0.13 à 1]). La probabilité de reproduction était négativement reliée à la couverture de neige printanière (β = -2.05 ± 0.96 SE) et était réduite durant les années de chasse printanière (β = -0.78 ± 0.35). La densité des nids dans la colonie reproductrice et le ratio jeunes/adultes à l'automne étaient de bons indices de la probabilité de reproduction, les densités de nids étant légèrement plus précises. Ces résultats suggèrent que les conditions rencontrées en période pré-reproductrice peuvent avoir un impact majeur sur la productivité des oiseaux se reproduisant dans l'arctique.

Abstract

Breeding propensity, the probability that a sexually mature adult will breed in a given year, is an important determinant of annual productivity. It is also one of the least known demographic parameters in vertebrates. We studied the relationship between breeding propensity and conditions encountered on the spring staging areas and the breeding grounds in Greater Snow Geese (*Chen caerulescens atlantica*), a long distance migrant that breeds in the High Arctic. We combined information from mark-recapture, telemetry, and nest survey data to estimate breeding propensity over a 7-year period. We tested the effects of spring snow cover and a spring conservation hunt on breeding propensity. True temporal variation in breeding propensity was considerable (mean breeding propensity: 0.574 [95% CI considering only true variation: 0.13 to 1]). Spring snow cover was negatively related to breeding propensity ($\beta_{snow} = -2.05 \pm 0.96$ SE) and tended to be reduced in years with a spring hunt ($\beta = -0.78 \pm 0.35$). Nest densities on the breeding colony and fall young/adult ratio were good indices of breeding propensity, with nest densities being slightly more precise. These results suggest that conditions encountered during the pre-breeding period can have a significant impact on productivity of Arctic-nesting birds.

Introduction

Breeding propensity, which can be defined as the probability that a sexually mature adult will breed in a given year, has a strong impact on the number of young produced. This parameter is thus of considerable interest in population dynamics, especially in long-lived species which may be more prone to skip a breeding year when conditions are not appropriate (Tickell and Pinder 1967, Chastel 1995, Nur and Sydeman 1999). Unfortunately, breeding propensity is very difficult to estimate in most species because non-breeders are often less conspicuous or simply absent from breeding colonies (Spendelow and Nichols 1989, Chastel 1995). Thus, it is probably one of the least known demographic parameter in vertebrates.

Absence of an individual at the breeding site due to a breeding skip will appear as temporary emigration. However, other factors may also cause temporary emigration, and can thus be easily confounded with breeding propensity: (1) home range of some individuals may not be completely enclosed in the study area, such that they are not exposed to sampling every year; (2) the capture process itself may cause an individual to temporarily leave the study area (e.g. Pradel et al. 1995); or (3) fidelity to specific breeding locations may be incomplete (e.g. Rohwer and Anderson 1988, Lindberg et al. 1998).

Breeding propensity may be especially variable in species living in unpredictable and highly heterogeneous environment such as the Arctic. In arctic-nesting geese, it has long been suggested that a large proportion of individuals may forego breeding in years of late snowmelt on the breeding grounds (Barry 1962, Prop and de Vries 1993, Reed et al. 1998). Delayed snowmelt denies access to nesting sites and prevents females from acquiring some nutrients used for egg-formation (Choinière and Gauthier 1995, Ganter and Cooke 1996). Recent studies of breeding propensity in waterfowl using robust statistical methods found rather high values for this parameter (0.74 - 0.90 of mature adults breeding in a given year: Kendall and Nichols 1995, Lindberg et al. 2001, Sedinger et al. 2001). Surprisingly, in contrast to previous suggestions, these studies detected little annual variation in breeding propensity (see also Cooch et al. 2001).

Events occurring during the spring migration may also have an impact on breeding propensity in long-distance migrants. In geese, nutrient reserves accumulated during spring staging are used to meet the energy cost of the spring migration and reproduction (Ankney and MacInnes 1978, Gauthier et al. 1992, Choinière and Gauthier 1995). Factors negatively affecting spring fattening such as reduced food availability due to drought or high disturbance due to spring hunting may thus lead to a reduced breeding effort (Davies and Cooke 1985, Féret 2002, Mainguy et al. 2002).

In open population mark-recapture models, apparent detection probabilities confound the probability of being present in the sampled area and the probability of being detected given presence (Kendall and Nichols 1995). Traditional sampling designs do not allow the separation of these two probabilities, as only their product is estimable. Thus, an ad hoc approach was developed in which multiple subsamples (secondary samples) within primary sampling periods are used to estimate probability of detection, conditioned on being present, which are then used to adjust estimates from standard mark-recapture techniques, assuming a closed population during secondary samples (Pollock 1982, Pollock et al. 1990). Recently, it was recognized that this approach could be used to estimate probability of breeding when presence is synonymous with breeding (Kendall and Nichols 1995, Kendall et al. 1997, Lindberg et al. 2001). In geese, this condition is met as non-breeders undergo a molt migration to specific areas away from the breeding sites (Salomonsen 1968, Abraham 1980, Reed et al. 2003a).

We quantified and examined annual variations in breeding propensity in Greater Snow Geese (*Chen caerulescens atlantica*), a long-lived migratory bird that breeds in the High Arctic, a highly variable environment. Building on a long-term capture-mark-recapture study at a major breeding site, we combined information from recapture, radio-tracking, and nest monitoring to estimate breeding propensity of adult female Greater Snow Geese over a 7-year period. Our objective was to investigate temporal variation of breeding propensity of adult females and evaluate the influence of 1) snow cover at the onset of nesting in the Arctic, and 2) a conservation hunt recently implemented on the spring staging area (Mainguy et al. 2002). We hypothesize that breeding propensity will be lower in years of high spring snow cover in the Arctic and in years with a spring conservation hunt on the staging area. We also seek to find out if other variables easier to sample were correlated with breeding propensity in order to use them as an index.

Study area

Data were collected at the Bylot Island breeding colony, Sirmilik National Park, Nunavut Territory. This area supports the largest concentration of breeding Greater Snow Geese, representing ca. 15 % (55 000 breeding adults in 1993) of the world breeding population (Reed et al. 1998). Field work was concentrated in two main study sites, separated by approximately 30 km: the Base-camp valley is an important brood rearing area where weather data collection and banding occurred; and the camp-2 area where the majority of geese nest and where nesting data were collected (Bêty et al. 2001). Most families that use the Base-camp area for brood rearing moved from camp-2 shortly after hatching (Mainguy unpublished data). We defined the superpopulation (*sensu* Kendall et al. 1997) as including all females that have nested on Bylot Island's south plain in at least one year of the study.

Methods

Capture and marking of geese

In early August, during the molting period, geese were rounded up with the help of a helicopter and by personnel on foot and driven into corral traps over a 5 to 8-day period from 1994 to 2001 (Menu et al. 2001). Captured birds are mostly successful parents with their young since non-breeders and failed-nesters leave the island for distant molting sites or have regained flight capacity at the time of banding (Reed et al. 2003a). This is referred to as the main banding operation.

All birds captured for the first time were fitted with a metal U.S. Fish and Wildlife Service leg band and a sample of adult females was fitted with individually coded plastic neck bands. Recaptures were noted systematically. Because we have evidence that neck bands affect breeding propensity of adult females (Chapitre 4), we restricted our analysis to leg-banded only females. Neck banded females that had lost their neck bands on a subsequent recapture were included, their first capture without the neck band being considered their initial capture. Similarly, leg-banded females that were subsequently fitted with a neck band were censored by considering their last capture as a leg-banded female as a loss on capture.

From 1995 to 1999, captures of individual families were also made at the same site to fit radio-transmitters affixed to neck bands (all years) or harnesses (1995 only) to adult females (Demers 2003). This operation was conducted shortly before the main banding operation but in some years both operations overlapped in time. In 2000-2001, incubating females were captured on their nest using bow traps and also marked with radio-transmitters affixed to neck bands. Presence of these females on Bylot Island in late summer was ascertained through aerial radio-tracking (see Reed et al. 2003a). We also determined the number of radio-marked females located in the banding area. Detection range of radios was approximately 3- 5 km from the ground and 10-15 km from the air (Bêty 2001).

Extent of banding area and brood-rearing site fidelity

The area that was covered by the main banding operation varied among years in response to goose densities. We always covered the base-camp valley before moving out into the adjacent plateau and other valleys (see map in Lesage and Gauthier 1998). The study area was bounded to the west by Navy Board Inlet and to the east by glaciers, so geese were constrained in a north - south corridor (ca. 10 km). Patches of suitable brood rearing habitat extended almost 65 km to the south of the base-camp valley but was limited to one valley to the north (ca. 5 km). The extent of the banding area was thus calculated as the distance between the most southerly and northerly capture sites each year (in km). In 1999, a year of almost complete reproductive failure (Mainguy et al. 2002), we covered the whole south plain of Bylot Island for banding.

We used the distance between inter-annual recaptures (independent from the main banding operations in most cases) of radio-marked females as an estimate of brood-rearing site fidelity. Mainguy (2002) found that 42.5 % of females were recaptured <5 km, 17.5 % 6 -

10 km, 10.0 % 11 - 15 km, 15.0 % 16 - 20 km, and 15.0 % 21 - 30 km of their previous capture location (n = 40 females). We estimated the proportion of females that were present on Bylot Island and that were at risk of capture (i.e. within our banding area) as the proportion of radio-marked females (from Mainguy 2002) recaptured in the distance class that included our median distance between extreme capture locations each year. For example, if the distance between our most northerly and most southerly capture during banding was 6 km (median = 3 km), we used the proportion of radio-marked females that were recaptured < 5 km from their previous capture location as an index of site fidelity.

Nest survival

GSG nests were found by systematic searches during incubation in 1995, and egg laying or early incubation from 1996 to 2001 at the camp-2 area (Bêty et al. 2001). Nests were revisited in the first half of incubation, during hatching and after the goslings had left the nest in order to determine their fate. Nesting parameters are generally not biased by our visits (Bêty and Gauthier 2001). We used the Mayfield method to calculate daily nest survival and the product method to evaluate nest survival probability for the whole nesting period (Johnson 1979). Nest survival for the years 1996 - 2000 were taken from Bêty et al. (2002).

Temporary emigration model

Background and notation

We estimated temporary emigration using the sampling design described by Kendall et al. (1997), i.e. individuals are captured during secondary samples (closed population) nested within primary periods (open population). Our model requires the combination of different sources of information under the Cormack-Jolly-Seber design to estimate temporary emigration. Model notation followed Lebreton et al. (1992) and Kendall et al. (1997).

First we define the following terms.

Φ_i = probability that an individual survives from primary period i to i+1 (apparent survival where permanent emigration and mortality are confounded), (i = 1, 2, …, k - 1)

p_i^0 = probability that an individual is caught in primary period *i*, given that the animal is alive and present in the superpopulation at period *i*, ($i = 1, 2, \ldots, k$)

p_i^* = probability that an individual is captured in at least one of the l_i secondary samples of primary period *i*, given that the individual is located in the sampled area during period *i*,

p_{ij} = probability that an individual is captured in secondary sample *j* of primary period *i*, given that it is alive and present in the sampled area during period *i*,

γ_i = probability that a marked individual is not at risk of capture during primary period *i* (i.e. is a temporary emigrant), given that it is in the superpopulation.

Kendall et al. (1997) described an ad hoc estimator of temporary emigration from the sampling area (banding area in our case). Temporary emigration from our study area is mainly due to non-breeding and nest failure (Reed et al. 2003a), but also incomplete fidelity to the brood-rearing areas sampled. Our goal was to estimate breeding propensity ($1-\gamma_i$) of the female segment of the Bylot Island breeding population, so we modified Kendall et al.'s (1997) estimator to take into account temporary emigration of breeding females due to nest failure and change in brood rearing site location:

$$\hat{\gamma}_i = 1 - \frac{\hat{p}_i^{js}}{\hat{p}_i^{cl}\,\hat{S}_i^{n}\,\hat{F}_i^{br}},$$

where p_i^{js} is the probability of capture estimated from CJS models (i.e. p_i^0), p_i^{cl} is the probability of capture given presence in the study area (closed population capture probability, i.e. p_i^*), S_i^n is the nest survival probability in year *i*, and F_i^{br} is the brood rearing site fidelity in year *i*. An appropriate variance estimate based on the delta method (Seber 1982:7) would be:

$$\widehat{\operatorname{var}}\left(\hat{\gamma}_i\right) =$$

$$\left(\frac{1}{\hat{p}_i^{cl}\,\hat{S}_i^{n}\,\hat{F}_i^{br}}\right)^2 \widehat{\operatorname{var}}\left(\hat{p}_i^{js}\right)+\left(\frac{\hat{p}_i^{js}}{(\hat{p}_i^{cl})^2\,\hat{S}_i^{n}\,\hat{F}_i^{br}}\right)^2 \widehat{\operatorname{var}}\left(\hat{p}_i^{cl}\right)+\left(\frac{\hat{p}_i^{js}}{\hat{p}_i^{cl}\,(\hat{S}_i^{n})^2\,\hat{F}_i^{br}}\right)^2 \widehat{\operatorname{var}}\left(\hat{S}_i^{n}\right)$$

$$+\left(\frac{\hat{p}_i^{js}}{\hat{p}_i^{cl}\,\hat{S}_i^{n}(\hat{F}_i^{br})^2}\right)^2 \widehat{\operatorname{var}}\left(\hat{F}_i^{br}\right)$$

We could ignore covariance terms because our samples were independent.

Primary period capture probabilities - CJS modeling

We used as a base model the Cormack-Jolly-Seber (CJS) model (Cormack 1964, Jolly 1965, Seber 1965) where survival (Φ_i) and capture (p_i) probabilities are time-specific (model Φ_t, p_t). We first tested the fit of this model using the goodness-of-fit (GOF) tests of program RELEASE (Burnham et al. 1987). Once we had a general model that provided a good fit to the data, we proceeded to assess the effect of time on survival and capture probabilities. We used Akaike's Information Criterion modified for small sample size (AICc) to select the best approximating model (lowest AICc value, Burnham and Anderson 1998). Other models were ranked relative to deviations from the best model (ΔAICc). We used program MARK v2.1 (White and Burnham 1999) for model selection and parameter estimation. We also used AICc weights (ωAICc), which represent the weight of evidence in support of each model in the candidate set (Burnham and Anderson 1998).

Secondary sample capture probabilities – radio-tracking

Capture probabilities for secondary sampling period (p_i^*) could not be estimated directly from the mark-recapture data because we avoid multiple recaptures of individuals in a given year. We used instead an independent sample of birds, the radio-marked females, to estimate closed population capture probabilities (p_i^{cl}). We assumed that radio-marked females, whose number was exactly known, provided a random sample of the geese present in the study area. Even though we sampled the banding area systematically rather than randomly, we did not search for radio-marked females during the main banding operations and our selection of banding sites was thus independent from these birds being present or not at the site. Few non radio-marked adults were captured more than once in the same year (3% of adult females between 1994 and 2001) so we can view our sampling as a simple random sampling without replacement.

Mean daily capture probabilities over the secondary samples ($\bar{p}_{ij}$) were estimated as the number of radio-marked females caught during the main banding operation on the sum of the number of radio-marked females present each day of capture over the whole banding period. Once a female was captured, she was removed from the sample of birds available for capture (only one radio-marked female was caught twice in the same year) and new females could be added when radio-marking overlapped the main banding operations.

The variance was computed as:

$$\widehat{\text{var}}\left(\hat{\bar{p}}_{ij}\right) = \hat{\bar{p}}_{ij} \bullet (1 - \hat{\bar{p}}_{ij}) \Big/ n_{ij} .$$

The probability that a female was captured in at least one of the secondary periods (p_i^{cl}) was calculated as:

$$\hat{p}_i^{cl} = 1 - \left(1 - \hat{\bar{p}}_{ij}\right)^k ,$$

where k was the number of days of banding in a given year. The variance was estimated as:

$$\widehat{\text{var}}\left(\hat{p}_i^{cl}\right) = \left(k\left(1 - \hat{\bar{p}}_{ij}\right)^{k-1}\right)^2 \bullet \widehat{\text{var}}\left(\hat{\bar{p}}_{ij}\right) .$$

In 1999, breeding was a general failure and less than 2 000 geese were still on Bylot Island during the banding operations (Gauthier, personal observation). The conventional main banding operations and the marking of females with radios took place at the same time, which prevented us to use the radio-marked females to estimate p_i^{cl}. Based on visual observations, we estimated that approximately 85% of the geese present on the Island were captured, but because of uncertainty on the exact number we added a SE of 0.05 to this estimate (thus assuming that between 0.75 and 0.95 of the geese were captured).

Covariates of breeding propensity

We tested whether breeding propensity varied among years using the sum of squares of breeding propensity probabilities weighted by their variances and the covariances of open population capture rates (p_i^{js}, other variables in the calculation of breeding propensity being independent). The statistic for the null hypothesis (homogeneity across years) follows a chi-square distribution with n - 1 degrees of freedom (where n is the number of breeding propensity rates) (Sauer and Williams 1989). This analysis was performed with program CONTRAST (Hines and Sauer 1989). Variance of breeding propensity estimates is contaminated by sampling error, which can lead to an overestimation of temporal variation in this parameter. Using a variance-components approach, we partitioned the total variability of estimated breeding propensity and calculated the percentage of the total variation that was accounted for by the sampling variation and covariation (Gould and Nichols 1998).

We then proceeded to test the effect of snow cover on the breeding grounds and the implementation of a spring conservation hunt on breeding propensity. Each year, a visual estimate of snow cover in the base-camp valley was made on 5 June (Lepage et al. 1996, Reed et al. 2003b). From 1997 to 2001, a simultaneous assessment of snow cover was made at camp-2, which showed that data from our base-camp valley was representative of the situation at camp-2. Snow cover on 5 June averaged 71% but was variable among years (range: 40% to 85%). In Quebec, a spring conservation hunt (hereafter called spring hunt) on Greater Snow Geese was allowed in 1999 - 2001. We categorized years with a binary variable (with or without spring hunt). We used a weighted least squares approach to estimate regression coefficients (± SE) with the covariates (Lebreton 1995, Link 1999). Thus, variances of the annual estimates of breeding propensity, as well as covariances of p_i^{js} were accounted for in the regression analysis. We fitted main effects only and tested for a negative effect of the covariates, i.e. $\beta < 0.0$ (β_{snow} = slope of the relationship between snow cover and breeding propensity; β_{hunt} = constant difference in breeding propensity between years with and without a spring hunt) with one-tailed *z*-tests.

Because the method used here to estimate breeding propensity is difficult and expensive in the field (e.g. requires large number of radio-marked birds), we looked for a simple index of breeding propensity that could be used for monitoring purposes. Two indices were examined: productivity surveys in fall and nest densities at the main breeding colony. Productivity surveys on the fall staging areas of this population have been conducted by the Canadian Wildlife Service (CWS) along the St-Lawrence River Estuary in Quebec, Canada since 1973. Proportion of young in the fall flight varied from 0.02 to 0.37 between 1995 and 2001 (Reed et al. 1998, A. Reed CWS unpublished data). Nest density (nests per 50 ha) was estimated as the number of nests found divided by the area of the search zone (data from Bêty et al. 2002). We transformed these estimates as nests per ha (1996: 1.0, 1997: 2.64, 1998: 6.52, 1999: 1.1, 2000: 1.64). We used the weighted least squares approach to test positive relations between these indices and breeding propensity ($\beta > 0.0$) with one-tailed *z*-tests. We also computed the total sums of squares (SS_t) of the breeding propensity estimators as well as the residual sums of squares (SS_r) from each model. We then calculated a coefficient of correlation ($R^2 = (SS_t - SS_r) / SS_t$)) for both indices to determine which fitted best the pattern of temporal variation in breeding propensity. Years 1996 to 2000 were used due to potential biases in point estimates for 1995 and 2001 (see below).

Results

From 1994 to 2001, we marked 1646 adult females with leg bands and subsequently recaptured 227 of these birds. The goodness of fit test of our general model indicated a good fit ($\chi^2_{32} = 26.82$, P = 0.14).

Our most parsimonious model had constant apparent survival and time dependent capture probabilities (Φ, p_t) and this model was strongly supported by the data (ωAICc = 0.98). The second best model was Φ_t, p_t (Δ AICc = 8.2). Apparent survival estimates from our best model were 0.87 ± 0.04 and capture probabilities given presence in the superpopulation (p_i^{js}) ranged from 0.02 to 0.07 (Table 1).

Between 1995 and 2001, 42 radio-marked females were recaptured during the main banding operations out of 1147 radio-days and these data were used to calculate an annual $\overline{p}_{ij}$ (1995: 2/64; 1996: 20/328; 1997: 4/304; 1998: 13/390; 2000: 2/24; 2001: 1/37). Estimated capture probabilities given presence in the sampled area (p_i^{cl}) was thus highly variable and ranged from 0.09 to 0.46 (Table 1).

We estimated nest survival from 179 to 326 nests each year. Nest survival was highly variable among years, being lowest in 1995 and 1999 and highest in 1997 and 2000 (Table 1). Fidelity to the brood rearing area was also variable and inversely related to the size of the sampled area. The extent of the banding area was 10.5 km in 1995, 12.3 in 1996, 17.2 in 1997, 6.1 in 1998, the entire south plain in 1999, 7.7 km in 2000, and 12.6 km in 2001. Thus, the probability that a female present on Bylot Island during banding was at risk of capture (i.e. present in our banding area) varied from 0.43 in 1998 and 2000 to 1.00 in 1999 (Table 1).

Estimated temporary emigration (γ_i) from Bylot Island's south plain varied considerably among years (Table 1). The large negative values for 1995 and 2001 indicated that their estimation was imprecise. However, variance of these two estimates was large and their confidence intervals included 0 (95% CI: [-4.45 to 1.89] and [-3.83 to 2.55] for 1995 and 2001 respectively). We thus excluded 1995 and 2001 from further analyses, although they did not have a large weight given their large variance.

Breeding propensity (1 - γ_i) varied across years (χ_4^2= 9.56, P=0.049) ranging from 1 in 1998 to 0.17 in 1999 (Table 1). We estimated total variation at 0.137 and true temporal variation at 0.051, indicating that sampling variation accounted for 62% of the total variation. Average breeding propensity for these 5 years was 0.574 [95% CI considering only true variation: 0.131 to 1.017]. Breeding propensity was negatively related to snow cover on 5 June (Fig. 1; β_{snow}: -2.05 ± 0.96, $z = -4.14$, $P = 0.02$) and was reduced in years with a spring hunt ($\beta_{hunt} = -0.78 \pm 0.35$, $z = -2.19$, $P = 0.01$).

Both nest density and young/adult ratio in the fall flight provided good indices of breeding propensity for the 1996 - 2000 period (Fig. 2). However, nest density (nest/ha) was a better predictor of breeding propensity (($\beta_{nest\ density}$: 0.59 ± 0.11, $R^2 = 0.97$, $z = 3.94$, $P < 0.001$) than was young/adult ratio in the fall flight ($\beta_{young/adult}$: 5.02 ± 1.06, $R^2 = 0.89$, $z = 4.04$, $P < 0.001$).

Discussion

Factors affecting breeding propensity

Breeding propensity of adult female Greater Snow Geese varied considerably between 1996 and 2000, ranging from 0.17 to 1. True temporal variation in breeding propensity was large (95% CI: 0.13 - 1.0), with an average of 57% of surviving adult females breeding (successfully or not) in any given year. These results confirm that intermittent breeding is common in this population. High rates of temporary non-breeding are well documented in seabirds (Tickell and Pinder 1967, Chastel 1995, Nur and Sydeman 1999) but not in waterfowl. Studies in Canvasback (*Aythya valisineria*), Black Brant (*Branta bernicla nigricans*) and Lesser Snow Geese (*Chen caerulescens caerulescens*) found high breeding probabilities with no detectable temporal variations (Cooch et al. 2001, Lindberg 2001, Sedinger et al. 2001). Only one study found temporal variation in breeding probability of geese, but the magnitude of variation was much less than in our study (Prop and de Vries 1993).

Several studies in seabirds have suggested that temporal variation in breeding probability may be due to variations in prey availability but the mechanism governing the decision to initiate breeding in herbivores such as geese is less obvious. Our results indicate that spring snow cover is an important determinant of breeding propensity (see also Prop and de Vries 1993). The other goose studies that showed no variation in breeding propensity, were conducted in low arctic regions, where environmental stochasticity is presumably less than at higher latitudes. Our results suggest that, in the High Arctic where the summer is very short, climatic conditions in spring are a key determinant of breeding propensity, with most females (>80%) breeding when snow cover is low and few of them (<30%) breeding when snow cover is high. Our results thus support early suggestions that reproductive effort of geese can be quite variable in the High Arctic (Prop and de Vries 1993), with widespread breeding failure in years of late snowmelt (Barry 1962).

Snow cover is one of the principal parameter influencing breeding propensity but air temperature, which influences the rate of snowmelt, may also be as important. At our study site, spring air temperature is highly correlated to snow cover on 5 June so we could not test these two variables separately (E. T. Reed, unpublished data). Climatic conditions could influence breeding propensity of herbivorous birds by limiting availability of food or nest sites. Geese feed intensively during the interval between arrival on the breeding grounds and egg-laying (Gauthier and Tardif 1991), and this nutrient intake contributes significantly to the energy invested in egg production (Bromley and Jarvis 1993, Choinière and Gauthier 1995, Ganter and Cooke 1996). Snow cover can thus limit access to high quality foraging sites, since primary production in the first snow free areas (mountain tops and ridges) is low due to wind exposure and good soil drainage (Prop and de Vries 1993). Early nesting is also important in seasonal environments because the date at which young hatch strongly influences their growth rate (Larsson and Forslund 1991, Lepage et al. 1998) and ultimately their survival and recruitment prospects (Spear and Nur 1994, Lepage et al. 2000, Prévot-Julliard et al. 2001). Although geese are flexible in the choice of their nest site when snowmelt is late (Lepage et al. 1996), a large proportion of adults may refrain from breeding if survival prospects of the young are too low at the date where nest sites become available.

In arctic-nesting geese, endogenous nutrient reserves acquired on the spring staging grounds are an important fuel source for the northward migration and can sometimes be a determinant of breeding success (Ankney and MacInnes 1978, Ebbinge 1989, Gauthier et al. 1992, Ebbinge and Spaans 1995). Davies and Cooke (1983) suggested that events occurring on the spring staging areas could influence the reproduction of arctic-nesting geese. In the first two years of the spring hunt (1999-2000), Féret (2002) found a marked reduction in nutrient accumulation of GSG during spring staging due to heavy hunting disturbance (Béchet 2002). This reduction of body condition was also detected in laying geese (Mainguy et al. 2002) and all reproductive parameters were apparently negatively affected in years with spring hunt at our study site: geese laid later and had smaller clutch size than in previous years, and radio-marked females showed a marked reduction in breeding effort (Mainguy et al. 2002, Bêty 2001). In our study, we found a reduction in breeding propensity during the years with a spring hunt (1999 to 2001). Breeding propensity was at a record low value in 1999, although it was not especially low in 2000 when considering snow cover and it could not be satisfactorily estimated in 2001. Even though we only had 2 good estimates, evidence suggests that the spring hunt impacts breeding propensity in GSG.

Overall, our results suggest that spring climatic conditions in the Arctic and nutrient reserves acquired during spring staging may be an important determinant of reproductive effort in GSG. This pattern should be increasingly true as one moves from low to high Arctic, since environmental stochasticity should increase with latitude. Moreover, the amount of endogenous nutrients remaining upon arrival in the Arctic should be reduced as the length and cost of the spring migration increases with latitudinal range (Choinière and Gauthier 1995).

Methodological considerations

Our results show that temporary emigration can be used to estimate breeding propensity when only breeding individuals are subject to capture. In the case where some breeders are not at risk of capture, temporary emigration must be corrected as was done in this study using information from radio-marked birds. In our study population, most non-breeders and failed nesters undertake a molt migration from our sampling area (Reed et al. 2003a), and those that remain on the island have regained flight capacity and are thus not sampled at banding. We could not rule out the possibility that some geese considered as non-breeders actually nested outside the study area, but a large proportion of adult females (including non-breeders) stage on Bylot Island from the pre-laying to the incubation period before leaving the island for the molt, too late for a breeding attempt (Reed et al. 2003a). Also, given the high level of breeding philopatry to Bylot Island previously found (Reed et al. 2003b), it seems unlikely that an important segment of the breeding population could temporarily settle elsewhere to breed.

Capture probabilities, given presence on the sampled area, varied considerably among years. Thus, estimates of capture probabilities from open population models (p_i^{js}) do not represent a valid index of breeding propensity. Because breeding propensity represents the probability that an adult will breed, irrespective of breeding success, we also had to correct our capture probability for individuals that leave Bylot Island following a nest failure. Furthermore, we did not sample all brood-rearing areas on Bylot Island but only specific ones, and the size of the sampling area varied in response to densities of geese. We therefore had to correct our estimates for incomplete fidelity of families to specific brood rearing areas (Mainguy 2002). Despite these corrections, biases may be associated with these estimates, especially the brood rearing site fidelity one which was rather crude.

The ad hoc method that we used was the best suited for estimation of breeding propensity and associated variance in our system. However, our first (1995) and last (2001) estimate of γ were << 0, because p_i^{js} >> (p_i^{cl} S_i^n F_i^{br}). In 1995, this result may be due to a negative bias in nest survival estimation resulting from nests being found late during incubation and followed over a short period of time. For the last encounter period (2001), capture probabilities for the CJS model are only separately identifiable if survival is fixed or constrained. Our CJS modeling indicated constant survival, but the last capture probability (2001) may nonetheless have been biased. The negative value of γ may thus be due to a positive bias on p^{js} in 2001. However, negative estimates are not unusual when γ is close to 0.

Predictors of breeding propensity

Nest density at the main nesting colony and young/adult ratio in the fall flight were positively related to breeding propensity. Based on their respective coefficient of correlation, nest density provided a better index of breeding propensity than young/adult fall ratios. The former is less sensitive to variations in nest success (when nests are found in the early phases of nesting), and insensitive of pre- and post fledging survival. Breeding effort of geese has often been inferred by fall or winter age ratios (e.g. Ebbinge 1989, Ebbinge and Spaans 1995). Our results indicate that fall age ratios can provide a reliable index of temporal variation in breeding propensity in this population. However, we believe that breeding ground indices should be preferred, as they are not influenced by factors occurring during the 3-month interval between the end of the egg-laying stage and arrival on the fall staging areas.

The proportion of young in the fall flight in 1999 (2.1%) was the lowest ever recorded since the inception of the productivity surveys in the St-Lawrence river estuary in 1973 (Reed et al. 1998). The combined occurrence of low breeding propensity and high predation pressure during the nesting period thus resulted in the near complete loss of this cohort. In contrast, most experienced females nested in 1998 and nest survival was high, resulting in a particularly strong cohort. Such variation across cohorts has been described for other species of waterfowl (Anderson et al. 2001). Other factors, such as gosling survival during their first year of life (Owen and Black 1989, Francis et al. 1992a), also contribute significantly to variations in productivity of Arctic nesting geese.

The frequency of occurrence of ‘bad’ and ‘good’ years has important consequences on the growth rate of this population (Gauthier and Brault 1998). We showed that breeding propensity was negatively correlated to spring snow cover such that this variable should be considered in future population models of Greater Snow Geese, or other arctic nesting birds that are likely to be affected by late snowmelt. The use of satellite imagery could be a useful monitoring tool for predicting breeding effort of Arctic goose populations from information on snow-cover on the breeding grounds in spring (Reeves et al. 1976).

Table 1. Estimate of capture probability, given presence in the superpopulation (p_i^{js}), from the open population CJS model (Φ, p_t); capture probabilities given presence in the sampling area (p_i^{cl}) obtained from radio-marked females; Mayfield estimate of nest survival (S_i^n) for the entire nesting period; fidelity to brood rearing sites (F_i^{br}) estimated as the proportion of individuals expected to be present in the banding area; probability of temporary emigration from the superpopulation of Greater Snow Geese on Bylot Island (γ_i) and breeding propensity of adults (1 - γ_i). Values are mean ± SE. See methods for details of calculations.

Year	p_i^{js}	p_i^{cl}	S_i^n	F_i^{br}	γ_i	$1 - \gamma_i$
1995	0.05 ± 0.01	0.20 ± 0.13	0.18 ± 0.03	0.60 ± 0.08	-1.28 ± 1.62	2.28 ± 1.62
1996	0.05 ± 0.01	0.40 ± 0.07	0.62 ± 0.03[b]	0.60 ± 0.08	0.65 ± 0.11	0.35 ± 0.11
1997	0.04 ± 0.01	0.09 ± 0.04	0.85 ± 0.02[b]	0.60 ± 0.08	0.19 ± 0.45	0.81 ± 0.45
1998	0.07 ± 0.01	0.18 ± 0.05	0.83 ± 0.02[b]	0.43 ± 0.08	-0.09 ± 0.39	1.09 ± 0.39
1999	0.02 ± 0.01	0.85 ± 0.05[a]	0.15 ± 0.02[b]	1.00 ± 0.00	0.83 ± 0.06	0.17 ± 0.06
2000	0.07 ± 0.02	0.46 ± 0.23	0.83 ± 0.03[b]	0.43 ± 0.08	0.56 ± 0.26	0.44 ± 0.26
2001	0.05 ± 0.01	0.10 ± 0.10	0.52 ± 0.03	0.60± 0.08	-0.64 ± 1.63	1.64 ± 1.63

[a] No radio-marked females were present on Bylot Island during banding; we visually estimated that 85% (range 75 - 95 %) of the of the geese present on Bylot Island were captured.

[b] Data from Bêty et al. 2002.

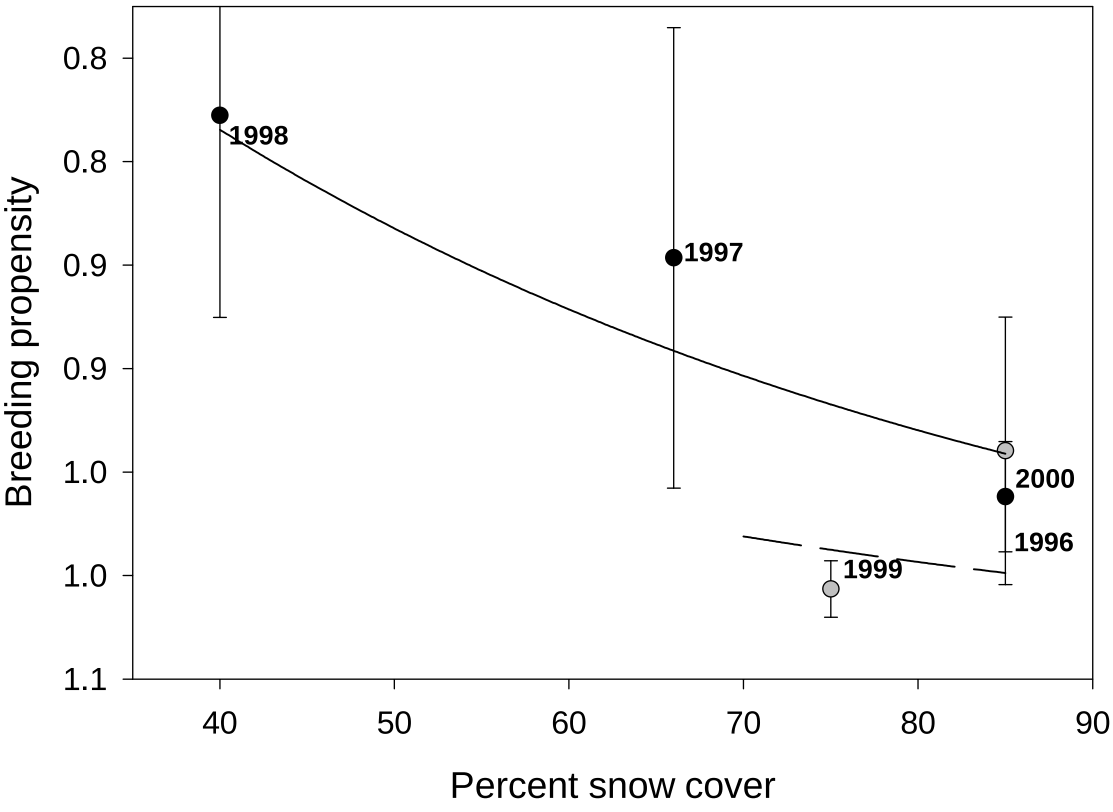

Figure 1. Relationship between snow cover on 5 June on Bylot Island and estimated breeding propensity (± SE) of female Greater Snow Geese. The solid line and dark dots represents years without a spring hunt and the dashed line and grey dots represent years with a spring hunt. Lines are predicted values of breeding propensity from model: logit (breeding propensity) = 0.79 [± 0.67] - 2.05 [± 0.96] * snow cover – 0.78 [± 0.35] * (0: no spring hunt; 1: spring hunt). Only estimates for years 1996 - 2000 are used due to imprecision of the 1995 and 2001 estimates.

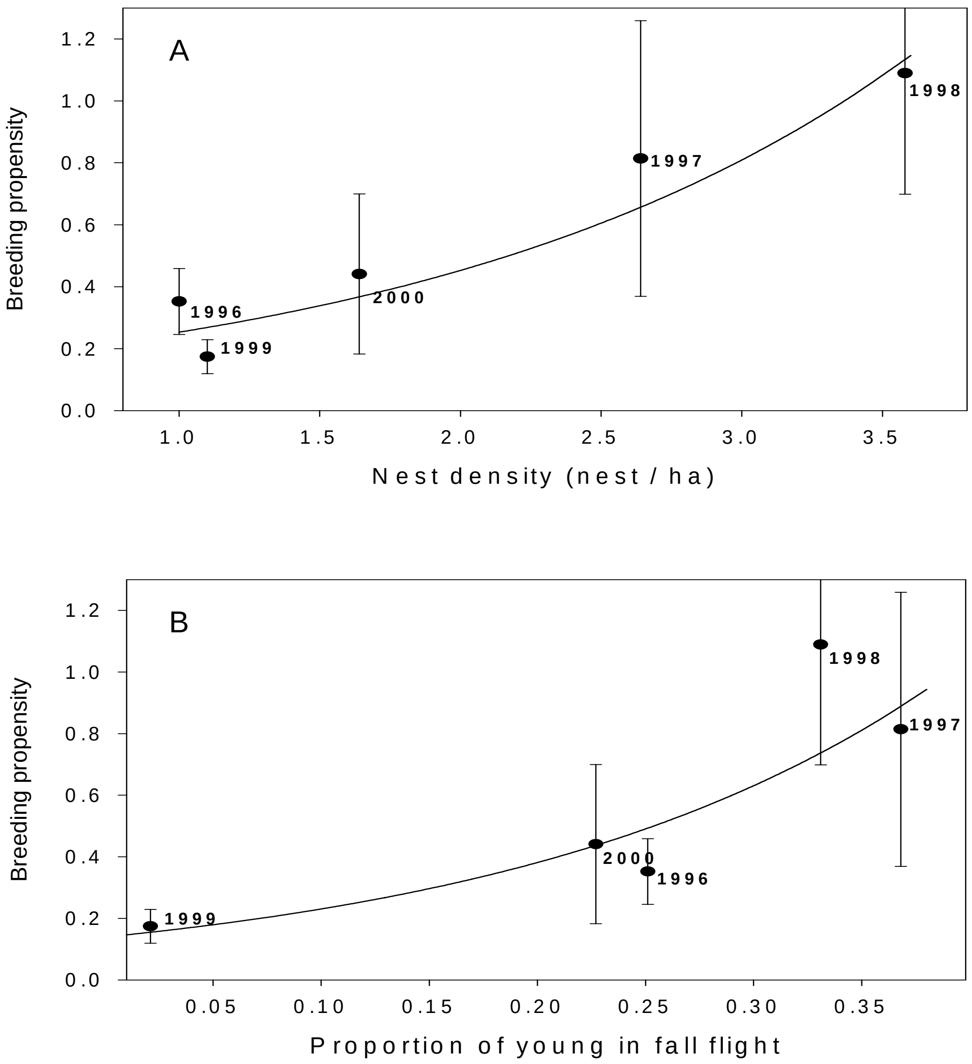

Figure 2. Relationship between estimates of breeding propensity (± SE) of female Greater Snow Geese at Bylot Island between 1996 and 2000 and: A) nest density (nest per ha) in the main nesting colony on Bylot Island (data from Bêty et al. 2002); and B) proportion of young in the fall flight in the St - Lawrence River estuary (data from Reed et al. 1998 and unpublished data). Nest density: $\beta = 0.59 \pm 0.33$, intercept = - 1.95 ± 0.58, $R^2 = 0.97$; Young/adult ratio in the fall flight: $\beta = 5.03 \pm 1.24$, intercept = - 1.97 ± 0.32, $R^2 = 0.89$ (logit scale).

Conclusion

Dans le cadre de ma thèse, j'ai abordé différents aspects associés à l'investissement dans la reproduction et à l'effet des facteurs biotiques et abiotiques du milieu sur les caractères démographiques des individus d'une population d'oiseaux migrateurs nichant dans le Haut-Arctique. Dans un premier temps, j'ai abordé le concept des compromis entre l'investissement dans la reproduction actuelle et la survie ou la reproduction future en étudiant la relation entre l'investissement dans la reproduction actuelle et les coûts (reproduction ou de survie future réduite) des parents. Ensuite, j'ai examiné l'effet des conditions environnementales sur la démographie, plus particulièrement sur le recrutement d'individus dans le segment reproducteur de la population et sur la probabilité de reproduction d'individus sexuellement matures. J'ai intégré dans cet ouvrage un contexte évolutif et des aspects démographiques au niveau de l'individu et de la population, tous des éléments essentiels à la compréhension de la dynamique des populations et des forces évolutives qui façonnent les traits d'histoire de vie.

Investissement parental et coûts de la reproduction

L'évaluation des coûts de la reproduction est un des principaux défis de l'application de la théorie des traits d'histoire de vie aux populations sauvages. Chez des espèces ou des populations vivant dans des habitats hétérogènes, les coûts de la reproduction risquent d'être variables d'une année à l'autre suite à des fluctuations dans les conditions environnementales. Ainsi, les coûts de la reproduction sont difficiles à mesurer car il y a souvent une variété de facteurs environnementaux (biotiques et abiotiques) qui peuvent masquer les coûts réels (Williams 1966, Stearns 1992, Cam et al. 1998), et parce que l'estimation des paramètres démographiques tels la survie et la probabilité de reproduction requièrent un suivi temporel prolongé des individus. Les corrélations phénotypiques entre l'effort reproducteur et le fitness des individus ont été critiquées car des facteurs génétiques et environnementaux y sont confondus (Reznick 1985, 1992; van Noordwijk et de Jong 1986). Malgré leurs limitations, les études de corrélations phénotypiques permettent néanmoins une évaluation des coûts liés aux soins parentaux et l'étude, dans un cadre évolutif, des comportements qui sont difficiles à manipuler en situation naturelle (Linden et

Møller 1989; Partridge 1992). La période d'association entre parents et jeunes chez des espèces qui ont des capacités de reconnaissance individuelle (ex. Radesäter 1976) est un exemple de comportement difficilement manipulable en nature.

Une corrélation phénotypique négative entre l'investissement dans la reproduction actuelle et la survie ou la reproduction future de femelles parentales pourrait être due à des différences de qualité individuelles ou à de vrais coûts liés à la reproduction. Mon étude n'examine pas la base génétique de ce compromis et n'est un test formel de l'occurrence de compromis physiologiques liés à la reproduction. Néanmoins, les hypothèses de coûts de la reproduction et de la qualité individuelle représentent un cadre utile à l'interprétation de la corrélation entre l'effort reproducteur et les paramètres démographiques étudiés.

Mon étude a permis de détecter un conflit parental apparent à la fin de la migration printanière menant aux sites de nidification (Chapitre 1). Ceci pourrait être le résultat d'un compromis entre les probabilités de survie et de recrutement des jeunes, et la probabilité de reproduction ou de survie future des parents. L'hypothèse selon laquelle la durée de l'association entre parents et jeunes est liée à la qualité individuelle des mères semble peu probable. D'une part, le patron de bris de familles observé dans mon étude est très comparable à celui détecté chez d'autres espèces d'oies. L'âge minimum des femelles n'était pas relié à la durée des liens familiaux, suggérant que ce ne soit pas seulement des femelles âgées ou sénescentes qui prodiguent des soins de longue durée. La durée des liens familiaux n'était pas non plus reliée à la taille de la couvée d'une femelle ni à la date de naissance (un index de qualité des jeunes) de sa progéniture.

Les résultats du chapitre 2 viennent également appuyer l'hypothèse qu'un conflit parental est présent au printemps. Plus spécifiquement, ces résultats suggèrent que l'extension des soins jusque dans la période pré-reproductrice suivante puisse être coûteuse pour les mères en terme de survie réduite, mais pas en terme de probabilité de reproduction future. La réduction de survie des mères accompagnées de jeunes jusqu'au printemps était de l'ordre de 9 à 15 %. Ces coûts peuvent donc représenter une réduction de fitness non-négligeable pour les parents mais ont probablement un effet réduit au niveau de la dynamique de la population vu que peu de couples sont associés à des jeunes pour une si longue période (environ 20% des couples, Chapitre 1). Par contre, ces coûts pourraient être compensés par une meilleure qualité de la progéniture, augmentant ainsi leurs probabilités de survie, de recrutement ou de reproduction à l'âge adulte. Deux mécanismes proximaux me semblent plus probables pour expliquer la réduction de survie de femelles prodiguant des soins de longue durée : 1) une diminution de la capacité immunitaire des individus les rendant plus susceptibles à la mortalité par infection parasitaire; 2) susceptibilité accrue des parents à des blessures à la chasse, résultant en une diminution de la survie subséquente. Une étude approfondie sur les causes de la réduction de survie des mères associées à leurs jeunes jusqu'au printemps ainsi que des bénéfices que les jeunes en retirent aiderait grandement la compréhension du compromis évolutif entre l'investissement dans la reproduction actuelle et la survie future.

L'utilisation de marqueurs auxiliaires tels les colliers représente un facteur de stress additionnel pour les individus marqués. Nous avons suggéré que l'effet principal de ce type de marqueur était de nature énergétique, probablement suite à une augmentation des dépenses lors du vol résultant d'une diminution de l'aérodynamisme. L'utilisation de colliers comme marqueur auxiliaire nous permet donc de tester de manière expérimentale certains facteurs qui peuvent influencer la survie et la reproduction des oies. Les résultats du chapitre 4 suggèrent que le coût énergétique se répercute plus particulièrement sur la reproduction, comme le fait foi la diminution de la probabilité de reproduction des femelles munies de colliers. Aucun effet du collier sur la survie n'a été noté dans mon étude ni dans une étude précédente (Menu et al. 2001).

Dynamique de la population

La population de la Grande Oie des neiges a plus que doublé au cours de la période 1990 - 2001. Malgré cette forte augmentation, aucun effet dépendant de la densité n'a été détecté sur les traits démographiques de base (survie juvénile et adulte, recrutement, probabilité de reproduction, succès reproducteur) de cette espèce (Menu et al. 2002, chapitre 5). Une étude prospective a démontré que la croissance démographique de la population (λ) était particulièrement sensible à des changements dans la survie adulte (Gauthier et Brault 1998). Toutefois, l'étude prospective ne nous apprend rien sur les facteurs qui ont mené au taux de croissance observé. Par contre, l'étude rétrospective relie la variation observée de λ à la variation observée dans les paramètres vitaux (Caswell 2000). L'approche employée dans ma thèse est rétrospective car elle quantifie la variation naturelle des paramètres démographiques à l'étude. Les paramètres vitaux ayant une grande variance sont reconnus comme étant ceux qui ont le plus fort effet sur λ en situation naturelle (Gaillard et al. 1998, Cooch et al. 2001). J'ai étudié la variation annuelle de plusieurs paramètres démographiques et deux de ceux-ci ressortent comme étant particulièrement variables : la survie juvénile (Chapitre 5) et la probabilité de reproduction des adultes (Chapitre 6). Les variations temporelles de la survie adulte et l'âge à la première reproduction étaient faibles et non détectables (sauf lors d'années de faible abondance de lemming pour l'âge à la première reproduction). Mes résultats suggèrent donc que des variations dans la survie juvénile et la probabilité de reproduction des adultes puissent avoir eu une forte influence sur la croissance récente de la population.

Dans le système étudié, les conditions environnementales expliquaient en bonne partie les variations temporelles observées dans les traits démographiques. Les conditions rencontrées en début de vie, plus particulièrement la date de naissance d'un individu, étaient négativement reliées à la survie juvénile (Chapitre 5). Ce déclin saisonnier abrupt de la survie juvénile implique donc que la probabilité de recrutement des jeunes produits dans les nichées tardives est faible, la majorité ne survivant pas jusqu'à l'âge de 2 ans (âge de la première reproduction possible). Ce résultat vient supporter de nombreuses études qui ont démontré un effet important de la date de naissance individuelle sur les traits d'histoire de vie chez les oiseaux (e.g. Cooke et al. 1984, Spear et Nur 1994, Sedinger et al. 1995, Verboven et Visser 1998, Dawson et Clark 2000, Prévot-Julliard et al. 2001). La survie juvénile a aussi montré une forte variation inter-cohortes mais celle-ci n'a pas pu être expliquée par les variables environnementales prises en compte. Je suspecte que les conditions rencontrées après l'envol, plus particulièrement lors de la première migration automnale d'un individu, aient un effet prépondérant sur la survie juvénile propre à une cohorte.

Les conditions rencontrées sur les sites de nidification, en période pré-reproductrice, ont aussi eu un effet sur les traits démographiques de la population à l'étude. Le recrutement a été pratiquement nul dans les années où les densités de lemmings étaient les plus basses (Chapitre 5). L'effet de la densité de lemmings est certainement un effet trophique indirect modulé par les réponses numériques et fonctionnelles des prédateurs aux cycles d'abondance des lemmings (Bêty et al. 2002). Ce résultat suggère soit que les femelles inexpérimentées ont un plus faible succès de nidification (et donc ont une probabilité plus grande de quitter le site d'étude avant la capture lors de la mue - Chapitre 3) que les femelles expérimentées, soit qu'elles retardent leur première reproduction due aux faibles probabilités de succès d'une reproduction en présence d'une forte pression de prédation. La couverture de neige au printemps sur les sites de reproduction n'avait pas d'effets sur le recrutement mais était reliée négativement à la probabilité de reproduction des adultes (Chapitre 6). La couverture de neige printanière influence la disponibilité des sites de reproduction et l'acquisition de réserves endogènes essentielles pour la nidification. Ainsi, les années où la couverture de neige au début de la période normale de ponte est supérieure à 75%, moins de 30% des femelles adultes ont tentées une reproduction. Il est surprenant de constater que les résultats du Chapitre 6 soient une des premières évidences directes d'une relation entre les conditions climatiques printanières sur les sites de reproduction et la probabilité de reproduction des oies nichant dans l'Arctique, alors que cette relation était soupçonnée depuis longtemps (Barry 1962).

L'importance des conditions environnementales sur divers aspects démographiques des oies suggère que celles-ci jouent un rôle prépondérant dans la dynamique de la population de la Grande Oie des neiges. Le Haut-Arctique étant un environnement imprévisible et fortement stochastique, il est probable que les relations entre les conditions environnementales et les caractères démographiques mises à jour dans mon étude s'appliquent à une variété d'autres espèces d'oiseaux se reproduisant dans ces milieux. Ces résultats sont donc importants alors qu'un réchauffement anticipé du climat planétaire risque d'entraîner des modifications majeures du climat des régions arctiques.

Approche statistique

Il est important de souligner l'approche méthodologique employée dans cet ouvrage, plus particulièrement celle fondée sur la modélisation de données de capture-marquage-recapture. Le potentiel des modèles multi-états pour l'étude des paramètres démographiques dans un contexte évolutif a été mis en évidence par Nichols et Kendall (1995), mais leur utilisation dans le cadre d'études empiriques est relativement récente. La possibilité de prendre en compte des probabilités de capture et de survie stratifiées par états, ainsi que d'estimer les probabilités de transition entre ces états, confère à ces modèles une place de choix dans l'étude des traits d'histoire de vie et de la dynamique des populations. Ces modèles sont d'une grande flexibilité et permettent de répondre à des questions très diverses.

L'approche multi-état pour l'étude du recrutement utilisée dans cet ouvrage (Chapitre 5) en fait foi. À notre connaissance, c'est la première fois que ce modèle, développé récemment, est utilisé avec des données empiriques. La combinaison d'informations provenant de différentes sources (Chapitre 6), quoique encore peu répandue, peut, elle aussi, s'avérer fort utile lorsque les méthodes traditionnelles de capture-recapture ne sont pas applicables dans leur intégralité. L'utilisation de ces méthodes m'a permis de répondre à des questions particulièrement difficiles. C'est ce qui m'a permis de quantifier le taux de bris des familles (Chapitre 1), de mettre en évidence des coûts reliés aux soins parentaux prolongés (Chapitre 2), d'évaluer l'effet du collier sur certains aspects la reproduction (Chapitre 4), et d'étudier les facteurs affectant le recrutement (Chapitre 5) et la probabilité de reproduction des adultes (Chapitre 6). J'espère que les méthodes développées ici pourront servir de point de référence pour des études futures.

Aspects pratiques

Les résultats présentés dans cet ouvrage ont certes un grand intérêt théorique, mais l'étude des paramètres démographiques revêt aussi un intérêt pratique certain. L'étude de certains paramètres mal connus chez la majorité des vertébrés, plus particulièrement le recrutement et la probabilité de reproduction des adultes, permettra une meilleure compréhension de la dynamique des populations animales. Ceci est particulièrement important dans le cas d’une espèce exploitée comme la Grande Oie des neiges.

Dans le but de stabiliser la population croissante de la Grande Oie des neiges, des mesures extraordinaires ont récemment été prises. Ainsi, pour la première fois depuis la signature du traité sur les oiseaux migrateurs entre le Canada et les États-Unis en 1917, une chasse de conservation printanière a été mise en place dans le sud du Québec en 1999. Cette mesure était basée en grande partie sur un modèle de population qui démontrait clairement l’importance de la survie adulte sur le taux de croissance de la population (Gauthier et Brault 1998). Les paramètres démographiques utilisés dans l’élaboration de ce modèle provenaient en grande partie de travaux menés sur la population de l’Île Bylot depuis 1989. Par contre, certains paramètres comme la probabilité de reproduction des adultes et le taux de recrutement avaient dû être ’empruntés’ à d’autres espèces, particulièrement la Petite Oie des neiges, faute d’information pertinente chez la Grande Oie des neiges. L’impact des conditions environnementales sur ces paramètres, méconnu jusqu’ici, pourra aussi être intégré dans un cadre décisionnel basé sur les connaissances du système. Mon étude devrait donc permettre l’élaboration de modèles de population plus précis pour la gestion de l’espèce.

L’évaluation des impacts des mesures de gestion exceptionnelles sur la population de Grandes oies des neiges, et en particulier sur les paramètres démographiques, est en cours (Béchet 2002, Féret 2002, Mainguy et al. 2002). L’estimation robuste des paramètres démographiques requiert un suivi à long terme d’individus marqués. Au moins 3 années de données sont nécessaires pour estimer la majorité de ces paramètres, et souvent davantage. Il a donc été difficile dans le cadre de ma thèse de tester l’impact de la chasse printanière sur la démographie de l’oie, sauf partiellement dans le cas de la probabilité de reproduction des adultes (Chapitre 6). La conclusion préliminaire qui ressort de cette analyse est que l’effet de la chasse sur les haltes printanières réduit la probabilité de reproduction des adultes, et que cet effet est additif à celui des conditions rencontrées sur les sites de reproduction en période de pré-ponte. Toutefois, nous disposons encore de peu d’années de suivi pour évaluer précisemment l’effet de la chasse printanière sur la probabilité de reproduction. Par contre, les approches développées aux chapitres 4, 5 et 6 de ma thèse devraient être de bons outils pour mieux évaluer, avec quelques années de suivi additionnelles, l'effet de la chasse sur la démographie dans un contexte de gestion évolutive de l'espèce. Selon cette philosophie, les décisions de gestion peuvent être vues comme des 'manipulations' expérimentales aidant à améliorer notre compréhension des processus de dynamique des populations (Williams et al. 1996, Johnson et al. 1997). Nous disposons maintenant d'une base de connaissances importantes sur la variation naturelle des traits vitaux de la Grande Oie des neiges et du taux de récolte, se prêtant particulièrement bien à cette approche de gestion évolutive.

Des études intensives de la Grande Oie des neiges au cours des 20 dernières années ont permis d'acquérir une compréhension globale de leur écologie et de leur utilisation de l'habitat durant la reproduction, sur les aires d'hivernage et lors de leur haltes migratoires automnales et printanières (Batt 1998). Par contre, à peu près rien n'est connu de leurs sites de mue et des conditions requises par les oies durant cette période importante de leur cycle vital. Longtemps suspectée, nous avons confirmé l'occurrence d'une migration de mue de l'Île Bylot vers des sites inconnus impliquant un segment significatif de la population adulte d'oies (Chapitre 3). Il appert que la majorité des non-nicheurs et des individus qui échouent durant la nidification quittent l'Île pour la mue. Ce comportement est particulièrement important dans les années de forte pression de prédation ou de faible effort reproducteur (e.g. 1999) alors qu'une majorité de la population adulte séjournera pendant au moins 1 mois sur ces sites. Avec l'accroissement dramatique de la population au cours des 30 dernières années, on peut s'attendre à ce que l'utilisation de certains sites ait pris de l'ampleur et/ou que le nombre de sites utilisés ait augmenté. Ceci pourrait avoir des conséquences au niveau de la population et des habitats arctiques si la capacité de support de ces milieux était atteinte. L'importance du comportement de migration de mue et le manque d'information sur les sites utilisés mettent en évidence le besoin pour des études approfondies de cette question.

Conclusions

En conclusion, mon travail contribue à l'étude des traits d'histoire de vie et en particulier à la théorie sur les coûts de la reproduction. Il met en évidence la nécessité primordiale, tant d'un point de vue scientifique qu'éthique, de vérifier l'impact des manipulations effectuées sur les individus afin d'ajuster nos interprétations en conséquence et de minimiser ces impacts dans le futur. Il apporte une connaissance accrue des paramètres démographiques d'une espèce longévive pouvant potentiellement être applicables à une grande variété d'espèces. Il souligne aussi l'importance des facteurs environnementaux sur les traits d'histoire de vie d'une espèce évoluant dans un environnement fortement stochastique et imprévisible. Finalement, il ouvre la voie à des études futures qui pourront examiner plus en détail les processus par lesquels les coûts de la reproduction sont encourus et étudier les conséquences d'une augmentation de la densité d'oies sur les paramètres vitaux. J'estime que ma thèse représente une contribution non-négligeable à la compréhension de l'évolution des traits d'histoire de vie et aux processus démographiques chez cette espèce. J'espère sincèrement que cette thèse facilitera et stimulera la poursuite de futurs travaux de recherche en écologie des populations.

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