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Stéphane MENU

Survie de la Grande Oie des neiges : Aspects méthodologiques et implications dans la dynamique de population

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 et Centre d'Études Nordiques
FACULTÉ DES SCIENCES ET DE GÉNIE
UNIVERSITÉ LAVAL
QUÉBEC

Septembre 1998

0-612-36301-5

UNIVERSITÉ LAVAL

Faculté des études supérieures

ATTESTATION

Ce 26ième jour du mois de août 1998, les personnes soussignées , en leur qualité de membres du jury de la thèse de STÉPHANE MENU, ont assisté à la soutenance de cette thèse.

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Austin Reed	Service canadien de la faune	
André Desrochers	Laval	
Gilles Gauthier	Laval	

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FES-63a (07-95)

Résumé succinct

L'objectif de la thèse était d'estimer les probabilités de survie de différentes composantes d'une population de la Grande Oie des neiges (*Chen caerulescens atlantica*), en utilisant des individus marqués pendant l'été à l'île Bylot (T.N.O., Canada) et l'automne à la Réserve Nationale de Faune du Cap Tourmente (Québec, Canada). Le marquage et les marques elles-mêmes n'ont pas eu d'effets négatifs sur la survie, ce qui permet d'extrapoler les résultats à l'ensemble de la population. Différents facteurs naturels et humains ont été examinés pour identifier leur contribution relative dans les variations intra- et inter-annuelles de la survie. La chasse est un élément majeur affectant négativement la survie et peut potentiellement contrôler la dynamique de la population. La survie des jeunes pendant la migration automnale a une grande influence sur leur survie annuelle et varie intra- et inter-annuellement en relation avec leurs masses corporelles à la fin de l'été et leurs date d'éclosion.

Stéphane Menu - Candidat

Gilles Gauthier - Directeur de recherche

Résumé

L'objectif de la thèse était d'estimer les probabilités de survie de différentes composantes d'une population de la Grande Oie des neiges (*Chen caerulescens atlantica*), en utilisant des individus marqués pendant l'été dans l'arctique canadien et durant l'automne au Cap Tourmente (Québec, Canada). Différents facteurs naturels et humains ont été examinés pour identifier leur contribution relative dans les variations intra- et inter-annuelles de la survie. L'effet potentiellement néfaste des techniques utilisées pour marquer le grand nombre d'individus nécessaires à une évaluation rigoureuse des probabilités de survie a également été évalué. Les probabilités de survie ont été estimées par des modélisations mathématiques utilisant des récupérations de bagues et des réobservations de colliers. Nos résultats montrent que le marquage et les marques elles-mêmes n'ont pas eu d'effets négatifs sur la survie des individus marqués, que ce soit à court ou à long terme, permettant ainsi l'extrapolation des estimés à l'ensemble de la population. La survie annuelle des adultes ne dépendait pas du sexe, ni du lieu de marquage des individus et était constante pour la période considérée. De plus, elle était similaire entre les années 1970 et 1990 alors que la population s'est accrue d'un facteur 10 entre-temps, suggérant l'absence d'effets dépendants de la densité de la population sur la survie. Les variations concomitantes de la croissance démographique et du taux de récolte par la chasse et l'absence de tendances temporelles évidentes dans la production de jeunes suggèrent que la chasse a le potentiel de contrôler la dynamique de la population, en agissant négativement sur la probabilité de survie. Bien qu'étant toujours nettement inférieure à celle des adultes, la survie des jeunes présentait des variations inter-annuelles prononcées, en grande partie dues aux variations de la survie pendant la migration automnale. Celles-ci étaient influencées par les variations dans la chronologie de nidification et la masse corporelle des jeunes à la fin de l'été. Que ce soit au niveau de la cohorte ou individuellement, une date d'éclosion hâtive et/ou une masse corporelle élevée à la fin de l'été augmentaient significativement la probabilité de survie des jeunes pendant la migration automnale, particulièrement lors des années de nidification tardive.

Stéphane Menu - Candidat

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Abstract

The objective of the thesis was to estimate the survival probabilities of different components of a population of Greater Snow Goose (*Chen caerulescens atlantica*), using individuals marked during summer in the Canadian Arctic and during fall at Cap Tourmente (Québec, Canada). Several natural and human factors were examined to identify their relative effects on intra- and inter-annual variations of survival. We also evaluated the potentially harmful effect of marking large number of birds, which is required for a reliable estimation of survival probabilities. Survival probabilities were estimated with mathematical modeling using band recoveries and neckband resightings. Our results show that the marking techniques and the marks themselves had no negative effect on survival of marked birds either in the short or long term. This allows us to extrapolate the estimates to the whole population. The annual survival of adults was not dependent on sex or banding location and was constant during the study period. Furthermore, adult survival rates between the 1970s and 1990s were similar, a period during which the population increased ten-fold, suggesting no density-dependent effect on survival yet. The concurrent variation of population growth and harvest rates, and the absence of clear temporal trend in the production of young, suggest that hunting could control the dynamics of the population by reducing survival rates. The survival rates of young were always lower than those of adults and varied greatly from year to year, mainly because of variations in the fall migration survival. These variations were affected by inter-annual differences in breeding chronology and body mass of young at the end of the summer. At the cohort or individual level, an early hatching date and/or a high body mass at the end of the summer increased significantly the survival probability of young during the fall migration, especially for years of late breeding.

Stéphane Menu - Candidat

Gilles Gauthier - Directeur de recherche

Avant-propos

Je voudrais tout d'abord remercier mon directeur de recherche, Gilles Gauthier, pour la confiance qu'il m'a accordé en m'acceptant dans son laboratoire, pour ses nombreux conseils et commentaires stimulants ainsi que pour sa grande disponibilité qui ont permis de mener à terme ce projet dans des délais raisonnables. Je considère comme une grande chance d'avoir eu l'opportunité de participer à un projet de recherche de cet envergure. Je tiens aussi à remercier Austin Reed, mon codirecteur, pour les longues discussions où il partageait sa passion et sa grande expérience de l'Arctique et des oies et pour les encouragements prodigués. Jay Hestbeck m'a initié à SURVIV. Je l'en remercie. J'ai également grandement apprécié son hospitalité. Je veux aussi remercier André Desrochers et Conrad Cloutier, pour leurs commentaires et leur supervision lors du déroulement de mon doctorat.

Naturellement, un projet d'une telle ampleur implique la participation d'un grand nombre de personnes, qu'il n'est pas possible de nommer tous. Néanmoins, je voudrais mentionner: Gérald Picard, technicien à l'Université Laval, maître d'oeuvre du baguage; Joël Bried, Isabelle Chouinard, Alexandre Daudé, Diane Dauphin, Nathalie Piedboeuf, et Catherine Poussart pour les observations de colliers à l'automne; et pour les bons moments passés à l'Ile Bylot, Julien Beaulieu, Joël Bêty, Jean-François Giroux, Kathy Jones, Diane Leclerc, Denis Lepage (en plus de discussions en tous genres sur la meilleure façon d'analyser telle ou telle donnée), Hélène Massé, Véronique Morez, Thomas Pewalatuk Chantal Pineau, Geneviève Pomerleau, Nathalie Piedboeuf (encore!), Monique Poulin, Catherine Poussart (encore!), Mathilde Renaud, Geneviève Simard, Jean-Pierre Tremblay.

De nombreux organismes ont rendu possible ce projet par leur soutien financier. Je voudrais remercier:
- l'Étude du plateau continental polaire (Ressources naturelles Canada)
- Canards Illimités Canada
- le Arctic Goose Joint Venture (Environnement Canada)
- le Service Canadien de la Faune (Environnement Canada)
- le Conseil de Recherche en Sciences Naturelles et en Génie du Canada
- le Fonds pour la Formation de Chercheurs et l'Aide à la Recherche (ministère de l'Éducation du Québec)
- le Centre d'Études Nordiques (Université Laval).

Enfin, merci aux gens du Hunter and Trappers Association de Pond Inlet pour leur précieuse collaboration.

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INTRODUCTION

L'étude des caractéristiques du cycle vital (*life history*) d'une espèce est particulièrement importante en écologie, notamment pour une meilleure compréhension des mécanismes de régulation des population (Stearns 1992). Dans ce contexte, un objectif majeur est de détecter et d'analyser les différences dans les traits du cycle vital parmi des groupes d'individus à travers le temps et l'espace, afin d'identifier les pressions de sélection qui contrôlent la dynamique de la population. Souvent, ces différences impliquent des variations dans la fécondité, la survie ou les deux, et donc des différences dans le fitness des individus. Selon la théorie de la sélection naturelle de Darwin (1859), le fitness d'un individu est défini comme son efficacité à transmettre ses gènes, à travers sa descendance, par rapport aux autres individus de la population. Pour cela, les individus doivent optimiser leur succès reproducteur en tenant compte d'un ensemble de contraintes et de compromis. La nécessité évidente de survivre pour pouvoir se reproduire fait de la survie un paramètre crucial dans la compréhension des mécanismes de sélection.

Les différents paramètres démographiques permettent de ranger les espèces selon un gradient de stratégie démographique appelé *r-K* (Pianka 1970). Les espèces de stratégie *r* ont en général une espérance de vie adulte faible, un âge à la première reproduction également faible et une fécondité élevée (nombreux descendants produits en peu d'événements reproducteurs). À l'autre extrême du gradient, les espèces de stratégie *K* présentent des caractéristiques opposées (espérance de vie adulte élevée, première reproduction tardive - maturité retardée - et faible nombre de descendants, qui requièrent souvent des soins parentaux prolongés). Pour ces espèces, le taux de survie des adultes est le paramètre qui influence le plus la croissance de la population.

La probabilité de survie est un paramètre dynamique, qui peut varier en fonction de caractéristiques individuelles comme l'âge, le sexe, le génotype ou le phénotype, et aussi en fonction de variables environnementales biotiques et abiotiques. La compétition intra- et inter-spécifique et la prédation peuvent également l'affecter.

Facteurs affectant la survie

De manière générale, il y a une amélioration des taux de survie au cours des premières années de la vie (Newton 1989). Ces différences sont habituellement attribuées à une expérience plus faible chez les juvéniles, tant pour les capacités de recherche et de prise de nourriture que d'évitement des prédateurs. De plus, certaines études ont également montré un déclin de la survie en fin de vie (sénescence), malgré la plus grande expérience des individus âgés. Par exemple, pour l'Épervier d'Europe (*Accipiter nisus*), il y a une amélioration de la survie des femelles des âges 1 à 3 ans, pour une longévité maximale de 10 ans, suivie d'une dégradation après l'âge de 5 ans (Newton et al. 1997). La diminution de la survie après un certain âge est attribuable à une usure généralisée, qui réduit l'efficacité de l'individu (Holmes and Austad 1995). Ainsi, l'usure des dents a été identifiée comme la principale raison pour la diminution de la survie des Chevreuils d'Europe (*Capreolus capreolus*) âgés de 7 ans et plus (Gaillard et al. 1993).

Les différences de survie entre les sexes, quand elles existent, peuvent s'expliquer par des différences de taille (dimorphisme sexuel), des différences dans les comportements migratoires et/ou dans les coûts de reproduction (Breitwisch 1989). La reproduction demande en effet un investissement de ressources important, surtout pour la femelle en général. Ainsi, chez les Otaries à fourrure de l'Antarctique (*Arctocephallus gazella*), les femelles adultes qui n'avaient pas de descendance avaient une probabilité de survie supérieure à celles avec descendance (Boyd et al. 1995). En revanche, d'autres études n'ont pas pu mettre en évidence de différence dans la probabilité de survie entre les sexes (e.g. Francis et al. 1992a, Cezilly et al. 1996). Cependant, même si les coûts associés à la reproduction n'impliquent pas une réduction de la survie, ils peuvent s'exprimer par des modifications comportementales, permettant d'éviter les effets négatifs de la reproduction sur la survie. Souvent, cela peut impliquer de compromettre le succès reproducteur actuel pour augmenter les chances de survie future (e.g. Cezilly et al. 1996).

À l'intérieur d'une population, la qualité des individus est variable, une conséquence des différences de génotype et des conditions environnementales rencontrées. Ces variations individuelles s'expriment notamment par des succès reproducteurs contrastés selon les individus. Ainsi, il a été montré, pour plusieurs populations, que la majorité des individus ne produisent aucun descendant viable, la presque totalité des descendants ne provenant que d'une faible proportion des individus (Newton 1989, Marti 1997). Les variations individuelles du fitness ont aussi des implications en termes de survie, bien que cela soit plus difficile à mesurer que le succès reproducteur. Par exemple, dans une colonie de Mouette tridactyle (*Rissa tridactyla*), les individus occupant le centre de la colonie avaient une meilleure survie que ceux en périphérie (Aebischer and Coulson 1990). Comme 99% de la mortalité se produit à l'extérieur de la colonie et que la fidélité au site de nidification est très forte, cette différence indique une variation importante de la qualité des individus, les individus nichant au centre de la colonie ayant un plus grand fitness (mis en évidence, également, par un meilleur succès reproducteur; Aebischer and Coulson 1990).

Les conditions environnementales peuvent aussi avoir une influence drastique sur la survie des individus, notamment lors d'événements extrêmes. Ainsi, une vague de froid majeure durant un hiver a réduit significativement (de 93% à 76%), mais de façon ponctuelle, la survie annuelle de Flamands roses adultes (*Phoenicopterus ruber roseus*; Cezilly et al. 1996). En revanche, la disparition d'une source de nourriture importante pour une population de Goélands argentés (*Larus argentatus*) n'a pas eu d'influence à court terme sur la survie des adultes, mais a modifié significativement d'autres paramètres biologiques (taille de ponte et production de jeunes, ainsi que masse corporelle des adultes; Pons and Migot 1995).

La dimension temporelle est en effet extrêmement importante dans les processus de variation de la probabilité de survie. Non seulement un individu vieillit, et ainsi sa probabilité de survie évolue, mais au cours de son cycle de vie annuel se produisent également des modifications physiologiques et comportementales majeures susceptibles d'induire des changements dans sa probabilité de survie. Ainsi, certaines périodes du cycle de vie peuvent présenter des risques de mortalité plus élevées: la reproduction et la migration, de part l'investissement considérable en énergie qu'elles requièrent et/ou l'exposition à des facteurs climatiques ou des environnements extrêmes, constituent des périodes critiques (e.g. Owen et Black 1989). De plus, au cours de sa vie, les conditions environnementales influençant la survie peuvent également se modifier. À une échelle temporelle supérieure à l'espérance de vie d'un individu, des modifications des probabilités de survie pour une population donnée peuvent aussi survenir à cause, notamment, de variations dans la densité de la population, dans la composition des communautés de prédateurs ou de compétiteurs, ou de changements majeurs des caractéristiques des habitats utilisés. Ainsi, la dégradation des conditions d'hivernage due à une sécheresse prolongée a provoqué une diminution importante de la survie chez la Cigogne blanche (*Ciconia ciconia*), et en conséquence un déclin marqué de la population considérée (Kanyamibwa et al. 1990).

La survie et la conservation des espèces

Une connaissance précise de la probabilité de survie et des facteurs qui l'influencent est d'une importance cruciale pour la conservation des espèces et la gestion des populations exploitées. En effet, dans le cas d'espèces menacées, il est essentiel d'identifier précisément les causes entraînant la diminution des populations afin d'y remédier éventuellement. Ainsi, le déclin des populations d'Albatross hurleur (*Diomedea exulans*) a été relié à une augmentation de la mortalité des adultes provoquée par les lignes de pêche des bateaux de haute-mer (Croxall et al. 1990). Comme cette espèce a une probabilité de survie très élevée (environ 95%), un faible taux de reproduction et un taux de recrutement également faible, la diminution de survie observée, même faible (1 à 2%) a eut de profondes conséquences sur la dynamique de la population (Croxall et al. 1990, Weimerskirch 1990).

Pour les espèces chassées, comme les canards et les oies, la relation entre la mortalité par la chasse et la mortalité naturelle constitue un important débat (Nichols 1991). Deux hypothèses extrêmes ont été proposées, soit l'hypothèse de mortalité complètement additive et l'hypothèse de mortalité complètement compensatoire. Sous l'hypothèse de mortalité additive, le taux de survie annuelle décroît de façon linéaire à mesure que la mortalité due à la chasse augmente. Quel que soit le niveau d'exploitation, la mortalité due à la chasse s'ajoute à la mortalité naturelle. En revanche, sous l'hypothèse de mortalité compensatoire, le taux de survie annuelle d'une population exploitée reste identique pour une certaine gamme d'intensité d'exploitation. Cela s'explique par le fait que, jusqu'à un certain point, la mortalité due à la chasse est compensée par une diminution de la mortalité naturelle. Cependant, au-delà d'un seuil d'intensité d'exploitation, de nouvelles augmentations de la mortalité due à la chasse entraînent une diminution linéaire de la survie (Nichols 1991). La validation de ces hypothèses est délicate et demande une expérimentation à grande échelle nécessitant la manipulation des réglementations de la chasse selon un protocole préétabli (Nichols et al. 1984, Anderson et al. 1987 et Nichols 1991). Il est pourtant essentiel de déterminer le type de réponse face à la chasse pour les populations ou les espèces exploitées, car les conséquences démographiques d'une mortalité compensatoire ou additive sont bien différentes et devraient influencer en conséquence les décisions sur les réglementations de la chasse

Estimation de la survie

L'estimation des taux de survie et l'identification des facteurs les influençant sont donc essentielles à la compréhension de la dynamique d'une population animale. Cependant, une estimation rigoureuse des taux de survie d'une population animale sauvage se heurte à de nombreuses difficultés méthodologiques: il faut procéder à un suivi à long terme (plusieurs années sont nécessaires pour obtenir des estimations de survie annuelle) et souvent le territoire à couvrir est de grande superficie (surtout pour les espèces migratrices). L'approche la plus pertinente consiste en une série d'échantillonnage successifs d'individus marqués individuellement (Lebreton et al. 1992). Selon le procédé d'échantillonnage utilisé, les informations subséquentes sur les individus marqués peuvent se répartir en trois types (Fig. 1): (1) enregistrement complet des survivants (ou de manière équivalente, des morts), (2) enregistrement incomplet des morts ("récupérations"), et, (3) enregistrement incomplet des survivants ("recaptures").

Dans ces 3 cas, des méthodes statistiques sont nécessaires pour estimer, comparer et modéliser les probabilités de survie. De plus, pour les types (2) et (3), comme l'enregistrement est incomplet, d'autres paramètres (probabilité de récupérations ou de recaptures) doivent être pris en compte. Bien que n'ayant pas toujours reçu l'attention souhaitée, l'introduction de ces paramètres est indispensable pour obtenir des estimations de survie non biaisées (Lebreton et al 1993). Ne pas prendre en compte les probabilités de détection des survivants (ou des morts) assume que tous les individus présents dans l'aire d'étude sont répertoriés (type (1): enregistrement complet), situation hautement improbable pour les populations naturelles. Même dans des cas particuliers où les individus sont facilement observables, car concentrés dans le temps et l'espace (i.e. colonie d'oiseaux marins), il est en effet illusoire d'espérer recenser *tous* les individus marqués qui ont survécu

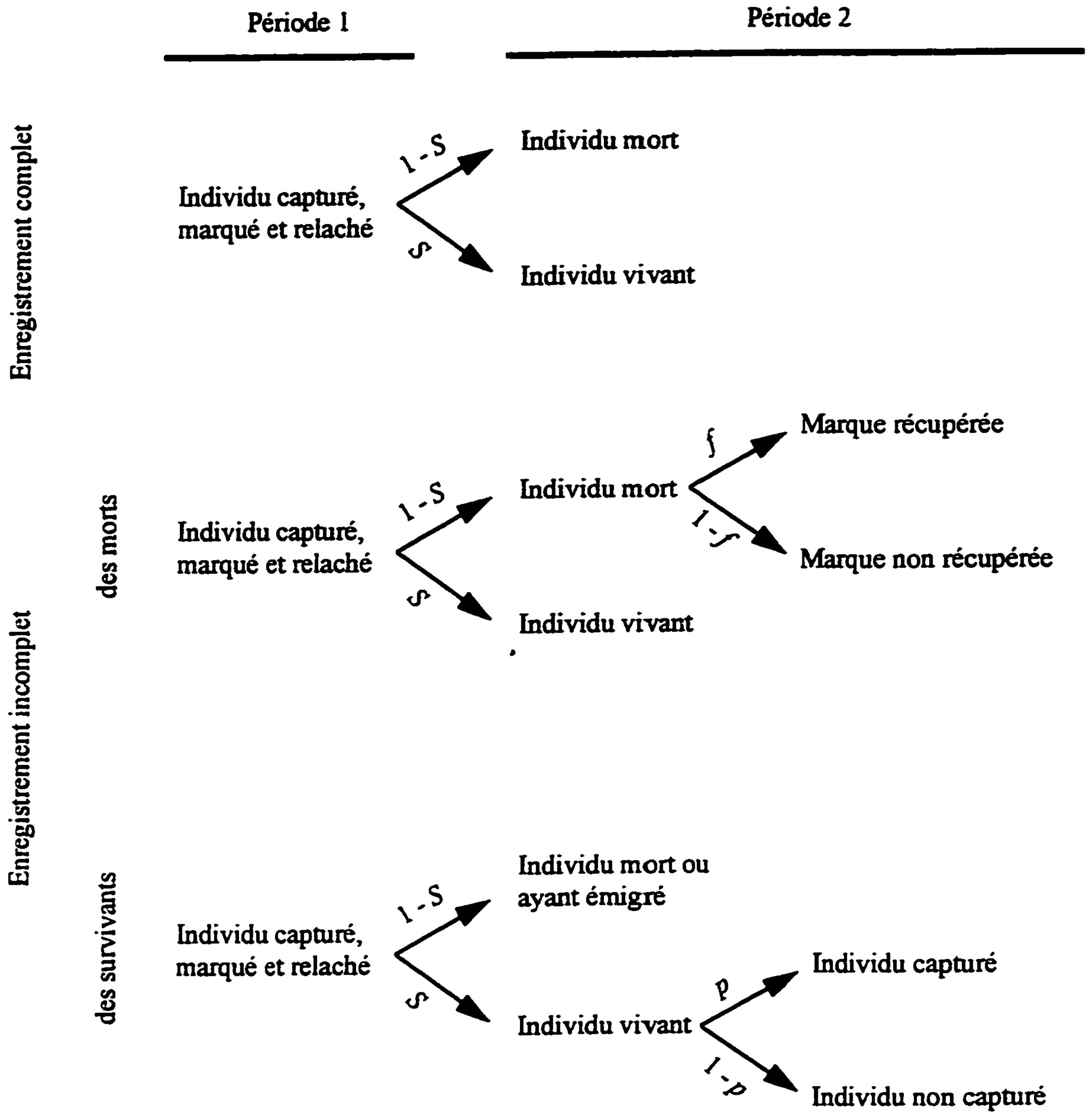


Fig. 1. Diagramme des évènements et de leurs probabilités associées pour un individu marqué et relaché à la première période d'une étude en comportant deux, selon les différents types de suivi possibles.

S = probabilité de survie
f = probabilité de récupération
p = probabilité de capture

et sont retournés à l'aire d'étude. C'est pourtant l'hypothèse émise lorsqu'est utilisé, pour l'analyse des taux de survie, le "taux de retour", qui correspond à la proportion d'individus capturés ou observés au temps t qui sont recapturés ou observés de nouveau au temps $t + 1$. Comme le souligne Clobert (1995), l'utilisation encore répandue du taux de retour pour l'estimation de probabilité de survie biaise les conclusions obtenues. Ainsi, pour des comparaisons entre groupes, toute différence observée pourra être attribuée à des différences réelles de la survie entre les groupes, mais aussi à de possibles différences de recaptures ou récupérations entre les groupes (Clobert 1995).

Sans rentrer dans les détails techniques, je présente rapidement la théorie et les méthodes utilisées dans l'estimation de la probabilité de survie à partir d'un échantillon d'individus marqués. Le principe général pour l'estimation des paramètres à l'étude est d'identifier le devenir possible de chaque individu marqué et de le modéliser selon une suite d'événements probabilistiques. En appliquant des généralisations ou des contraintes spécifiques sur la probabilité de survie, et le cas échéant, sur la probabilité de récupération ou de recapture, un modèle stochastique est généré, représentant la distribution attendue des histoires observées des individus marqués. Selon le principe de maximum de vraisemblance (*maximum likelihood*), il est alors possible de produire des estimations des probabilités pour obtenir une distribution attendue des histoires la plus proche de la distribution observée (Brownie et al. 1985, Pollock et al. 1990, Lebreton et al. 1992).

Enregistrement complet des survivants (ou des morts)

Cette situation est plus souvent rencontrée pour des populations humaines où il est possible de suivre tous les individus de la naissance à leur mort. Pour des populations animales, des cas particuliers permettent un suivi exhaustif (i.e. individus fixés à un substrat, télémétrie). Le devenir d'un individu ne s'exprime alors que par deux possibilités mutuellement indépendantes, la survie ou la mort (Fig. 1). Pour un groupe d'individus marqués, la succession des événements peut ainsi être modélisée comme une suite de lois binomiales. Les méthodes itératives de calcul, aisément accessibles avec des logiciels informatiques, permettent une estimation des paramètres et une mesure de la concordance des données utilisées dans les modèles.

Enregistrement incomplet des morts: récupérations

L'exemple typique d'enregistrement incomplet des morts est celui des récupérations de bagues d'oiseaux trouvés morts ou tués à la chasse. Ces récupérations ne concernent en fait qu'une fraction, souvent minime, des individus morts durant la période de temps considérée (Fig. 1). Afin de modéliser correctement la probabilité de survie à partir de ces données, il faut donc introduire au modèle un autre paramètre, la probabilité de récupération, f. Plusieurs modèles peuvent être construits pour tester des hypothèses spécifiques sur les probabilités de survie et de récupération (Brownie et al. 1985). Cependant, le complément de la probabilité de survie contient la perte du marqueur en plus de la mortalité. Mais, de part les marqueurs utilisés, la perte est en général considérée comme négligeable (Hestbeck et al. 1990). Très souvent, la proportion d'oiseaux marqués récupérés est très faible (moins de 10%), produisant des estimations à précision réduite, ce qui peut limiter la puissance des conclusions. Par contre, un avantage certain de cette méthode est la possibilité de couvrir une aire géographique relativement importante à moindre coût. Cela permet le plus souvent d'éviter les problèmes d'immigration et de dispersion, notamment pour les populations exploitées par la chasse.

Enregistrement incomplet des survivants: recaptures

Au contraire des récupérations de bagues, les recaptures, qu'elles soient physiques ou non (une marque observée à distance est considérée comme une recapture), n'impliquent pas la disparition de l'individu marqué. Un même individu peut donc être recapturé plusieurs fois, et avoir ainsi une "histoire de capture" plus détaillé. Les histoires de captures individuelles sont généralement représentées par une suite de 1 et de 0, le 1 signifiant une capture et le 0 pas de capture. A chaque numéro correspond une occasion de capture (i.e. une période d'échantillonnage). Dans la même logique que précédemment, une certaine fraction des individus vivants ne sont pas répertoriés lors des occasions de capture (Fig. 1). Il faut donc considérer la probabilité de recapture p, en plus de la probabilité de survie, dans la modélisation des devenirs possibles d'un individu marqué.

A partir du modèle initial de Cormack-Jolly-Seber (i.e. probabilités de survie et de recapture dépendantes du temps; Cormack 1964, Jolly 1965, Seber 1965), plusieurs développements sont possibles: paramètres dépendants de l'âge, de groupes, différents entre anciennement marqués et nouveaux, etc. (Pollock et al. 1990, Lebreton et al 1992). Par rapport aux récupérations, la proportion d'individus recapturés est souvent relativement élevée (bien que dépendent de l'effort appliqué), ce qui permet d'avoir une meilleure précision sur les estimés. En revanche, le complément à la probabilité de survie avec les modèles de capture-recapture contient, en plus de la mortalité, l'émigration permanente et la perte du marqueur. Les recaptures ou réobservations, de part l'investissement qu'elles requièrent, sont souvent limitées géographiquement. En conséquence, tout individu marqué émigrant définitivement hors de l'aire d'étude est considéré comme mort, alors que ce n'est pas le cas. Cela a comme conséquence, si l'émigration permanente est importante, de biaiser négativement les probabilités de survie. Il faut donc avoir un protocole d'échantillonnage limitant au mieux les possibilités d'émigration permanente en plus d'estimer le taux de perte du marqueur (avec un double marquage; Hestbeck et al. 1990).

Comparaisons des 3 méthodes

Pour chaque méthode, le suivi des individus marqués engendre une histoire qu'il est possible de décrire par différentes probabilités selon le type de suivi considéré. Des prémisses associées à la modélisation probabilistique sont à respecter afin de limiter les biais dans l'estimation des paramètres. Commune aux trois types de suivi, l'indépendance des devenirs et l'identité des taux des individus marqués de la population à l'étude (*independence of fates and identity of rates among individuals*) constituent des prémisses fondamentales (Lebreton et al. 1992). Pour les respecter, les procédures de capture doivent être le plus aléatoire possible afin de réaliser un échantillonnage non biaisé de la population. Cependant, cela ne constitue une condition ni suffisante ni nécessaire et il convient également de procéder à un examen attentif des données. Souvent, il est nécessaire de fractionner en plusieurs sous-catégories l'échantillon d'individus marqués pour remplir les conditions de la prémisse. La répartition en différentes catégories peut se baser sur des critères biologiques (âge, sexe, individus reproducteurs ou non, etc.) ou méthodologiques (périodes et sites d'échantillonnage), ce qui permet d'assurer une certaine homogénéité dans les probabilités de survie et de récupération ou capture à l'intérieur d'une sous-catégorie (Lebreton et al. 1992).

Chaque méthode présente des avantages et des inconvénients, que ce soit en termes de précision des estimés, d'efforts nécessaires à la capture et la récolte des données, etc. (Hestbeck et al. 1990). Leur utilisation concomitante (par exemple, récupérations et recaptures) permet d'améliorer la confiance dans les estimés obtenus et d'identifier les limites de chacune d'elles.

Objectifs de la thèse

Mes objectifs, au cours de ce travail, seront d'une part d'évaluer l'impact des techniques de marquage et des marqueurs sur la survie des individus ainsi marqués, et d'autre part, d'estimer la probabilités de survie de différentes classes de la population de la Grande Oie des neiges (*Chen caerulescens atlantica*), à des échelles temporelles variables, et d'identifier les facteurs naturels et humains qui l'influencent.

La Grande Oie des neiges niche de façon semi-coloniale dans le Haut-Arctique canadien. Elle entreprend deux fois par an une migration de près de 4000 km entre ses sites de nidification et les lieux d'hivernage le long de la côte Atlantique des Etats-Unis d'Amérique (du New Jersey à la Caroline du Nord; Annexe E). Au printemps et à l'automne, les oies se concentrent le long du fleuve St-Laurent, au Québec, qui constitue une halte migratoire de grande importance. Elles s'alimentent alors dans les marais fluviaux, ainsi que dans les terres agricoles. Chez cette espèce, la nidification dans un environnement extrêmement saisonnier et imprévisible et une longue migration après la période de croissance des jeunes imposent des contraintes sélectives importantes pouvant influencer la survie.

La Grande Oie des neiges présente un intérêt économique certain, à cause principalement de l'exploitation qui en est fait par la chasse et le tourisme écologique. De plus, les oies peuvent occasionner des dégâts aux cultures agricoles par endroits. En conséquence, au delà d'une problématique purement biologique, il est essentiel d'étudier en détail sa dynamique de population pour la mise en place de plans de gestion de la population.

Le comportement grégaire des oies, tant lors de l'élevage des jeunes qu'en migration, facilite la capture et le marquage d'un grand nombre d'individus. De plus, l'utilisation d'un corridor de migration relativement restreint et une chasse assez intensive permettent des taux élevés de réobservation et de récupération des oiseaux marqués. Ces caractéristiques font de la Grande Oie des neiges un sujet idéal pour effectuer cette étude.

Première partie: Les effets du marquage

Les taux de survie obtenus avec les modèles ne s'appliquent en définitive qu'aux individus marqués de la population à l'étude. Cependant, il est naturellement désirable de vouloir extrapoler les résultats à l'ensemble de la population. Pour que l'extrapolation soit valide, bien que cela ne puisse être testée directement, il faut principalement que les captures pour le marquage soient le plus aléatoire possible, et ce pour toutes les catégories visées de la population. Il faut aussi garder à l'esprit que les extrapolations ne pourront s'appliquer qu'aux individus de la zone à l'étude, qui est le plus souvent une région favorable pour l'espèce. Par contre, il est évident que si la capture et/ou les marques appliquées induisent une modification significative de la probabilité de survie des individus marqués, il n'est alors plus valide d'extrapoler les résultats obtenus aux individus non marqués. La difficulté d'évaluer un effet potentiellement négatif du marquage sur la survie découle du fait qu'il n'est pas possible d'estimer de manière rigoureuse la survie d'individus non marqués: il n'y a pas de groupes témoins. Seules des méthodes indirectes peuvent être employées.

Il m'est donc apparu indispensable d'analyser en détail les effets potentiels du marquage sur la survie afin d'assurer la validité des conclusions subséquentes. Dans le premier chapitre, j'aborderai plus précisément les effets à court terme que peut provoquer la capture en elle-même. Impliquant un grand nombre d'individus retenus dans un espace restreint pendant un laps de temps relativement long, la capture peut induire une mortalité directe (dans les heures ou les quelques jours qui la suivent), provoquée soit par le stress, l'incapacité à s'alimenter, ou des blessures physiques occasionnées lors des manipulations. Un éventuel impact non négligeable de la capture sur la survie directe des individus capturés remettrait sérieusement en question l'approche utilisée et nécessiterait une modification des techniques employées.

Les chapitres 2 et 3 porteront plus particulièrement sur les effets potentiels à moyen et long terme qui peuvent se produire si les marqueurs utilisés sont susceptibles de provoquer une gêne importante due à leur taille et/ou leur poids. Ce peut être le cas pour des marqueurs télémétriques ou ceux pouvant être lus à grande distance sans recapture de l'individu (i.e. colliers, marques patagiales). En général, les individus ainsi marqués sont un sous-échantillon d'un marquage impliquant un autre marqueur beaucoup moins volumineux et dont l'impact est considéré comme négligeable (une bague tarsale dans le cas des oiseaux, par exemple). Ainsi, sont constitués un groupe d'individus doublement marqués ("traitement") et un groupe d'individus marqués simplement avec le marqueur dit inoffensif ("témoin"). Il est alors possible de tester les effets potentiels du plus gros marqueur en comparant la survie du groupe "traitement" avec le groupe "témoin". Les effets peuvent s'avérer transitoires: après une période d'adaptation pendant laquelle une certaine mortalité pourrait avoir lieu, il n'y aurait ensuite plus de différence entre les deux groupes (cette question est examinée au chapitre 2). Au contraire, l'effet pourrait perdurer de manière constante sur une longue période entraînant alors une baisse significative de la survie à long terme des oiseaux ainsi marqués (chapitre 3).

Deuxième partie: dynamique de population

Cette partie vise à examiner des questions de nature davantage biologique sur les facteurs qui influencent la survie et leur lien avec la dynamique de la population. Deux aspects seront donc abordés dans cette partie. Tout d'abord, au chapitre 4, la survie annuelle des oies des neiges sera estimée et mise en relation avec différents facteurs biotiques et abiotiques pouvant l'influencer. Les effets de l'âge, du sexe, du temps et des sites de nidification sur les probabilités de survie seront testés. Les variations temporelles dans la survie et le régime d'exploitation par la chasse seront mises en relation avec le suivi à long terme de la taille de la population de la Grande Oie des neiges afin de mesurer le rôle de chacun de ces paramètres dans la croissance démographique de l'espèce. Cette question est d'un intérêt particulier pour la gestion de la population sachant que l'impact de la chasse sur la dynamique des populations d'oies et de canards reste sujet à débat. Les résultats de ce chapitre fourniront également les bases à une modélisation plus détaillée de la dynamique de la population de la Grande Oie des neiges.

Les chapitres 5 et 6 concerneront plus particulièrement une période précise du cycle de vie de la Grande Oie des neiges, la migration automnale. Je me suis intéressé aux contraintes imposées par cette période critique sur la survie des jeunes. La mortalité pendant la migration automnale peut constituer une part considérable de la mortalité annuelle des jeunes et représenter ainsi un facteur primordial déterminant le recrutement. Cependant, elle n'est pas souvent estimée, car il est rarement possible de mesurer directement les pertes encourues pendant la migration ou de séparer la survie annuelle en estimés saisonniers. En plus d'estimer la survie des jeunes pendant la migration automnale, je me suis également attaché à rechercher les facteurs pouvant l'influencer, que ce soit au niveau de la cohorte (chapitre 5) ou au niveau individuel (chapitre 6). Les éléments les plus déterminants dans la survie des jeunes après envol sont leur masse corporelle et leur date d'envol (ce dernier paramètre étant en étroite relation avec la date d'éclosion). Les variations tant intra- (i.e. saisonnières) qu'inter-annuelles de ces paramètres ont des conséquences profondes sur la probabilité de survie après l'envol, et, en définitive, sur la démographie de la population.

CHAPITRE 1

SURVIVAL OF JUVENILE GREATER SNOW GEESE IMMEDIATLY AFTER BANDING.

RÉSUMÉ

Nous avons étudié la survie immédiatement après baguage d'individus de la Grande Oie des neiges (*Chen caerulescens atlantica*) capturés et marqués à la fin de l'été à l'île Bylot (T.N.O., Canada). Immédiatement après le baguage, les sites utilisés et leurs environs ont été inspectés pour les oiseaux bagués morts. La régression logistique a été utilisée pour modéliser la survie après baguage en relation avec l'âge et la masse au baguage des oiseaux, la taille de la capture, l'année de baguage et leurs interactions. Entre 1993 et 1996, 6577 adultes et 6736 jeunes furent bagués. 192 jeunes et seulement 6 adultes furent retrouvés morts lors de l'inspection des sites. L'âge au baguage a eu un effet significatif sur la survie post-baguage des jeunes, en interaction avec la taille de la capture et l'année de baguage. La survie apparente post-baguage était la plus faible pour les oisons les plus jeunes lors des plus grosses captures. La survie était aussi affectée positivement par la masse au baguage, étant significativement moins élevée pour les oisons les plus légers, principalement pour des grosses captures. La survie apparente immédiatement après baguage était très élevée pour les jeunes (0.971) et proche de 1 pour les adultes. Cela suggère que le baguage a un effet mineur sur la survie post-baguage des oisons et pratiquement aucun effet sur les adultes.

ABSTRACT

We studied the post-banding survival of Greater Snow Geese (*Chen caerulescens atlantica*) captured and marked during mass-banding drives on Bylot Island (N.W.T., Canada). Immediately after banding, the banding sites and the surrounding areas were checked for dead banded birds. Logistic regression was used to model post-banding survival in relation with age and mass at banding, size of catch, banding year and their interactions. Between 1993 and 1996, 6,577 adults and 6,736 juvenile were banded, of which 6 adults and 192 juvenile were found dead. Apparent survival immediately after banding was very high for juvenile (0.971) and close to 1 for adults. Effect of age on the post-banding survival of young was significant but the magnitude varied with catch size and year. Apparent post-banding survival was reduced for the youngest goslings captured in the largest catch size. Mass at banding also affected survival in interaction with catch size as survival was reduced for light goslings in large catch size. This suggests that banding has a minor effect on post-banding survival of juvenile and virtually no effect on adults.

INTRODUCTION

Individual marking of large number of birds is a valuable tool for long-term population studies designed for research and management purposes. A method commonly used to capture ducks and especially geese is mass driving of flightless birds (e.g. Cooch 1953, Raveling 1977, Cooke and Sulzbach 1978, Lepage et al. 1998). Because the technique involves the capture of large numbers of individuals held in pens for several hours with minimal feeding opportunities, it could have a negative effect on the survival of birds after their release (Williams et al. 1993). Any negative effect on survival is likely to be more pronounced in young than in adults because of the lower body mass and smaller size of the former. We tested the effects of mass driving on the survival of juvenile Greater Snow Geese (*Chen caerulescens atlantica*) immediately after release in relation with the size of the catch, and gosling age and mass at banding.

METHODS

Study area and banding method

This study was conducted at the Greater Snow Goose colony on Bylot Island (73°N 80°W), Northwest Territories, Canada (see Hughes et al. 1994 for a description of the study area). From 1993 to 1996, goose families were captured during a one-week period in early August when the adults were moulting and before the juvenile could fly. Flocks of up to several hundred birds were rounded up with 3-4 people on the ground assisted by a helicopter. Flocks were driven by people to a large holding pen (7.3 m in diameter, 1.3 m high) made of flexible plastic netting. Goslings were then caught individually in the main holding pen and put into a separate pen to minimize the risk of trampling by adults. Birds were processed individually for banding and measurements (goslings first) and then put back into another separate pen. All birds were sexed by cloacal eversion and they received a metal US Fish and Wildlife Service band. Goslings were measured (culmen, head, tarsus and 9th primary length; Dzubin and Cooch 1992), weighed to the nearest 25 g with a spring scale in 1993 and 1994 or to the nearest gram with an electronic balance in 1995 and 1996. We also checked for the presence of web-tags, which were put on a sample of goslings during the hatching period (Lepage et al. 1998). At the end of the operation, we first released the juvenile, followed a few minutes later by the release of adults in the same direction taken by the juvenile. Bands of birds seriously injured (broken wings or legs; these birds were immediately killed) or found dead in the holding pens were recovered at release. A few days after banding, we checked all banding sites for the presence of dead geese: three people walked up to one hour from the banding site in the direction taken by the released birds, recording the number of all banded geese found dead. Fox dens known to be active in the area were also checked after banding.

Estimation of gosling age

Every year, goslings that had been web-tagged at hatch were captured and were thus of known age. We estimated the age of unmarked goslings from year-specific linear relationships between age of marked goslings and length of their 9th primary (see appendix B and Lepage et al. 1998 for details).

Data analysis

Let θ_j denote the probability that individual j coming from a sample of banded birds is found dead during or shortly after release. θ_j is the apparent post-banding mortality and is the product of two probabilities:

$$\theta_j = (1 - \phi_j)*p_j$$

where ϕ_j is the probability that a banded bird survives the banding and p_j is the probability of finding a bird if it dies. p_j could depend on the distance walked during the post-banding visit because it is reasonable to think that a bird in better condition could walk a longer distance before dying. However, most of the dead birds were found close to the banding sites. So, we assumed that p_j did not depend on physical condition. A test of the null hypothesis that θ_j was not related to an external variable, x_j (e.g. age and mass at banding, size of catch, banding year), therefore, tested whether ϕ_j (post-banding survival) was related to this external variable. We used the apparent post-banding survival $(1 - \theta_j)$ for the analysis.

As the dependent variable is binary (i.e. a banded juvenile is either found dead or not), we used logistic regression procedure to simultaneously evaluate the effect of several variables and their interactions on $(1 - \theta_j)$ (Cox 1970, Trexler and Travis 1993). We first built a general model with all variables (banding year, catch size, age and mass at banding) and their interactions. Interactions were then deleted, one at a time, from higher to lower levels, until only significant interactions remained. This procedure was repeated until we reached the simplest model which still fitted the data. At each step, the reduced model was compared with the previous model with a likelihood ratio test (LRT) and the Akaike's Information Criterion (AIC; Burnham et al. 1995). These analyses were performed with the LOGISTIC procedure of SAS (SAS Institute Inc. 1988).

RESULTS

During the four annual banding periods, a total of 6,577 adults and 6,736 juvenile were banded (Table 1). The average catch size was 446 birds (SE = 30) but varied considerably (range: 117 - 792; N = 30). The time required to band and measure all birds depended on the number of birds caught. For an average catch size, the time elapsed between birds entering the pens and their release was about 5 hours. During and after release, 192 juvenile and only 6 adults were found dead (Table 1). Because so few adults died during banding, we restricted subsequent analyses to the juvenile.

Low vegetation on Bylot Island facilitated detection of dead birds during the post-banding visits. Furthermore, most dead birds were found in the vicinity of the banding sites, which suggests that p_j, the probability that a dead juvenile was found, was very high in all years. We thus believe that the ratio of birds found dead to total banded birds gave a reliable estimation of the post-banding mortality. The apparent immediate post-banding survival for juvenile ($1 - \theta_j$) was high in all years, with an average at 0.971 (Table 1).

The general model, which included all variables and their interactions, fitted well the data (Hosmer and Lemeshow Goodness-of-Fit = 11.64, df = 8, P = 0.17). However, a reduced model was selected based on LRT and its AIC. The reduced model excluded interactions not significant in the general model (Table 2) and also fitted well the data (Hosmer and Lemeshow Goodness-of-Fit = 6.26, df = 8, P = 0.62). The post-banding survival of goslings increased with age in a non-linear fashion as survival was almost constant for goslings older than 35 days old (Fig. 1). However, the effect of age on survival varied with catch size and year.

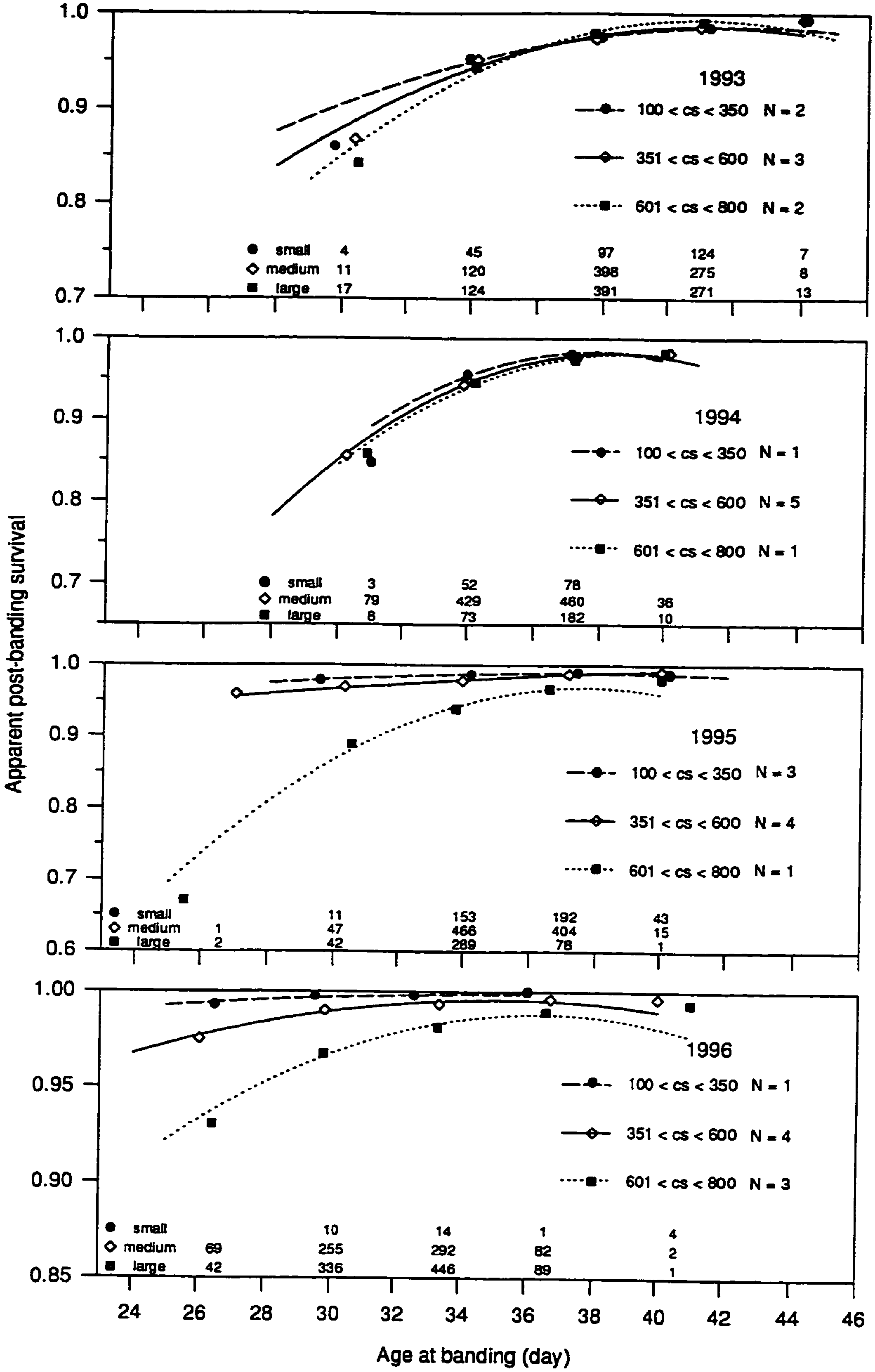
Table 1. Number of Greater Snow Geese banded at Bylot Island, found dead after banding and the apparent post-banding survival, 1993-1996.

Year	Adults		Juvenile		
	Banded	Found dead	Banded	Found dead	Apparent survival
1993	1244	2	1919	59	0.969
1994	1846	2	1412	47	0.967
1995	1590	0	1754	56	0.968
1996	1897	2	1651	30	0.982
Total	6577	6	6736	192	0.971

Table 2. Parameter coefficients of the reduced model estimating the apparent post-banding survival for juvenile Greater Snow Geese banded on Bylot Island.

Parameter	Estimates	SE	χ^2	df	*P*
Constant	-187.5	64.5	8.45	1	0.0036
Age at banding	5.185	1.900	7.45	1	0.0064
Mass at banding	0.008	0.001	32.3	1	0.0001
Catch size	-0.016	0.005	9.28	1	0.0023
Banding year	2.067	0.687	9.05	1	0.0026
Age*Catch size	7.78e-4	1.89e-4	16.9	1	0.0001
Age*Banding year	-0.060	0.020	8.67	1	0.0032
Mass*Catch size	8.52e-6	2.59e-6	10.8	1	0.0010

Fig. 1. Relationship between age at banding and apparent post-banding survival of juvenile Greater Snow Geese. To depict the interaction between age, catch size (cs) and year, the data were divided into three catch sizes (small, medium and large) and by cohorts (1993-96). The dots represent mean survival estimates on data grouped over 4-day intervals. Sample sizes of groups are given at the bottom of the graph. The lines show the predicted values calculated according to the logistic regression analysis.


Apparent post-banding survival
1993
—●— 100 < cs < 350 N = 2
—◇— 351 < cs < 600 N = 3
···■··· 601 < cs < 800 N = 2
● small 4 45 97 124 7
◇ medium 11 120 398 275 8
■ large 17 124 391 271 13
1.0
0.9
0.8
0.7
1994
—●— 100 < cs < 350 N = 1
—◇— 351 < cs < 600 N = 5
···■··· 601 < cs < 800 N = 1
● small 3 52 78
◇ medium 79 429 460 36
■ large 8 73 182 10
1.0
0.9
0.8
0.7
1995
—●— 100 < cs < 350 N = 3
—◇— 351 < cs < 600 N = 4
···■··· 601 < cs < 800 N = 1
● small 11 153 192 43
◇ medium 1 47 466 404 15
■ large 2 42 289 78 1
1.0
0.9
0.8
0.7
0.6
1996
—●— 100 < cs < 350 N = 1
—◇— 351 < cs < 600 N = 4
···■··· 601 < cs < 800 N = 3
● small 10 14 1 4
◇ medium 69 255 292 82 2
■ large 42 336 446 89 1
1.00
0.95
0.90
0.85
24
26
28
30
32
34
36
38
40
42
44
46
Age at banding (day)

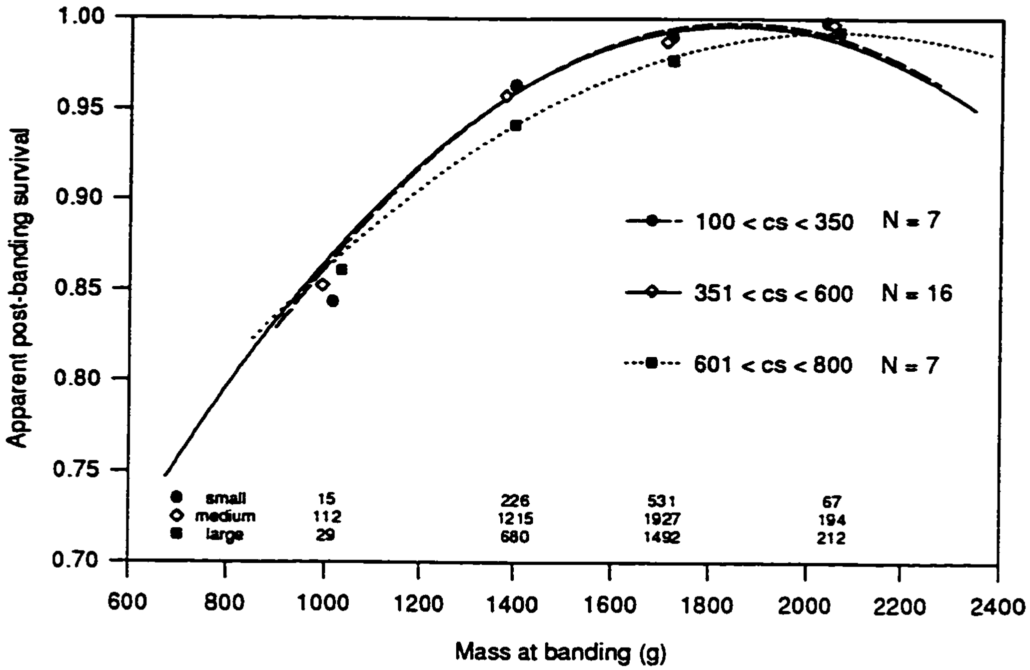


Fig. 2. Relationship between mass at banding and apparent post-banding survival of juvenile Greater Snow Geese (cohorts 1993-96 grouped). To depict the interaction between mass and catch size (cs), the data were divided into three groups of catch size (small, medium and large). The dots represent mean survival estimates on data grouped over 425 g intervals, in relation with mean mass of each group. Sample sizes of groups are given at the bottom of the graph. The lines show the predicted values calculated according to the logistic regression analysis.

Younger goslings had a lower survival in 1993 and especially in 1994 whereas survival was high and nearly constant in 1996. Survival tended to be lower in larger catches but only in some years (e.g. 1995 and 1996) and, again, only for younger goslings. Mass at banding also had a strong effect on survival. As with age, the effect was non-linear, with survival declining rapidly with mass below 1500 g (Fig. 2).

DISCUSSION

Our study suggests that mass-banding drives generally have a minor effect on post-banding survival of juvenile, and virtually no effect on adults. However, we cannot rule out entirely the possibility of birds dying at a greater distance than the one covered during the post-banding visits (especially for adults), which would tend to overestimate survival. This could happen, for example, if predation risk is increased by banding up to several hours or days after the release, because of either reduced physical condition or family break-up (Prevett and MacInnes 1980, Williams et al. 1993). When captured flocks were released, the reaction of some goslings was to stop and feed, whereas most of the adults left the banding site immediately. To facilitate reunification of families, we released goslings first and pushed them over some distance before releasing the adults, which then ran rapidly towards the goslings but usually slowed down upon joining them. The large area used by birds after banding and their tendency to disperse at that time (Hughes et al. 1994) precluded observing family reunification. Therefore, our results applied only to the immediate effects of banding.

Age and mass of goslings both affected the probability of mortality during banding. As these two variables are highly correlated in juvenile during this period (Lepage et al. 1998), it is not possible to separate specific effect of each one. Older and heavier juvenile survived better to this stressful period: above a threshold value of about 35 days and/or 1500 g, goslings were little affected by banding whereas below these values, mortality increased rapidly. Catch size also influenced post-banding survival: large catch sizes (> 600 birds) tended to increase mortality, but only in some years and affecting only younger goslings. Differences in magnitude among years could be explained partially by mean banding age and mass, weather, banding site conditions (dry vs. wet) and predation risk. A combination of these factors could increase the post-banding mortality. For example, in

1995, 36 of the 56 juvenile found dead (64%) originated from the biggest catch ever done (792 banded birds) during a cold, rainy day, at a muddy and wet site, and early in the banding period. In 1993, predation risk was presumably high because of the high fox density (three active fox dens were present in the study area at banding) and many bands were found at dens. In contrast to our study, Williams et al. (1993) showed that mass-banding caused significant increased mortality for juvenile Lesser Snow Geese (*Chen caerulescens caerulescens*) at La Pérouse Bay, at least from 1984 to 1991. However, this effect was explained by the long-term decline in gosling growth and body condition associated with habitat degradation, rather than to the banding procedure per se. Thus, Williams et al. (1993) concluded that this effect was a local phenomenon. No negative effect of banding on survival was found in a population of Black Brant (*Branta bernicla nigricans*; Sedinger et al. 1997).

It is also possible that the slight mortality induced by mass-banding drives is largely compensatory to natural mortality. We have shown that during the fall migration, mortality of juvenile Greater Snow Geese was positively correlated with their hatching date and mass (chapter 6). Young and/or light goslings that die immediately after banding may therefore be those individuals that would have been more likely to die during migration.

When properly done, mass-banding drives have virtually no effect on adults and only slight negative effect on survival of juvenile. Based on the results of our study, we should avoid to band goslings much younger than 35 days or much lighter than 1,500 g because mortality increases rapidly below these values. Large catch sizes (> 600) should also be avoided, especially when goslings are small or conditions are poor (rain and wet sites).

CHAPITRE 2

IS THERE A TRANSIENT EFFECT OF MARKING WITH NECK BANDS ON THE SURVIVAL OF ADULT GREATER SNOW GEESE?

RÉSUMÉ

Nous avons évalué si la capture initiale et la pose d'un collier avait un effet transitoire négatif sur la survie d'individus marqués chez la Grande Oie des neiges (*Chen caerulescens atlantica*). Entre 1990 et 1995, 2431 colliers ont été posés sur des femelles adultes pendant l'été à l'île Bylot (T.N.O., Canada). Les analyses ont été réalisées avec le logiciel SURGE à partir de 4234 réobservations de colliers obtenues pendant l'été dans l'Arctique, et le printemps et l'automne dans le sud du Québec. Malgré une concordance médiocre des données avec le modèle général de Cormack-Jolly-Seber, il a été possible d'identifier et de corriger les sources d'hétérogénéité dans l'ensemble des données. Les taux de réobservation étaient variables selon les saisons et les années (de <0.05 à 0.48) mais généralement assez élevés, permettant une bonne précision pour les estimés des taux de survie. Les taux de survie des individus nouvellement marqués ne différaient pas de ceux des anciennement marqués, indiquant l'absence d'effet transitoire du marquage et/ou du collier sur la survie des femelles adultes. Les taux de survie de l'automne et de l'hiver étaient similaires (0.93) et supérieurs à ceux de l'été (0.87). Rapportés sur une base mensuelle, le taux de survie était supérieur en hiver (0.99), intermédiaire à l'automne (0.97) et le plus bas pendant l'été (0.96).

ABSTRACT

We evaluated whether the initial capture and marking with a neck band had a transient negative effect on survival of Greater Snow Geese (*Chen caerulescens atlantica*). Between 1990 and 1995, we neck-banded 2,431 adult female snow geese during the summer on Bylot Island (N.W.T., Canada). The analyses were conducted with the software SURGE using 4,234 resightings of birds in the Arctic in summer, and in spring and fall in southern Québec. Although goodness-of-fit tests indicated that the data fitted poorly the Cormack-Jolly-Seber model, sources of heterogeneity could be identified and corrected. Resighting rates were variable among years and seasons (from <0.05 to 0.48) but were generally relatively high, enabling us to obtain good precision on survival rate estimates. The survival rates of newly marked birds did not differ from those of previously marked ones, indicating that there was no transient effect of marking and/or of the neck band on the survival of adult females. Fall and winter survival rates were similar (0.93) and were higher than summer survival rates (0.87). On a monthly basis, survival rate was highest for the winter period (0.99), intermediate for the fall migration period (0.97), and lowest for the summer period (0.96).

INTRODUCTION

It is reasonable to question whether the stress associated with the capture, handling and marking of an animal could negatively affect its survival over the first days or weeks following its release. In many instances, this effect could be transient and disappear once the animal recuperates from the stress of capture or becomes accustomed to wearing a marker. We have already shown that capture in mass-banding drives had a slight negative impact on the post-banding survival of goslings, especially the young ones or those with low body mass, but no apparent effect on adults (chapter 1). Use of neck bands is common in goose research (Rusch et al. 1985, Hestbeck and Malecki 1989, Raveling et al 1992, Schmutz et al 1994) and this is a fairly invasive technique because of the marker's size. Our objectives were to evaluate a possible transient effect of marking with a neck band on the survival of Greater Snow Geese (*Chen caerulescens atlantica*). We tested the hypothesis that survival was equal between previously marked birds and newly marked ones. A secondary objective was to examine seasonal variations in survival rates of adult females.

METHODS

Banding method and observations of neckbanded geese

From 1990 to 1995, goose families were captured annually on Bylot Island, NWT (73°08'N 80°00'W) (see description of the study area in Hughes et al. 1994) during a one-week period in early-August when the adults are molting and before the young could fly. Birds were classified as adults (> one year old) or young based upon plumage, and their sex was determined by cloacal eversion. Banding occurred after non-breeders (including yearlings), who molt earlier, had regained flight abilities. Therefore, virtually all adults captured were breeders and were at least two years old since snow geese do not breed as yearlings (Cooke at al. 1995). All birds received a metal US Fish and Wildlife Service band and some adult females (chosen randomly) received yellow neck bands with black, 4-digit alphanumeric codes. The neck bands were made of rigid single-wrap, thick (1.5 mm) plastic, 57 mm high (weight 20 g). They were glued with cyanoacrylic on a 25 mm wide overlapping area. Overall, 2,431 adult females received a neck band.

Observations of neckbanded geese were made throughout the year at several sites from fall 1990 to spring 1996. During the summer, geese were observed at our study area on Bylot Island. Recaptures of neckbanded geese during banding were included in the resighting data. Intensive observations were also made during 4-6 weeks in spring and fall along the St. Lawrence River (Québec, 47°N 72°W), the most important staging area during migration (see details in chapter 3). There was therefore 3 discrete periods of observations (spring, summer and fall) each year. A particularity of this design was that marking only occurred during the summer. Therefore, there were no newly marked birds during the spring and fall. On the basis of approximate midpoints of resighting periods, survival periods pertained to the following: fall migration = 13 August - 15 October, winter = 16 October - 5 May, summer = 6 May - 12 August. Because of uneven duration of periods, we calculated monthly survival estimates for each one to make estimates comparable among them.

Data analyses

Survival of adult females was estimated with neck band resighting data using Cormack-Jolly-Seber (CJS) capture-mark-recapture models (Cormack 1964, Jolly 1965, Seber 1965) and computer programs RELEASE (Burnham et al. 1987) and SURGE (Lebreton et al. 1992). Model notation follows Lebreton et al. (1992). The most general model tested included the effect of release following initial marking (r), season (s) and year (y) on both survival (ϕ) and resighting rates (p). In this model ($\phi_{r*s*y}\, p_{r*s*y}$), the survival and resighting rates of the newly marked birds are different from the survival and resighting rates of the previously marked ones during the first period (i.e. from summer to fall). The goodness-of-fit (GOF) of the data to the CJS model was assessed with RELEASE, which tests for permanent or temporary heterogeneity in resightings for each cohort. RELEASE generates 2 standard tests. Test 2 compares the subsequent capture histories of individuals known to be alive at time i, whether they were seen or not at time i. Test 3 compares the subsequent capture histories of individuals captured at time i, whether they were previously or newly marked at time i. A hierarchy of models sequentially constraining some parameters was fitted by the maximum likelihood method using SURGE. To determine the most parsimonious list of parameters needed to model the data, the significance of various effects was tested by likelihood ratio tests (LRT) and the best model was selected with the Akaike's (1973) information criterion (AIC). LRT are χ^2 tests based on differences in deviance (DEV) between models. Use of this test requires that one of the models is a special case of (i.e. nested within) the more general model. This enabled us to test specific hypotheses such as equality of survival between newly banded and previously banded birds. AIC is defined as AIC = DEV + 2*np*, where *np* is the number of separately estimable parameters in the model. The model with the smallest AIC value is selected (Lebreton et al. 1992, Burnham et al. 1995). This search for parsimonious models enhances the robustness of the conclusions, keeping only important (i.e. significant) parameters to describe the data, and providing precise estimates of those parameters.

RESULTS

Preliminary tests

The results of the GOF tests (obtained with RELEASE) indicated heterogeneity within groups with sparse data, especially for Test 2 (Table 1). Even when the component C_{92} of Test 2 (the one with the highest chi-square value - see below for details) was omitted, the GOF still showed heterogeneity, therefore rejecting the CJS model. The first marked cohort was deleted because of small sample size. Restricting the analysis to capture years 1991-1995 resulted in acceptance of the CJS model by Test 2 if the component $2.Ct_{92}$ was omitted (Table 2). The test $2.Ct_{92}$ indicated a strong heterogeneity during the fall 1992 observation period between birds newly marked in summer 1992 ("seen in summer 1992") and previously marked birds ("not seen in summer 1992"): the newly marked birds were more likely to be observed during fall 1992 than the previously marked ones (Table 3). This heterogeneity can be controlled by using different resighting parameters for the 1992 cohort and the other ones during the fall period. This suggests that the general model ($\phi_{r\cdot s\cdot y}p_{r\cdot s\cdot y}$), where all the fall resighting parameters are different between newly marked birds and previously marked ones, could be reduced to a model with different fall resighting parameters only for 1992. This reduced model is noted ($\phi_{r\cdot s\cdot t}p_{r92,s\cdot y}$).

Table 1. Goodness-of-fit tests of the Cormack-Jolly-Seber model for neckbanded Greater Snow Goose resightings data by cohort, for capture years 1991 to 1995 (output from program RELEASE).

	Test 3.SR			Test 3.Sm			Test 2		
Year	$\chi2$	df	*P*	$\chi2$	df	*P*	$\chi2$	df	*P*
1991	-	-	- *	-	-	- *	16.75	8	0.03
1992	-	-	- *	-	-	- *	32.67	9	0.00
1993	0.003	1	0.96	0.96	1	0.33	8.08	7	0.33
1994	4.47	1	0.03	1.30	1	0.25	2.45	4	0.65
1995	7.97	1	0.00	0.09	1	0.77	0.06	1	0.81
Total	12.44	3	0.01	2.35	3	0.50	60.01	29	0.00
Test 3	14.79	6	0.02						
Test 2+3	74.79	35	0.00						

* = insufficient data for valid test

Table 2. Goodness-of-fit tests of the Cormack-Jolly-Seber model for neckbanded Greater Snow Goose resightings data by cohort, for capture years 1991 to 1995 (output from program RELEASE).

Test 2

	Test 2.Ct			Test 2.Cm		
Year	$\chi2$	df	*P*	$\chi2$	df	*P*
1992	12.58	1	0.00	9.71	8	0.29
1993	0.10	1	0.75	7.97	6	0.24
1994	0.04	1	0.85	3.39	3	0.33
1995	0.00	1	0.96	-	-	-
Total	12.72	4	0.01	20.97	17	0.23
Total without $2.Ct_{92}$	0.14	3	0.99			
Test 2	33.70	21	0.04			
Test 2 without $2.Ct_{92}$	21.11	20	0.39			

Test 3

	Test 3.SR			Test 3.Sm		
Year	$\chi2$	df	*P*	$\chi2$	df	*P*
1992	-	-	- *	-	-	- *
1993	0.13	1	0.72	-	-	- *
1994	2.02	1	0.15	1.71	2	0.42
1995	7.87	1	0.01	0.07	1	0.79
Total	10.01	3	0.02	1.78	3	0.62
Test 3	12.79	6	0.07			

* = insufficient data for valid test

Test 2 + 3

	$\chi2$	df	*P*
Test 2 + 3	46.31	28	0.02
Test 2 + 3 without $2.Ct_{92}$	32.73	27	0.17

Table 3. Data for Test $2.\mathrm{Ct}_{92}$ of neckbanded Greater Snow Goose resightings for the fall 1992 (output from program RELEASE).

		Next seen at		
		Fall 1992	After fall 1992	Total
Not seen in summer 1992	Observed	50	95	145
	Expected	66.3	78.7	
Seen in summer 1992 (observed and marked birds)	Observed	110	95	205
	Expected	93.7	111.3	
Total		160	190	350

Table 4. Modeling of the resighting and survival rates of neckbanded Greater Snow Geese with SURGE. For each model, we give the number of identifiable parameters (*np*), deviance (DEV) and the Akaike Information Criterion (AIC). Boldface denotes the AIC value for the selected model.

Model	*np*	DEV	AIC	Tests between models
(1) ($\phi_{r*s*y}\,p_{r*s*y}$)	34	12295	12363	
(2) ($\phi_{r*s*y}\,p_{r92,\,s*y}$)	31	12295	12357	Effect of release on resighting rate (except 1992 cohort) (2) vs. (1): $\chi^2_3 = 0.26, P = 0.97$
(3) ($\phi_{r*s*y}\,p_{s*y}$)	30	12308	12368	Effect of release of 1992 cohort on resighting rate (3) vs. (2): $\chi^2_1 = 12.57, P = 0.00$
(4) ($\phi_{r*s*y}\,p_{r92,\,s-y}$)	21	12322	12366	Linear temporal trend of seasonal resighting rates (4) vs. (2): $\chi^2_{10} = 27, P = 0.00$
(5) ($\phi_{s*y}\,p_{r92,\,s*y}$)	27	12302	12356	Effect of release on survival rate (5) vs. (2): $\chi^2_4 = 6.89, P = 0.14$
(6) ($\phi_{s*y'}\,p_{r92,\,s*y}$)	20	12312	12352	Effect of year on fall and winter survival rate (6) vs. (5): $\chi^2_7 = 9.61, P = 0.21$
(7) ($\phi_{s'*y'}\,p_{r92,\,s*y}$)	19	12313	**12351**	Effect of season on fall and winter survival rate (7) vs. (6): $\chi^2_1 = 1.61, P = 0.20$
(8) ($\phi_{s'}\,p_{r92,\,s*y}$)	17	12321	12355	Effect of year on summer survival rate (8) vs. (7): $\chi^2_2 = 9.97, P = 0.00$

The test 3.SR for the year 1995 indicated that fewer birds marked prior to the summer 1995 were ever resighted afterwards (i.e. during the fall 1995 and the spring 1996) than birds marked during the summer 1995 (Table 2). This could be due to a different survival rate between these two groups. For birds seen again after the summer 1995, there was no difference between the two groups in their resighting pattern (component 3.Sm_{95} not significant). This indicated that if a difference in survival existed, it was more likely to occur between the summer and the fall periods. This possible difference is tested under the general model, ($\phi_{r*s*y} p_{r*s*y}$). Overall, Test 3 was not significant.

Model testing

The structure of the model by itself determines the maximum number of parameters which may be potentially estimated. All parameters may not always be identifiable, either because of the sparseness of the data or other structural problems. A close examination of the results under the various models tested indicated that the summer survival of 1992 was not identifiable, likely because of very few observations during that summer (p_{92} = 0.004 (SE = 0.004)). Therefore, this parameter was not included in *np*. Our most general model had 34 parameters.

We started by reducing as much as possible the number of parameters associated with the resighting rates, in order to keep maximum power for the tests involving the survival rates (Table 4). The fall resighting rates of newly released birds did not differ from the ones of other birds for all cohorts except the 1992 cohort (as outlined by the test 2 of RELEASE). The fall 1992 resighting rate of the 1992 cohort (the newly marked birds) was 0.39 (0.03), compared to 0.26 (SE = 0.03) for the previously marked ones. The year effect on the resighting rate was clearly significant: *p* ranged from 0.07 to 0.40 in spring, from 0.16 to 0.48 in fall and was less than 0.05 in summer (Fig. 1). There was an apparent increasing trend for resighting rates over the years but models with linear trends for seasonal resighting rates were rejected.

There was no effect of the release on the survival rate: the newly marked birds had the same fall migration survival as those previously marked. There was also no annual variation in fall migration and winter survival rates, although the summer survival rates were year-specific. The hypothesis of equality of survival between the fall and winter seasons was supported although the hypothesis of equality of survival rate between summer and the other seasons was rejected. Therefore, the best reduced model was $(\phi_{s'*y}, p_{t92, s*y})$.

According to the selected model, the fall migration and winter survival was estimated at 0.93 (SE = 0.01), compared to a mean summer survival of 0.87 (0.10). Monthly survival rate was highest for the winter period, intermediate for the fall migration period, and lowest for the summer period (Table 5). The composite annual survival rate (product of the seasonal rates), taking into account the neck band retention rate (estimated at 0.97 (0.01) in this population; see chapter 3 for details), was 0.77 (0.09). Because of the very high retention rate and the relatively short duration of the periods, seasonal survival rates were not corrected for the neck band retention rate.

Table 5. Estimates of seasonal and monthly survival for adult female Greater Snow Geese, 1991-1996. Fall migration = 13 August - 15 October, winter = 16 October - 5 May, summer = 6 May - 12 August.

		Seasonal survival		Monthly survival	
Season	Year	ϕ	SE	ϕ	SE
Fall migration	1991-95	0.93	0.01	0.97	0.01
Winter	1992-96	0.93	0.01	0.99	0.01
Summer[a]	1993	0.79	0.05	0.93	0.11
	1994	0.96	0.04	0.99	0.08
	1995	0.87	0.04	0.96	0.08
	mean	0.87	0.10	0.96	0.06

a: Summer survival was not identifiable in 1992 because of sparse data.

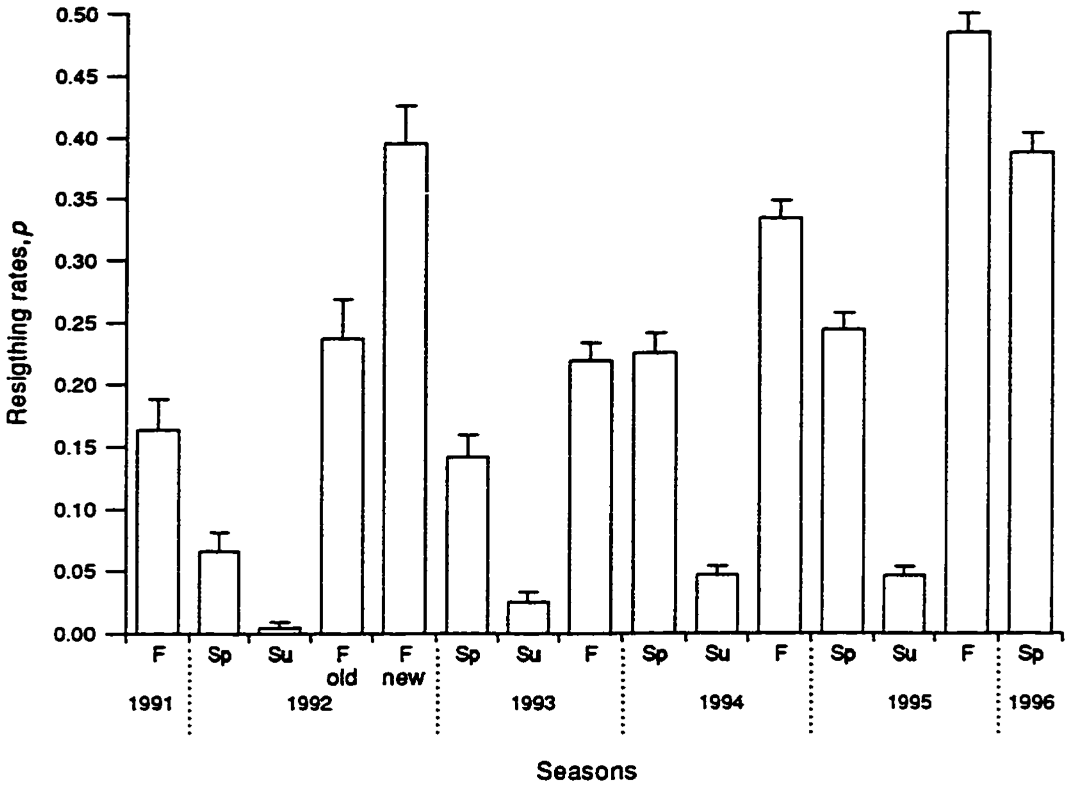


Fig. 1. Seasonal resighting rates (mean + SE) of neckbanded Greater Snow Geese, from fall 1991 to spring 1996, under the model $(\phi_{s*y}, p_{t92,s*y})$.
F: fall; Sp: spring; Su: summer.
F old: fall resighting rate of the birds marked before 1992.
F new: fall resighting rate of the birds marked in 1992.

DISCUSSION

Initial effect of marking

The survival rate of newly marked birds was not different from that of previously marked ones. We therefore concluded that there was no initial effect of marking and/or of neck band on the survival of adult female Greater Snow Geese after banding on Bylot Island. Furthermore, less than 0.2% of neckbanded adults were found dead during surveys of banding sites done immediately after banding (chapter 1). This result is also supported by behavioral observations made after the banding period on Bylot Island and during the fall on the staging areas. Although geese tried to back out of their neckband of frantically preened them immediately after marking, afterwards, neckbanded geese did not seem to be affected by the neck band as they fed, preened, rested and interacted with other geese (marked or not) like other birds.

Resighting rates

The resighting rates were moderate to high for the spring and fall samples, leading to a fairly good precision of the survival estimates. Resighting rates were quite variable among seasons and years, mostly because of variable observation efforts (spring and fall) and difficulty of access to the birds (summer). For the fall of 1992, the newly marked birds were resighted much more often than the previously marked ones. This heterogeneity is probably the result of a large difference in breeding success between the two groups. The summer of 1992 was characterized by poor weather on the breeding grounds, causing a nearly complete breeding failure (5.4% of young in the fall population; Reed at al. 1998). Nevertheless, because of the selective banding procedure (see methods), newly banded geese in 1992 were largely successful breeders, in contrast to the rest of the population, including previously marked birds. In the fall staging areas, Maisonneuve and Bédard (1992) reported that the length of the stopover by Greater Snow Geese depended on the breeding status, adults with young staying longer than those without young. This could explain why the probability of resighting a bird marked during the summer of 1992 was higher than for previously marked ones that fall. In contrast, the very low resighting rate of previously marked birds for that summer was likely a consequence of geese dispersing away from the study area following their failed breeding attempt. Nevertheless, this precluded the estimation of only one survival rate.

Seasonal estimates of survival rate

Fall migration and winter survival rates did not differ and showed no sign of annual variation, in contrast to the summer survival rates. A higher survival rate during winter (when most of the hunting takes place) than during summer is surprising and, although the differences were small, is contrary to expectations. Indeed, most studies have suggested that hunting is the most important source of mortality of adult geese and this occurs mainly during fall and winter (Owen and Black 1989, Francis et al. 1992b, Rexstad 1992, Hestbeck 1994). Few studies, however, have been able to partition survival on a seasonal basis. Schmutz et al. (1994) estimated survival rates on a seasonal basis in the Emperor Goose (*Chen canagica*) and found lower survival during winter even though harvest was higher in summer than in winter in that population. Seasonal survival of adult Pacific Brant (*Branta bernicla nigricans*) was lowest in late spring migration subsistence harvest occurred on the breeding grounds, and highest in winter when sport harvest occurred (Ward et al. 1997).

The low survival rate of females during summer could be a consequence of predation by arctic foxes (*Alopex lagopus*) on incubating females, a period of high vulnerability. In some years, fox activity at goose colonies can be high on Bylot Island (Tremblay et al. 1997). Alternatively, some emigration could occur during the summer, reducing the survival rate estimate. The area surveyed was relatively small compared to the total area used by nesting females on Bylot Island, the fidelity to the breeding sites is low in this population (Lepage et al 1996) and home range during brood rearing is large (Hughes et al. 1994). This also explains why summer resighting probabilities are fairly low. The summer survival estimate could therefore be underestimated. The sparseness of the summer resightings data also calls for caution in the interpretation of differences in seasonal survival rates. In contrast to the summer period, the fall and spring resightings should be less affected by emigration because staging geese use a small, easily accessible area in southern Québec where temporal and spatial mixing of individuals is considerable (Maisonneuve and Bédard 1993). However, some heterogeneity among individuals in lengths of stay on the staging areas during fall could also bias the fall migration survival estimate (Appendix D).

CHAPITRE 3

EFFECT OF NECK BANDS ON THE SURVIVAL OF ADULT FEMALE GREATER SNOW GEESE

RÉSUMÉ

Le marquage par des colliers est répandu pour l'étude des populations sauvages d'oies, mais son effet sur la survie a rarement été mesuré. Nous avons testé l'effet potentiellement négatif du collier sur la survie annuelle de femelles adultes de la Grande Oie des neiges (*Chen caerulescens atlantica*) en utilisant, pour la même population marquée pendant l'été à l'île Bylot (T.N.O., Canada), les retours de bagues, les réobservations de colliers et les recaptures durant le baguage. Les retours de bagues, analysées avec le logiciel SURVIV, ont permis de tester directement l'égalité de survie entre les 2 groupes d'individus marqués (uniquement avec bague ou avec bague et collier). Selon la façon de modéliser les probabilités de récupération, le résultat était divergent. Dans un cas, la survie des oiseaux marqués uniquement avec bague étaient significativement supérieure (S = 0.77) à celle des oiseaux marqués avec un collier (S = 0.58). Dans l'autre cas, la survie des deux groupes était identique (S = 0.82). Les réobservations de colliers ont été analysées avec le logiciel JOLLY, qui ne permet une estimation de la survie que pour les femelles à collier. La survie annuelle moyenne a été estimée à 0.83. Cette estimation indépendante des précédentes suggère que le collier n'a pas d'effet sur la survie. Enfin, les recaptures pendant le baguage ne donnent qu'une survie apparente, puisque les probabilités de survie et de recapture n'ont pas pu être séparées à cause d'un nombre trop faible de recaptures. Les taux de recapture étaient significativement plus faibles pour les oiseaux à collier (4.6% vs. 12.1%). Si la survie entre les 2 groupes est similaire, cela suggère que la propension à nicher des femelles à collier est plus faible et/ou que leur taux d'émigration permanente en dehors de la région de marquage est plus élevé, à cause d'un effet du marquage en lui-même ("trap-shyness"). En conclusion, les colliers posés sur les oies ne semblent pas avoir d'effet sur leur survie, mais pourraient éventuellement affecter d'autres paramètres démographiques.

ABSTRACT

Neck bands are widely used as a marker in goose research. However, few studies have investigated a possible negative effect on survival of this marker. We tested the effect of neck bands on the annual survival of adult female Greater Snow Geese (*Chen caerulescens atlantica*) marked on Bylot Island (N.W.T., Canada) using legband recoveries in fall and winter, neckband resightings in spring and fall and recaptures during summer banding. Band recoveries were analysed with program SURVIV which allowed a direct test of equality of survival between legbanded only birds and leg- and neckbanded ones. Depending on the modeling of the recovery probabilities, results were not convergent. In one case, survival of legbanded birds was significantly higher ($S = 0.77$) than survival of neckbanded ones ($S = 0.58$). In the other case, survival was similar for the 2 groups ($S = 0.82$). With resighting data, only the survival of neckbanded birds could be estimated, using program JOLLY. Mean annual survival was estimated at 0.83. This estimation independent from the preceding ones suggests that neckbands have no effect on survival. Recaptures during banding drives yielded only apparent survival, as the survival and recapture probabilities could not be separated due to small sample sizes. Recapture rates were significantly lower for neckbanded birds than legbanded ones (4.6% vs. 12.1%). If survival between these 2 groups is similar, this suggests that breeding propensity of neckbanded birds is lower and/or that their rate of permanent emigration from the banding areas is higher due a handling effect ("trap-shyness"). We conclude that neck bands seem not to have an effect on survival of Greater Snow Geese, but could possibly affect other demographic traits.

INTRODUCTION

The use of neck bands in goose research has become common in North America (Rusch et al. 1985, Hestbeck and Malecki 1989, Raveling et al. 1992, Schmutz et al. 1994) to: (1) study the distribution and movements of geese, (2) estimate annual or seasonal survival rates, (3) determine population size, (4) conduct behavioral observations. Because a neckbanded individual can be resighted several times, more information can be gathered on known individuals. This leads to improved precision in the survival rate estimates compared to those obtained with leg band recoveries.

However, neck bands, like any other markers, could negatively affect behavior and/or survival of geese. Direct mortality can be caused by accumulation of ice on neck bands in winter (see Ballou and Martin 1964, MacInnes 1966, Greenwood and Blair 1974, Craven 1979, Zicus et al. 1983) and through starvation (Ankney 1975 but see Raveling 1976). Neck bands have also been shown to increase recovery rates (Samuel et al. 1990). Increased recovery rates could result from selective harvesting of neckbanded geese by hunters or from a higher reporting rate of neckbanded geese compared to legbanded ones.

A negative effect of neck bands on the survival of marked individuals is potentially a serious problem because estimates obtained from marked populations are often extrapolated to the entire population. To obtain unbiased estimates, the marking techniques and the markers must have a negligible impact on the behavior and survival of the marked individuals. There have been at least three evaluations of the effects of neck bands on goose survival. Samuel et al. (1990) found a lower survival rates for immature neckbanded Canada Geese (*Branta canadensis*) compared to legbanded birds but only in 2 of 6 years. Another study with Canada Geese (Castelli and Trost 1996) also concluded that, over a 5-year period, survival of neckbanded birds was lower compared to legbanded only ones. Alisauskas (1996) reached a similar conclusion based on recaptures of Canada Geese and White-Fronted Geese (*Anser albifrons*) on their breeding grounds: neck bands appeared to have a strong negative influence for survival for Canada geese but a weaker one in white-fronted geese.

Our objective was to evaluate possible long-term effects of neck bands on survival of Greater Snow Geese (*Chen caerulescens atlantica*) banded in the Canadian Arctic. In a previous analysis, we showed that there was no transient negative effect of marking on survival of newly neckbanded geese (chapter 2, Gauthier and Menu 1997). In this paper, we estimated survival rates with two independent methods for the same marked populations and during the same period, using band recoveries of neckbanded and legbanded birds (incomplete registration of deaths) and multiple resightings of neckbanded birds only (incomplete registration of survivors). A third method, recapture rate on the breeding grounds of the two categories of marked birds (neckbanded and legbanded), provided an estimate of "apparent" survival rate.

METHODS

Banding method and recoveries

This study is part of a long-term banding program of Greater Snow Geese started in 1990. The study area is located in a glacial valley on Bylot Island, NWT (73°N 80°W) (see description in Hughes et al. 1994). Bylot Island is the largest breeding colony of Greater Snow Geese (Reed et al. 1992). From 1990 to 1995, goose families were captured annually for banding during a 7-day period in early-August when the adults were molting and before the young could fly. Birds were classified as adults (> one year old) or young based upon plumage, and their sex was determined by cloacal eversion. Banding occurred after non-breeders (including yearlings), who molt earlier, had regained flight abilities. Therefore, virtually all adults captured were breeders and were at least two years old since snow geese do not breed as yearlings (Cooke et al. 1995). All birds received a metal US Fish and Wildlife Service band and some adult females (chosen randomly) received neck bands. The neck bands were made of rigid single-wrap, thick (1.5 mm) plastic, 57 mm high (weight 20 g). They were glued with cyanoacrylic on a 25 mm wide overlapping area. The neck bands were yellow with black, 4-digit alphanumeric codes (2 letters and 2 numbers). Overall, 3,538 adult females were legbanded, of which 2,431 also received a neck band, and 4,123 young females were leg-banded (Table 1). All recaptures of banded birds in subsequent years were recorded and the presence or absence of a neck band noted.

Recoveries occurred during the fall and winter hunting season in southern Québec and the eastern United States of America, and came from the Bird Banding Laboratory. In the upper estuary of the Saint Lawrence river (Québec, 47°N 72°W), outfitters were also solicited by letters or personal contact to report bands directly to us. We used recoveries for the period 1990 to 1994 (Table 1).

Observation of neckbanded geese

Observation of neckbanded geese were made throughout the year at several sites from 1990 to 1996 (Fig. 1 and appendix E). During the summer, geese were observed at our study area on Bylot Island. Recaptures of neckbanded geese during the banding drives were also included in the resighting data. Intensive observations were made at the most important staging area in the fall, the upper estuary of the St. Lawrence river (Québec, 47°N 72°W), from the end of September to the beginning of November. Depending on the year, from one to 4 people made daily observations at the sites most heavily used by geese (Cap Tourmente National Wildlife Area on the north shore of the river, Iles-aux-Grues/Iles-aux-Oies islands, and bird sanctuaries scattered on the south shore between Québec City and La Pocatière). Fall observations took place during the hunting season. A small number of winter observations were reported to us by regular observers in the Lake Champlain area (New York and Vermont) in November and December, and along the Atlantic coast (New Jersey to North Carolina) from November to March. Intensive observations were again made during the spring (15 March-25 May) when the geese staged along the St. Lawrence river, from Lac St. Pierre to Isle Verte. From 1991 to 1993, spring resightings came mostly from reliable birdwatchers but afterwards, observations were made primarily by our team.

Table 1. Banding and recovery matrix of female Greater Snow Geese banded on Bylot Island (N.W.T) from 1990 to 1995.

				Recoveries						
Age	Collar	Year	No. banded	1990	1991	1992	1993	1994	1995	Total
Adult	No	1990	65	2	1	2	4	1	0	**10**
		1991	126		2	3	3	0	2	**10**
		1992	249			10	1	4	3	**18**
		1993	103				6	1	0	**7**
		1994	395					6	4	**10**
		1995	169						5	**5**
		Total	**1107**	**2**	**3**	**15**	**14**	**12**	**14**	**60**
Adult	Yes	1990	108	12	7	4	1	0	1	**27**
		1991	262		13	12	5	2	3	**35**
		1992	303			27	6	1	0	**34**
		1993	525				19	10	12	**41**
		1994	527					22	7	**29**
		1995	686						30	**30**
		Total	**2431**	**14**	**20**	**43**	**31**	**35**	**53**	**196**
Young	No	1990	191	12	3	4	1	1	0	**21**
		1991	550		40	5	4	1	1	**51**
		1992	416			34	4	0	0	**38**
		1993	929				84	16	2	**102**
		1994	911					26	5	**31**
		1995	1126						68	**68**
		Total	**4123**	**12**	**43**	**43**	**93**	**44**	**76**	**311**
Adults + young		Total	**7661**	**28**	**66**	**101**	**138**	**91**	**143**	**567**

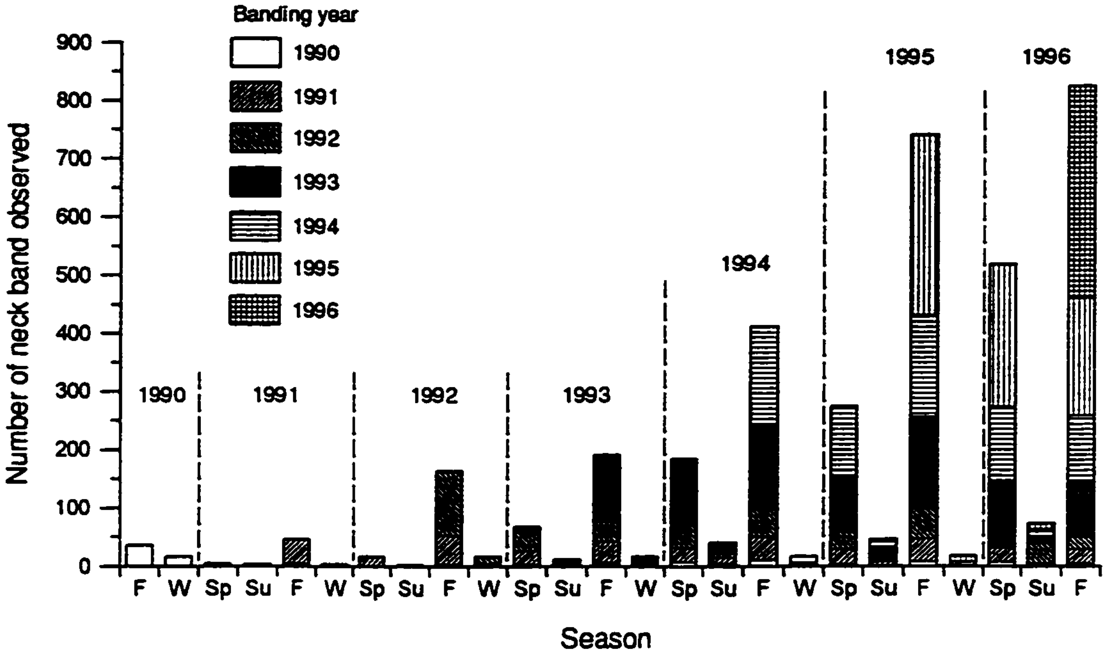


Fig. 1. Observations of neckbanded geese by year of banding, from fall 1990 to fall 1996.
F: fall; W: winter; Sp: spring; Su: summer.

Data analyses

Band recovery analyses were conducted following the procedures of Brownie et al. (1985) using the computer program SURVIV (White 1983). The most general model tested included the effect of age (a; two age classes: young and adults), presence of a neck band (n; adult females with or without neck band) and time (t) on both survival and recovery rates. Newly-banded adult females were not a random sample of the population because most of them were successful breeders, i.e. they had young with them. To account for that in the general model, the recovery rates of newly marked adults (direct recovery rate, f^*) were set different from the ones of previously banded birds (indirect recovery rate, f), both for each group of adult females (legbanded only and neckbanded). Previous analyses showed that the survival rate of newly neckbanded adult females did not differ from that of previously banded birds (chapter 2, Gauthier and Menu 1997). After their first year, the recovery and survival rates of females banded as young were assumed to be the same as those of adults without neck band.

A hierarchy of models sequentially constraining some parameters was tested to determine the most parsimonious list of parameters needed to model the data. Apart from the effect of neck bands on survival, we were interested to test for differences in recovery rates between and within groups (legbanded only and neckbanded adults). Likelihood ratio tests (Brownie et al. 1985) between models and the Akaike Information Criterion (AIC; Burnham et al. 1995) were used to select the best model among subsets of the general one.

For resighting data, we estimated survival and resighting rates using Cormack-Jolly-Seber mark-recapture models (Cormack 1964, Jolly 1965, Seber 1965) and program JOLLY (Pollock et al. 1990). The largest number of observations per season came from the fall and spring samples in southern Québec (Fig. 1). We estimated survival of neckbanded geese from spring to spring, rather than fall to fall, to avoid any potential biases related to the hunting mortality occurring during the fall observation period. We used the first resighting of an individual as its time of marking. The model AX of JOLLY (survival and resighting rates are time-dependent) was used. A particularity of this model is to include resightings made between the spring sampling periods (i.e. during the summer, fall and winter; Pollock et al. 1990). For example, a bird could not be seen in sample i, resighted after this period but not seen in the next sample ($i+1$). A bird seen only during the inter-sampling period (between i and $i+1$) is thus known to be alive at i. Inclusion of these observations improves the estimation of survival.

We estimated neck band retention rate with geese recaptured during banding every year. We used program SURVIV to estimate annual probabilities of retaining a neck band, θ_j , k years after initial banding. Annual retention probability (θ_j) is defined as the probability that a bird that is alive and still has its neck band at time k, will retain its neck band from k to $k+1$ given that the bird also survives. The expected number of recaptured geese with neck bands (T_k) among geese recaptured i years after banding (N_k) is estimated by the general model:

$$E[T_k] = N_k \prod_{j=1}^{k} \theta_j$$

where θ_j is the annual neck band retention rate for the jth year. We modeled annual probability of neck band retention as a function of its age rather than as a function of calendar year because we believed that the principal cause of neck band loss was ageing of the plastic. We also used a reduced-parameter model in which annual retention rate was considered to be constant regardless of the number of years since banding, and likelihood-ratio tests to compare the most general model with the reduced-parameter one. Survival rates based on resighting data were then corrected for the neck band retention rate (Hestbeck et al. 1990).

Among birds recaptured during banding drives, we compared raw recapture rates of legbanded only versus neckbanded adult females by year of banding using 2-way contingency table analysis. Recapture rate was too low to estimate separately survival and recapture rates in a CJS model with this data set alone.

RESULTS

Recovery data

The most general model (Snat $f$nat f^*nt) fitted the data though not very well based on the Goodness-of-Fit (Fig. 2). From this model, two strategies were possible for testing the hypothesis of equality of direct (f^*) and indirect recovery rates (f) in adult females: between the two groups of females (legbanded only, lb vs. neckbanded, nb) or within each group. Depending on the strategy of modelisation used, results were not convergent (Fig. 2). With the between-groups strategy, we tested the hypothesis of equal direct recovery rates (H0: $f^*_{nb} = f^*_{lb}$) and equal indirect recovery rates (H0: $f_{lb} = f_{nb}$). The hypothesis of equal direct recovery rates was strongly rejected ($P = 0.002$), indicating that neckbanded geese had a higher direct recovery rates than legbanded ones. However, the hypothesis of equal indirect recovery rate hypothesis was not rejected ($P = 0.29$). Thus, indirect recovery rates were set similar between legbanded and neckbanded females (model (Snat $f$at f^*nt)). The hypothesis of equality between direct recovery rates of legbanded only adults and indirect recovery rates was also accepted ($P = 0.66$), leaving a different direct recovery rate only for the neckbanded birds (model (Snat $f$at f^{*n}t)). Other attempts to further reduce the number of parameters associated with recovery rate failed. From this model, we then tested effects on survival rates. The effect of time on the adult survival rates was not significant but was significant for young. Finally, the effect of neck bands on survival was not significant (P = 0.81, model (Sat' $f$at f^{*n}t), AIC = 219). This model fitted the data well and had the lowest AIC (Fig. 2) and was thus selected. It yielded a constant annual survival rate of 0.82 (SE = 0.09) for legbanded and neckbanded adult females. Survival rates of young were about half of the adults but varied among years and were poorly estimated for 1994 (Table 2). Recovery rates of adults were about half of the values in young (0.032 vs. 0.067 on average, respectively) except for direct recovery rates of neckbanded females (0.065) which were twice as high as in legbanded females.

The within-groups modeling strategy started with the same general model (model (Snat $f$nat f^*nt)) but first tested the hypothesis of equal direct and indirect recovery rates (H0: $f = f^*$) within legbanded and neckbanded birds (Fig. 2). This hypothesis was not rejected ($P = 0.78$), indicating no difference between the direct and indirect recovery rates within each group. We then tested the hypothesis of equal recovery rates between legbanded and neckbanded females (this test was different from previously because direct and indirect recovery rates were here set equal in each group). This hypothesis was strongly rejected (P = 0.0003), leaving recovery rates specific for each group. The effect of time on the recovery rate was not significant for the legbanded females ($P = 0.18$) but was significant in neckbanded ones ($P = 0.005$). So we used model (Snat $f$nat$'^{n}$) (Fig. 2) as a new starting point for modeling survival rates. As with the between-group modeling, the effect of time on adult survival rates was not significant but was significant for young. The effect of neck bands was strongly significant ($P < 0.001$). Therefore, the selected model was (*S*nat' *f*nat'^{n}), based on its lowest AIC (219). According to this model, annual survival of legbanded adult females was 0.77 (0.10) compared to only 0.58 (0.07) for neckbanded ones. Under this model, recovery rates of neckbanded birds were similar to their direct recovery rates estimated by model (*S*at' *f*at *f*^{*n}t) (Table 2 vs. Table 3) and were more than twice as high as recovery rate of legbanded birds (0.067 vs. 0.027 on average). Recovery rates of neckbanded geese also tended to decrease over time.

Resighting data

Survival estimated from resighting data is critically dependent on the retention rate of neck bands. Overall, 111 adult females which originally received a neck band were recaptured during banding on Bylot Island up to 6 years after the initial banding. Only 7 geese had lost their neck band at the time of the recapture (Fig. 3). The model with a constant retention rate (AIC = 16.4) was selected against the model with an age-dependent retention rate (AIC = 25.0). The annual probability of retaining a neck band was 0.97 (SE = 0.01), a rather high value.

The spring to spring estimation of survival rate was based on the observation of 1,426 neck bands. The model AX of JOLLY fitted well the data ($\chi^2 = 1.68$, df = 7, $P = 0.97$; data of 1990 were excluded because of too few resightings that year). When corrected for neck band loss, the average annual survival rate of adult females with neck bands was 0.83 (0.06), and the average resighting rate was 0.27 (0.05; Table 4).

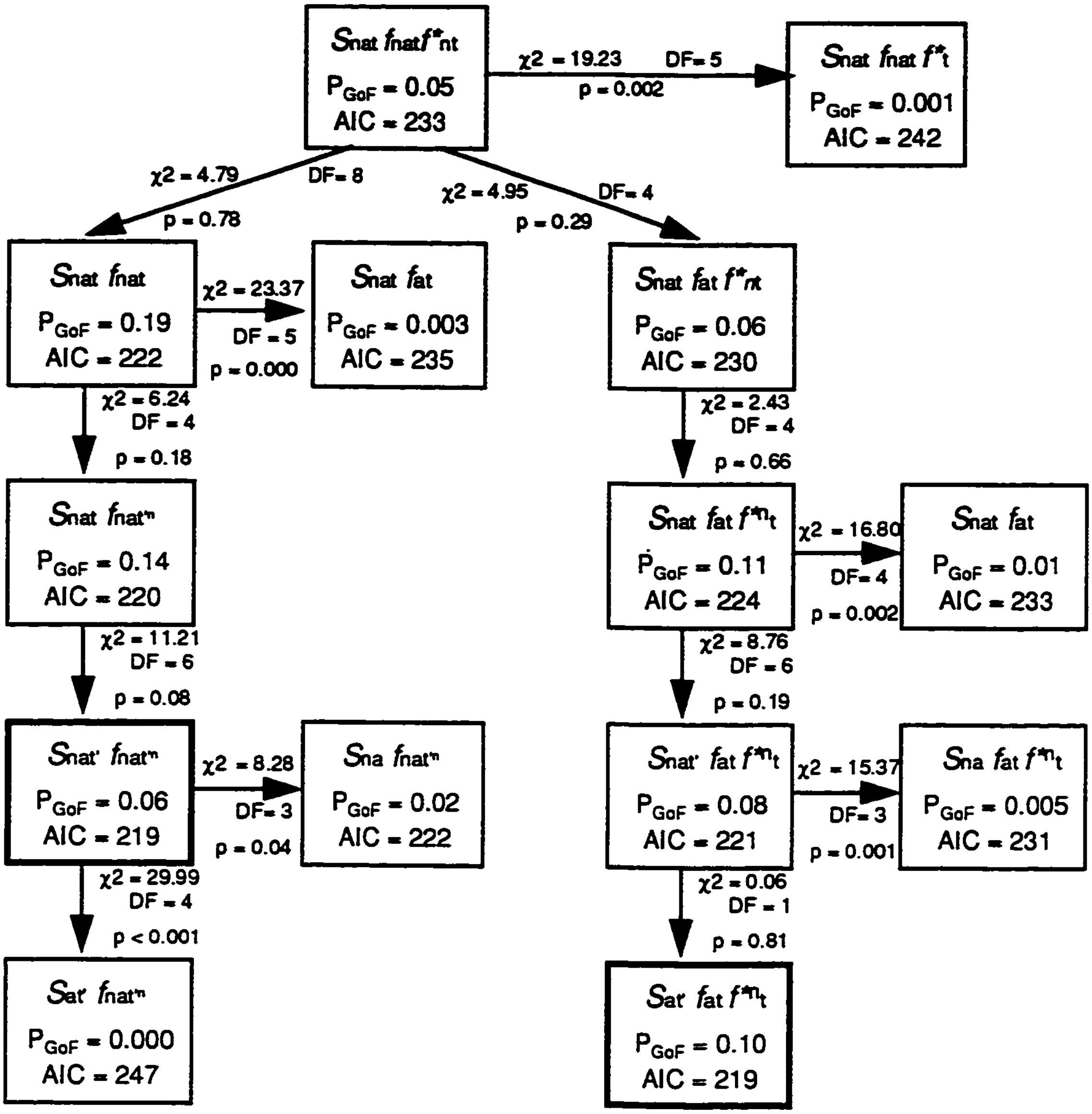


Fig. 2. Modeling of survival and recovery rates for greater snow geese banded on Bylot Island with SURVIV. Banding and recovery years are from 1990 to 1994. The best models are in the bold boxes. The left-hand side shows the within-group modelisation strategy and the right-hand side the between-group strategy (see results).

S: survival rate; *f*: recovery rate. GoF: Goodness-of-Fit. AIC: Akaike's Information Criterion

f^*: specific direct recovery rate

f^{*n} : specific direct recovery rate for neckbanded females only

t: time-dependent

t': time-dependent for the young only

t'^n: time-dependent for the young and the neckbanded adults only

a: age-dependent

n: neck band-dependent

Table 2. Annual survival (S) and recovery (f; f^{*}: direct recovery) rates (mean ± SE) of Greater Snow Geese legbanded and neckbanded at Bylot Island, 1990-94, under the model (Sat' $f$at f^{*n}t).

	Adults				Young			
	Neckbanded		Neck- and legbanded					
Year	f^{*}	SE	f	SE	f	SE	S	SE
1990	0.114	0.030	0.032	0.022	0.063	0.017		
1991	0.050	0.013	0.036	0.011	0.073	0.011	0.460	0.161
1992	0.088	0.016	0.045	0.008	0.082	0.013	0.226	0.076
1993	0.036	0.008	0.030	0.007	0.091	0.009	0.225	0.120
1994	0.042	0.009	0.016	0.004	0.028	0.005	1.000	0.364
Mean	0.065	0.009	0.032	0.007	0.067	0.006	0.478	0.210

Table 3. Annual survival (S) and recovery (f) rates (mean ± SE) of Greater Snow Geese legbanded and neckbanded at Bylot Island, 1990-94, under the model (Snat' $f$nat'^{n}). Recovery rates of young are identical to model (Sat'$f$at f^{*n}t).

	Adults				Young	
	Neckbanded		Legbanded			
Year	f	SE	f	SE	S	SE
1990	0.115	0.031				
1991	0.061	0.013			0.623	0.224
1992	0.087	0.014	rate constant		0.082	0.099
1993	0.038	0.007			0.203	0.105
1994	0.035	0.006			0.645	0.195
Mean	0.067	0.009	0.027	0.005	0.439	0.243

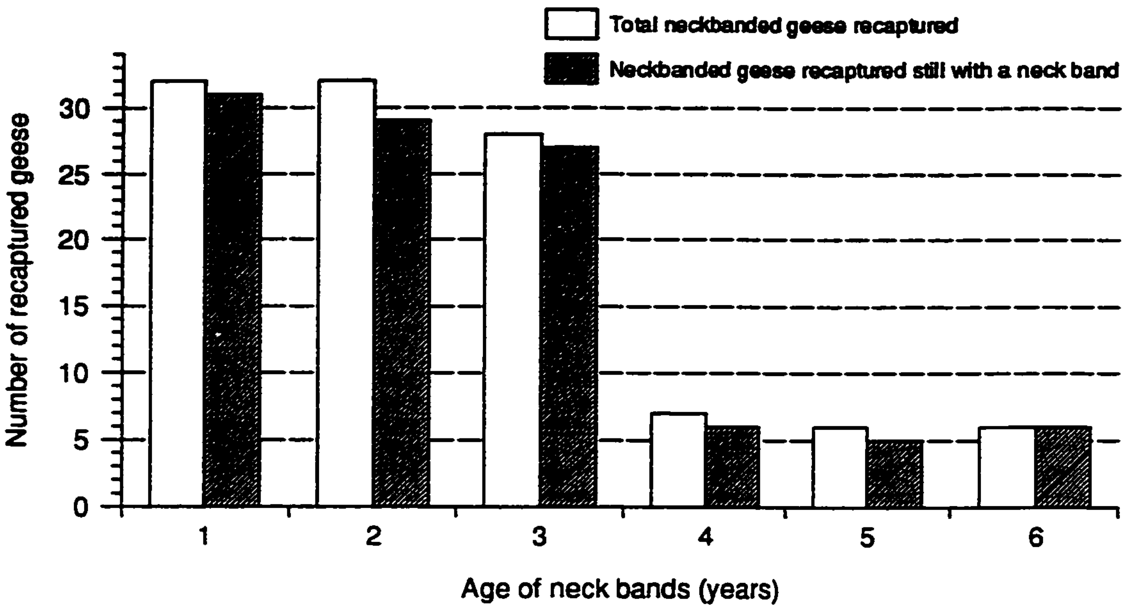


Fig. 3. Retention of neck bands for adult female geese banded on Bylot Island, from 1990 to 1995. Recaptures are from 1991 to 1996.

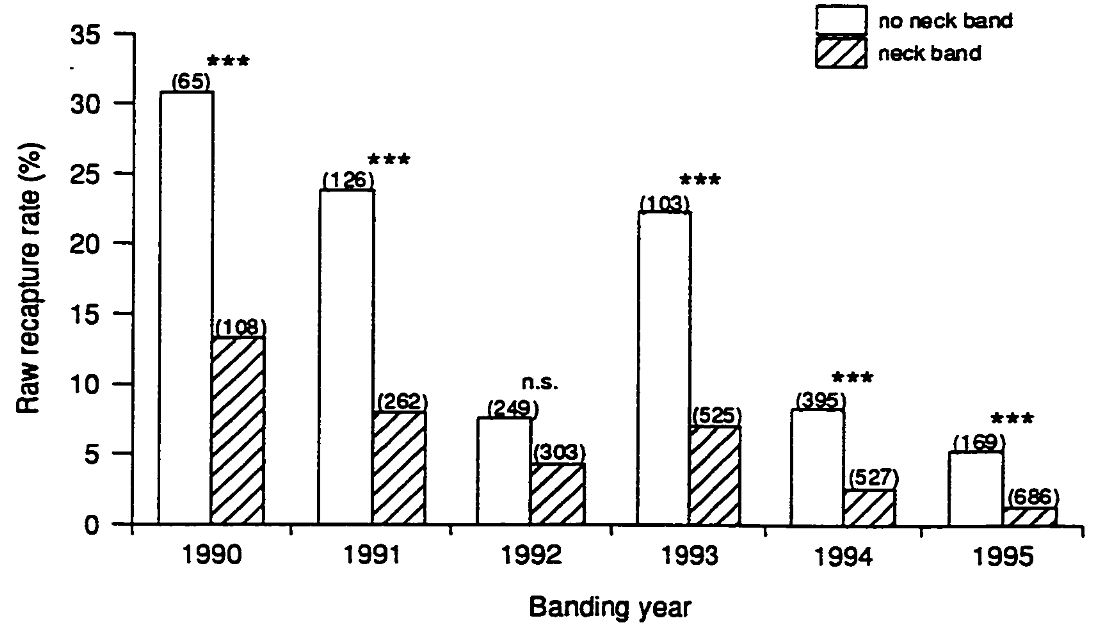


Fig. 4. Raw recapture rates of adult female geese banded on Bylot Island, 1990-1996. Numbers of birds banded are in brackets. ***: $P < 0.001$; n.s.= not significant.

Table 4. Survival (ϕ) and resighting (p) rates (mean ± SE) of neckbanded Greater Snow Geese, spring 1991 to spring 1996, under model AX of JOLLY. Survival rates are corrected for the neck band retention rate.

Year	ϕ	SE	p	SE
1992	0.85	0.16	0.15	0.1
1993	0.83	0.08	0.28	0.06
1994	0.78	0.05	0.25	0.04
1995	0.87	0.13	0.38	0.06
Mean	0.83	0.06	0.27	0.05

Simpler models with constant survival and/or constant resighting rates cannot be tested when inter-sampling resightings are used.

Recapture data

Of the 1,107 adult females which received only a leg band, a total of 134 (12.1%) were subsequently recaptured at least once during banding, compared to only 111 females with neck bands, out of the 2,431 banded (4.6%). Differences were significant for all banding years except 1992, though the trend was in the same direction (Fig. 4).

DISCUSSION

Effect of neck band on survival

The effect of neck bands on survival of marked individuals has been a controversial topic since the use of such markers on geese began. Our study provided an excellent opportunity to compare survival of neckbanded and legbanded birds, simultaneously estimated by several methods. The raw recapture rate during banding suggested a negative impact of neck band on survival, the band recovery analysis gave contradictory results, and the resighting method yielded a high survival value for neckbanded birds. However, one of these methods, recaptures on the breeding grounds, gave only an estimate of "apparent" survival because survival and recapture probabilities were confounded. Thus, no strong inference from this data set can be made on survival without further information. We are therefore left with two methods that have partly contradictory results.

Depending on how the recovery rates were parameterized, the band recovery analyses yielded contradictory results on the effect of neck bands. It is unclear why such a contradiction was found but could partly result from instability in the data. In one analysis, we found no difference between direct and indirect recovery rates within groups. This yielded a mean recovery rate for neckbanded birds twice as high as that for legbanded ones (model (Snat' $f$nat'^{n})). Higher reporting rate in neck-banded birds could be due to differences between leg- and neckbanded birds in hunting mortality (either because of a higher vulnerability to hunting of neckbanded birds or selection for them by hunters), or because of an increased reporting rate of geese with neck band by hunters. Under model (Snat' $f$nat'^{n}), the recovery rate of neckbanded birds also showed a decreasing trend over time. It is possible that the novelty of neck bands increased the reporting rate by hunters at first but that this effect wore out over time as these birds became more common. This would suggest that the higher recovery rate of neckbanded geese was more a consequence of higher reporting rate rather than an increase in hunting mortality. However, this analysis also showed that the survival rate of neckbanded birds was lower than that of legbanded birds only.

Using an alternative strategy of modeling with the same data set, the hypothesis of equal recovery rates between neckbanded and legbanded birds was accepted except for the direct recoveries of neckbanded geese, which was twice as high. A higher direct recovery rate of neckbanded birds could result from a greater reporting rate as outlined above, or a higher vulnerability to hunting. Newly-marked birds were more likely to be accompanied by young than previously marked ones and Giroux and Bédard (1986) showed that the presence of young with adults, especially females, increased their vulnerability to hunting in the St. Lawrence estuary. According to the preferred model in this analysis (model (Sat' $f$at f^{*n}t)), the survival rate of neckbanded geese was equal to that of legbanded birds.

The preferred models in each of these two analyses had the same AIC. Without further information, it would have been difficult to conclude on the effect of neck bands on survival. At best, we could have issued a cautionary note on the use of neck bands. Under these conditions, selection of the “best” model should therefore be made on grounds external to the data (Lebreton et al. 1992). In our case, it was another method of estimating the survival rate of marked snow geese.

The resighting analysis estimated survival only for the neckbanded geese. The model fitted well the data and the high resighting rate (p = 0.27, SE = 0.06), compared to the recovery rates (f = 0.03 to 0.06), increased the precision of the estimates. Overall, 71% of all neckbanded birds were resighted at least once and nearly all of the staging areas used in spring and fall were surveyed, so the risk of permanent emigration was negligible. All these conditions should lead to a reliable estimate of survival. The average annual (spring to spring) survival rate adjusted for neck band retention rate (0.83) was very similar to the annual survival rate estimated by model (Sat’ $f$at f^{*n}t) for both legbanded and neckbanded adult females (0.82) but was much higher than the survival rate estimated by model (Snat’ $f$nat’^{n}) for neckbanded birds (0.58). A separate analysis of survival on a seasonal basis with software SURGE yielded an annual survival of 0.77 for neckbanded females (chapter 2), a value similar to here. This strongly suggests that model (Sat’ $f$at f^{*n}t) should be the preferred model for the band recovery analysis. We therefore conclude that neck bands had no effect on the survival of marked birds. Furthermore, we did not find any evidence of a transient effect of marking and/or of neck band on survival immediately after banding (see chapter 2).

Samuel et al. (1990) examined survival in Canada geese neckbanded during fall migration. They did not detect any consistent reduction in survival of adult or juvenile geese associated with neck bands. In contrast, Castelli and Trost (1996) did find a negative effect of neck band on survival of Canada geese banded during the summer in New Jersey. Both of these studies used band recovery analyses, but the latter did not test for differences in direct and indirect recovery rates. Failure to do so in our analysis would also have lead us to conclude that neck band had a negative effect on survival. Alisauskas (1996) found an effect of neck band on recapture rates of Canada geese and white-fronted geese in the central Arctic. Capture-recapture analysis showed a lower survival for neckbanded Canada geese, compared to legbanded ones but the difference was not significant in white-fronted geese even if the trend was in the same direction. It appears that no general conclusion can be drawn on the effect of neck bands on survival of geese. Any possible effects could depend on the type of neck band, the species marked and its migratory habits or the weather conditions encountered by wintering birds. Presently, there is a need to asses the effect of neck bands for each program using this kind of marker, and especially for those designed to estimate survival rate using only resighting data as no control group (legbanded birds only) would be available in this case.

Other effects of neck bands

Overall recapture rates of adult geese on Bylot Island were low, likely a consequence of a low fidelity to breeding sites (Lepage et al. 1996). However, for geese marked in the Arctic, recapture rates were significantly lower for those marked with neck bands than for those marked with legbands only. Recapture of a marked individual during banding drives on Bylot Island depends on its survival and its probability of being captured if alive. If results of our previous analyses showing no difference in survival between the neckbanded and the legbanded birds are correct, this suggests a difference in capture probabilities between these two groups. There are at least two hypotheses to explain this difference. First, because our banding included mostly successful breeders, it is possible that the difference is due to different breeding propensities between the two groups. If neck bands somehow reduce the probability of breeding, then these birds could disperse more widely and/or molt earlier, thereby escaping capture during banding at the end of the summer. Neck bands could have a negative effect on body condition large enough to decrease the probability of breeding without affecting survival. Gessaman and Nagy (1988) showed that homing pigeon fitted with a harness and a transmitter weighing between 2.5% and 5% of the body mass increased both the time and the energy needed for flights of 90 km to 320 km. The neck band used on geese weighs only 0.75% of the bird's body mass but the spring migratory flight from the last staging area is at least 3,000 km (Gauthier et al. 1992). Whether there is an increased cost associated with the neck band during migration is unknown but arrival dates in the fall staging areas for neckbanded geese are similar to those of unmarked geese (Menu, unp. data, Maisonneuve and Bédard 1993). Schmutz et al. (1994) noticed increased feather wear beneath neck bands on recaptured Emperor Geese, which could increase thermoregulation costs. No such wear was detected for neckbanded geese recaptured on Bylot Island.

An alternative explanation for a low capture probability in neckbanded geese could be a handling effect of banding. Because neckbanded birds were handled longer and received a large marker, they could have experienced more stress than those marked with legbands only, provoking a higher rate of permanent emigration from the banding areas ("trap-shyness"). Pradel et al. (1995) suggested that handling effect explained why 25 to 30% of lesser snow geese which are banded for the first time as adults permanently emigrate from the sampling area (in their case, birds received only leg bands). These two factors could act simultaneously: some geese may not breed because of the neck band, while other ones may move away from the banding area because of the handling effect.

CONCLUSION

Our results emphasize the usefulness of different methods to estimate survival rates for the same population. With only band recovery analysis, results were contradictory. Analysis of resighting data lead to much stronger conclusions. Finally, a third analysis, recapture on the breeding grounds, pointed out differences not addressed by the other two analyses.

We urge those conducting studies using neckbanded geese to design experiments in order to assess the effects of neck bands on the demographic parameters of the population (survival, breeding propensity, etc.). Our analyses also suggest that other studies which have assessed the effect of neck bands on goose survival using only band recovery analyses may be biased.

CHAPITRE 4

CHANGES IN SURVIVAL RATES AND POPULATION DYNAMICS OF GREATER SNOW GEESE DURING AN EXTENDED GROWTH PHASE

RÉSUMÉ

La population de la Grande Oie des neiges (*Chen caerulescens atlantica*) a augmenté pendant les trois dernières décennies à un taux annuel d'environ 9%. Il y a eu deux phases de croissance importante séparées par une période de 8 ans sans augmentation de population. Cependant, le recrutement est resté constant pendant l'ensemble de la période considérée et ne semblait pas non plus dépendant de la densité. Nous avons estimé les probabilités annuelles de survie et de récupération de populations de la Grande Oie des neiges baguées dans l'Arctique, en relation avec l'âge, le sexe, le site de nidification et le temps. Nous avons aussi évalué les variations temporelles des taux de récolte par la chasse, indépendamment des données de baguage, pour examiner la relation entre la croissance démographique et la mortalité due à la chasse. La survie des adultes ne dépendait pas du sexe, ni de l'origine des individus et était constante pour la période considérée. De plus, elle était similaire entre le début des années 1970 ($S = 0.81$) et le début des années 1990 ($S = 0.79$) alors que la population s'est accrue d'un facteur 10 entre-temps, suggérant l'absence d'effets dépendants de la densité sur la survie. Au contraire des adultes, la survie des jeunes présentait des variations inter-annuelles prononcées, pendant la période (1990-1996) où elle a pu être estimée, pour une valeur moyenne de 0.32 (extrêmes: 0.11 - 0.42). Trois périodes distinctes de croissance démographique ont été reliées à trois niveaux différents de taux de récolte, le niveau le plus élevé correspondant à la période sans croissance de population. Ces variations concomitantes suggèrent que la chasse a le potentiel de contrôler la dynamique de la population, en agissant négativement sur la probabilité de survie des adultes.

ABSTRACT

The population of Greater Snow Geese (*Chen caerulescens atlantica*) has been increasing throughout most of the last three decades at an annual rate of about 9%. We examined changes in several demographic parameters during this period. There were two phases of important population growth interrupted by an 8-year period with no increase. However, recruitment stayed constant across the periods and also showed no evidence of density dependence. Annual survival and recovery rates of Greater Snow Geese banded in the arctic was estimated in relation to age, sex, breeding locations and time. Long-term changes in harvest rates were also assessed independently from banding data to examine relationship between population growth and hunting mortality. Adult survival rates were not specific of sex, breeding location and time for the duration of the study. Survival rates of the early 70s (S = 0.81) were similar of those of the early 90s (S = 0.79) while the population increased 10-fold, suggesting as yet no density-dependent effect on survival. In contrast to adult survival, survival rates of young varied greatly from year to year during the period (1990-1996) where they could be estimated, with a mean of 0.32 (range: 0.11 - 0.42). The three distinct periods of population growth were related to three different levels of harvest rate, the highest level occurring during the period of no growth. These concurrent variations suggest that hunting could control population dynamics by reducing adult survival rate.

INTRODUCTION

Understanding the dynamics of a population or a group of individuals is of primary importance both in evolutionary biology (Stearns 1992) and in conservation biology (e.g. Doak 1995). In long-lived species, adult survival is the key parameter to which population growth is the most sensitive (Lebreton and Clobert 1991). Variations in survival rates among groups and over time can therefore have a strong effect on the life history of a species and population dynamics. Numerous intrinsic factors may affect survival, such as age (e.g. Newton et al. 1997), sex (Breitwisch 1989), reproductive status (Francis et al. 1992a), or individual quality (Aebischer and Coulson 1990). External factors such as breeding location (Newton et al. 1993), environmental changes (Pons and Migot 1995), or hunting pressure in exploited populations (Nichols 1991) could also affect survival.

Some studies have documented long-term changes in survival rates of animals. For example, Kayamibwa et al. (1990) found a significant decline in survival rates of White Storks (*Ciconia ciconia*) between 1956 and 1976, apparently due to drought conditions on the wintering grounds in West Africa. Croxall et al. (1990) suggested that decline in population size of Wandering Albatrosses (*Diomeda exulans*) was due to increased mortality from fishing lines. In contrast, survival rates of adult Greater Flamingos (*Phoenicopterus ruber roseus*) was found constant over time (from 1983 to 1991), except during a very cold and unusual winter where it was significantly reduced (Cézilly et al. 1996). Similarly, survival of adult European Shags (*Phalcrocorax aristotelis*) at a British colony was estimated to be constant over a 24-year period (Harris et al. 1994).

Knowledge of systematic changes in survival rates and of factors influencing them is particularly important for management of exploited populations. In birds, the most common form of exploitation is hunting, which may negatively affect survival rates and thus population dynamics. However, the extent to which hunting affects survival rates of waterfowl is still poorly understood, in particular because hunting mortality could be either compensatory or additive to natural mortality (Nichols 1991). It is often assumed that hunting is the most significant source of adult mortality in geese, although few supporting data are available (Owen 1980). Adult Lesser Snow Geese (*Chen caerulescens caerulescens*) from the Mid-continent population experienced an increase in survival, which was related to a decrease in hunting mortality (Francis et al. 1992b). Similarly, a negative relationship between survival and harvest rates was found for Canada Geese (*Branta canadensis*; Hestbeck 1994).

The population of the Greater Snow Goose (*Chen caerulescens atlantica*) has increased dramatically since the beginning of the century. Fewer than 10,000 birds were present at the turn of the century (Lemieux 1959), leading to strict protective measures: A year-round prohibition of hunting in the USA and an open season limited to the fall in Canada allowed the population to slowly recover to 50,000 birds in 1967 (Gauvin and Reed 1987). Following a further increase in population, hunting was resumed in 1975 in the USA. Despite increased hunting pressure, the population continued to increase and the spring population estimate for 1997 was 657,500 (Reed et al. 1998). Our objective was to determine the relative contribution of recruitment and mortality on recent changes in population dynamic of the Greater Snow Geese. We estimated annual survival and recovery rates of Geese banded in the arctic in relation to age, sex, breeding locations and we used fall age ratios as index of recruitment. We also assessed long-term changes in harvest rates independently from banding data in order to examine the relationship between survival and hunting mortality.

METHODS

Population census

The Greater Snow Goose spring population has been censused using aerial photography during surveys conducted by the Canadian Wildlife Service on the staging areas of the St. Lawrence river since 1969. This census yielded an almost complete photographic coverage at a time when the entire population of the Greater Snow Goose was present in a relatively small, well-defined area (see Gauvin and Reed 1987 for details). This census thus estimates population size with a much greater accuracy than the mid-winter population counts of waterfowl populations (Reed at al. 1998). To characterize population growth, we divided the period in three time intervals: the early period, from 1970 to 1974; the mid period, from 1975 (re-opening of US hunt) to 1982, and the late period, from 1983 to 1996.

For each interval, we estimated mean annual growth rate, λ ($\lambda = N_{i+1}/N_i$ where N_i = spring population size in year *i*) as the natural logarithm of the slope of the relationship between lnN and i.

Recruitment

From 1970 to 1996, the proportion of juvenile in the fall flock was determined by visual observations, along the St. Lawrence estuary, as well as brood sizes since 1973 (Reed at al. 1998). These observations were made at several sites along the fall staging area during most of the period when geese were present. The mean proportion of young and mean brood size in fall were compared among periods with an analysis of variance (ANOVA procedure; SAS Institute Inc. 1988).

Banding data

Between 1970 and 1974, mass banding of Greater Snow Geese was conducted at several colonies throughout their arctic breeding range by the Ministère de l'Environnement et de la Faune (Québec Province). Goose families were captured annually in summer (during two distinct periods: 3 to 6 July and 1 to 3 August) when the adults were molting and before the young could fly. Birds were classified as adults (> one year old) or young based upon plumage, and their sex was determined by cloacal eversion. All birds received a metal US Fish and Wildlife Service band. Because of the timing of the banding procedures and of two years of nearly complete breeding failure (1972 and 1974), few goslings were banded, precluding the estimation of their survival rate (Table 1 in appendix A).

Between 1990 and 1996, another banding operation was done at one of the major breeding colony, Bylot Island (N.W.T. 73°N 80°W), as part of a long-term project on the Greater Snow Goose (see Hughes et al. 1994 for description of the study area and chapter 3 for general methods). Each year, flightless geese (adults and geese) were captured for banding in late summer (mid-August). The same standard procedures as above were applied. Furthermore, most of the adult females received a yellow plastic collar with an alphanumeric code (Table 2 in appendix A).

Recoveries occurred during the fall and winter hunting seasons in southern Québec and the eastern United States of America, and came from the Bird Banding Laboratory. Since 1990, outfitters from the upper estuary of the St. Lawrence River (Québec, 47°N 72°W), have also been solicited by letters or personal contact to report bands directly to us.

Survival rate analysis

We estimated survival with band recovery analyses using the program SURVIV (White 1983). For the early period, we used recoveries from 1970 to 1989, and recoveries from 1990 to 1996 for the late period. We used the general models and methodology described by Brownie et al. (1985), and followed their terminology. Recovery rate (f_i) is the probability that an individual banded bird alive at the time of banding in year i will be shot and retrieved during the hunting season in year i, and its band reported to a wildlife agency. Survival rate (S_i) is the probability that a bird alive in a particular age and sex class at the time of banding in year i will survive to the time of banding in year $i + 1$.

We tested for possible differences in survival rates in relation to breeding latitudes by grouping the geese banded during the early period into two groups, South or North of the 74°N. The southern group corresponds to birds banded on Baffin, Bylot and Sommerset islands and the northern one to birds banded on Devon, Ellesmere and Axel-Heiberg Islands. Because there were too many parameters compared to the number of cohorts (i.e. banding years) for the early period, it was not possible to test all the effects at the same time (sex, group and time). Therefore, we first tested the effect of sex (s; male or female) on both survival and recovery rates for each group separately. In the absence of sex differences, sexes were pooled and we started a new analysis with all the data to test the hypotheses of equality of survival and recovery rates between the two groups (g; south or north of the 74°N) and over time (t). A hierarchy of models sequentially constraining each parameter was then tested to determine the most parsimonious list of parameters needed to model the data. Likelihood ratio tests (LRT; Brownie et al. 1985) between models and the Akaike Information Criterion (AIC; Burnham et al. 1995) were used to select the best model among subsets of the general one. For the late period, we modeled the effect of age (a; two age classes: young and adults), sex (s), presence of a neck band (n; adult females with or without neck band) and time (t) on both survival and recovery rates. Recovery rates of the newly marked adult females (direct recovery rate, f^*) were set different from previously banded birds, for both group of adult females (legbanded only and neckbanded; see details in chapter 3). As above, a hierarchy of models was tested to select the best model.

Harvest rates

We estimated harvest rates independently from the banding data. Harvest rate was estimated with the ratio of total number of geese harvested by the estimated total fall population size. Total harvest was obtained from annual reports issued by the Canadian Wildlife Service and the US Fish and Wildlife Service. Total numbers of Snow Geese killed by sport hunting are estimated annually in Canada and USA through the national harvest surveys designed for all migratory waterfowl species (see Boyd and Finney 1978). Because Greater Snow Geese are restricted to the Atlantic Flyway and overlaps little with other snow goose populations during migration and winter, we defined the harvest for this population as geese killed from Québec and all the US states within the Atlantic Flyway (15 states reported harvest of geese with major ones being New Jersey, Delaware, Maryland and North Carolina; Reed et al. 1998). Age ratio in the harvest were determined from tail fans of shot geese collected through the parts collection survey. Although the sample sizes were sometimes small (mean annual number of tails = 344, range: 25 - 1081), age ratios in the harvest were highly correlated (R^2 = 0.86 and 0.90 for Québec and USA harvest, respectively) with the proportion of juvenile in the fall flock (Fig. 1) and were thus considered accurate.

Two methods were used to determine the size of the fall population for the harvest rate calculations. First, the fall population size of adults in year *i* (NF_i^*) was estimated using the preceding spring count of the population (Ns_i) multiplied by a seasonal survival rate value for adults (from May to October: oversummer survival, S_{su}). As summer survival rates determined with resighting data may be biased (see chapter 2 and appendix D), we used the annual survival rate determined with band recovery (this study) to estimate the oversummer survival rate, assuming a constant survival rate throughout the year ($S_{su} = S_y^{5/12}$). With the second method, the fall population (NF_i) was estimated with the following spring population (Ns_{i+1}) plus the total estimated harvest (H_i), assuming no natural mortality during the hunting season. For the two methods, the fall population was further divided into young and adult segments, using the proportion of young in the fall flock. We then estimated a harvest rate for the two age classes (young, y, and adult, a; see formulas in appendix).

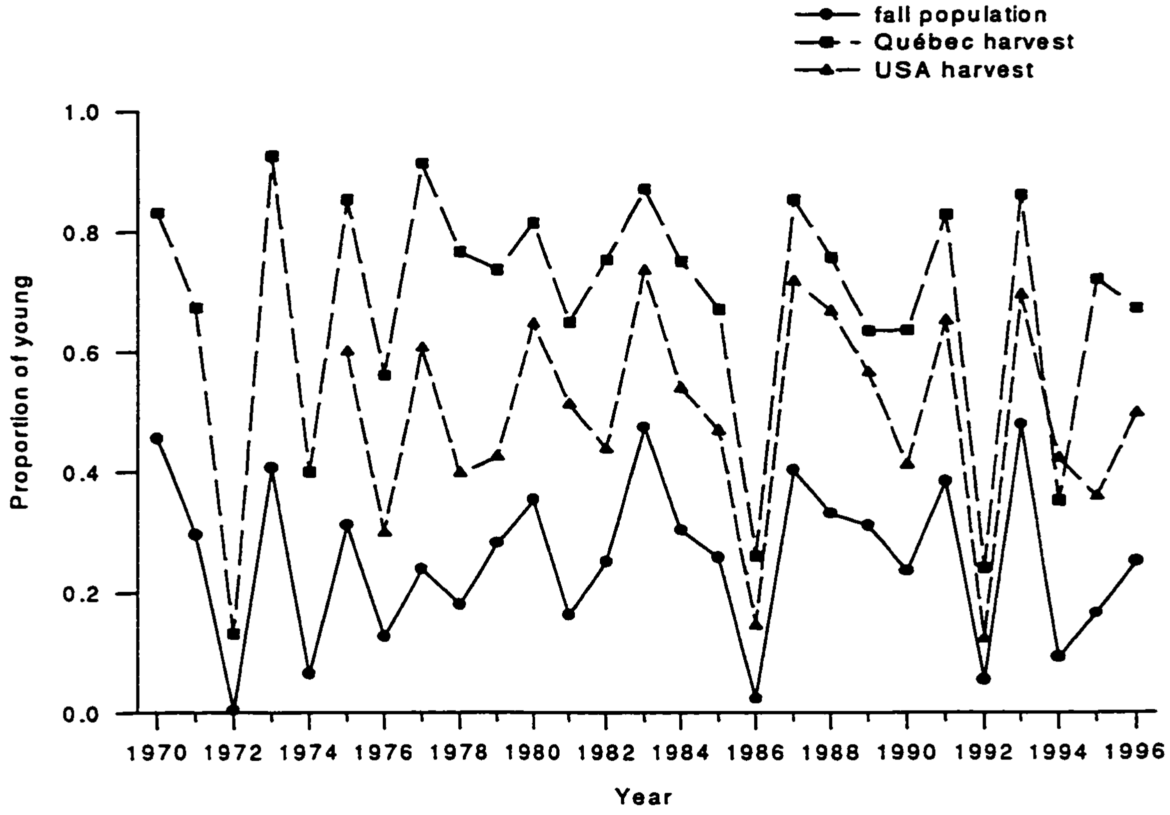


Fig.1. Proportion of young Greater Snow Geese in the fall population and in the Québec and USA harvest, as estimated by CWS and USFWS national surveys, from 1970 to 1996.

RESULTS

Population size and recruitment

The spring population has increased ten-fold from 1970 to 1996, although the rate of increase varied significantly over the period (Fig. 2). Three different phases of population growth can be distinguished (Table 1). From 1970 to 1974, the population increased from 89,620 to 165,000, with a mean annual growth rate of 14.7%. In contrast, there was no increase from 1975 to 1982 (0.9%). However, the population started to grow again after 1982, from 185,000 in 1983 to 657,500 in 1996, a mean annual growth rate of 9.6%.

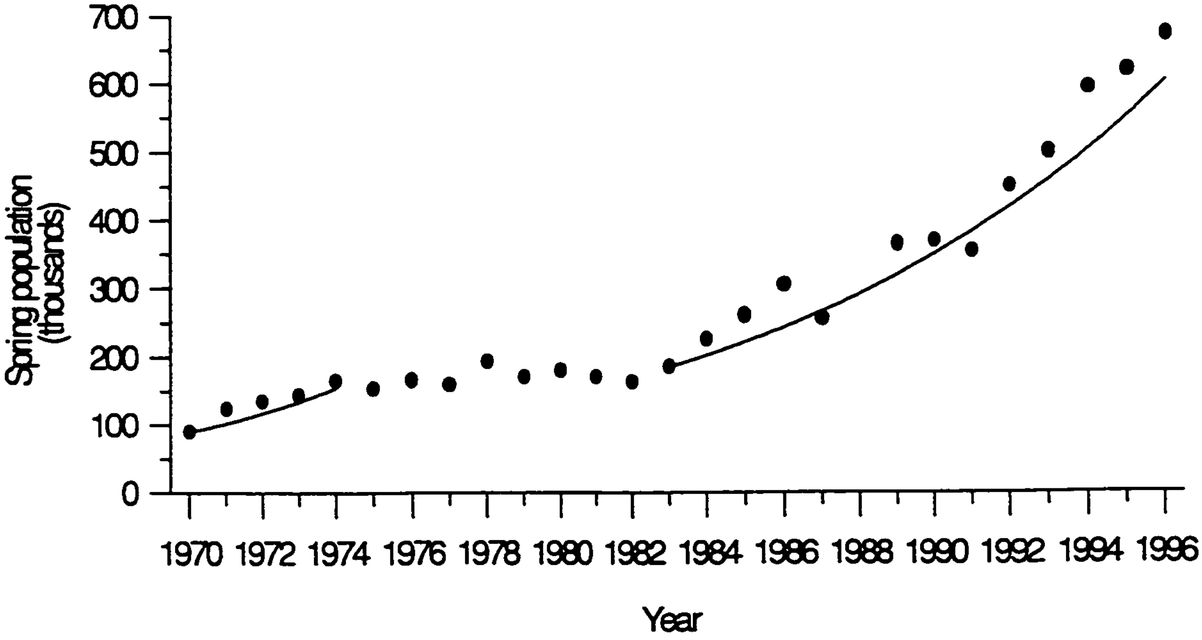


Fig. 2. Spring counts of the Greater Snow Goose population obtained from aerial surveys conducted in southern Québec from 1970 to 1995 (no survey done in 1988). The solid line represents the exponential model for periods 1970-1974 and 1983-1996.

Table 1. Demographic parameters of the Greater Snow Goose population for the different time intervals (Mean ± SE).

	Interval period			
	1970-1974	1975-1982	1983-1996	1970-1996
Observed growth rate, λ [a]	1.147	1.009	1.096	1.068
P-value of exponential model	0.01	0.43	0.0001	0.0001
Fall proportion of young (%) [b]	24.5 ± 20.2	23.8 ± 7.8	27.0 ± 15.1	25.5 ± 13.9
Mean brood size [c]	2.56 ± 0.53	2.50 ± 0.19	2.53 ± 0.28	2.52 ± 0.26
Adult survival	0.83 ± 0.03	-	0.79 ± 0.03 [d]	-
Young survival	-	-	0.32 ± 0.14 [d]	-
Adult recovery rates [e]	0.015 ± 0.002	0.032 ± 0.003	0.023 ± 0.004	0.024 ± 0.004
Adult harvest rate	0.04 ± 0.01	0.11 ± 0.01	0.07 ± 0.01	0.08 ± 0.01
Young harvest rate	0.42 ± 0.15	0.74 ± 0.06	0.37 ± 0.03	0.52 ± 0.06

a: Mean annual growth rate, $\lambda = N_{t+1}/N_t$.

b: one-way ANOVA among periods: $F = 0.14$, df = 2, $P = 0.87$.

c: one-way ANOVA among periods: $F = 0.01$, df = 2, $P = 0.93$.

d: Birds banded between 1990 and 1996.

e: No banding between 1975 and 1989. For the 1983-1996 period, recovery rates were estimated with birds banded during the early (1970-1974) and late (1990-1996) periods.

During this period, annual recruitment fluctuated widely, with proportion of young in the fall flock ranging from 0.4% to 48%. However, there was no difference among the three contrasting periods of population growth in the mean proportion of young in fall and the mean brood size (*P* = 0.87 and 0.93, respectively; Table 1), despite the high annual variability in these measures and the very contrasting periods of population growth This suggests that changes in recruitment were not responsible for variations in population growth over this period.

Survival and recovery rates

For the early period, the hypothesis of equality of survival and recovery rates between sexes was accepted for both birds banded south or north of 74°N (Fig. 3). Sexes were therefore pooled together for subsequent analyses. For the pooled data, the most general model (*S*gt *f*gt) did not fit well the data based on the Goodness-of-Fit because of non estimable parameters (recovery and survival rates could only be estimated for the banding years, 1970 to 1974). The effect of latitude on the recovery and survival rates was not significant (Fig. 3). The effect of time on the survival rates was not significant but was strongly significant for the recovery rates (Fig. 3). Therefore, our analysis suggests that there was no effect of breeding latitudes and time in survival rate of adults during the early period (Fig. 3). Survival rate was estimated at 0.83 (SE = 0.03). With acceptation of the hypothesis of constant survival over time, it was then possible to estimate recovery rates during the period 1975-1989. The recovery rates were generally low from 1970 to 1974 (mean *f* = 0.015), but increased sharply in 1975 and remained fairly high until 1981 (mean *f* = 0.032). Recovery rates declined afterwards (mean *f* = 0.017; Fig. 4). Precision of recovery rates declined over time because no new birds were banded after 1974.

For the late period, the most general model (*S*nast *f*nast *f**nt) did not fit the data based on the Goodness-of-Fit test (*P* = 0.0003). Inspection of contingency tables indicated that only a few cells contributed to the large chi-square value. This suggests that the lack of fit was not severe and that the analysis could be pursued further. We started by reducing the number of parameters associated with the recovery rates as much as possible, in order to

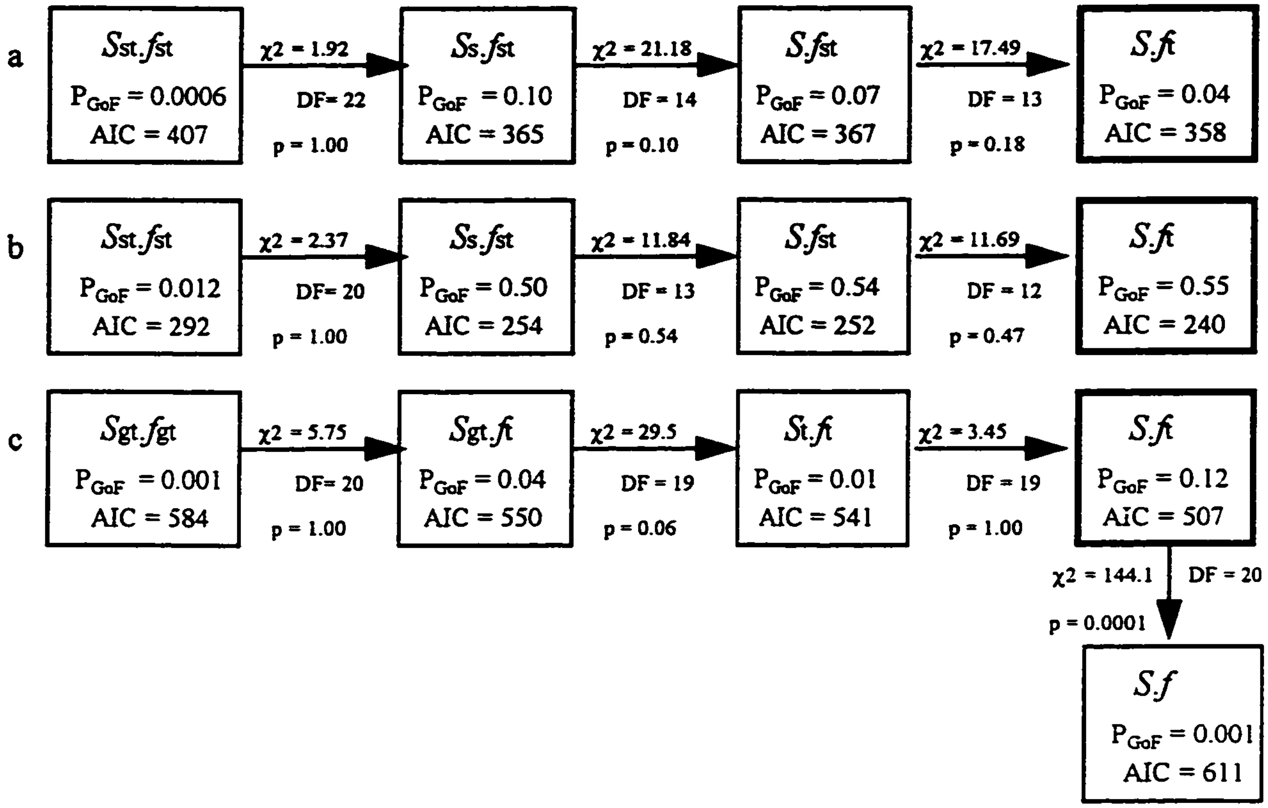


Fig. 3. Modeling of survival and recovery rates for Greater Snow Geese banded in the Arctic during the early period with SURVIV. Recoveries are from1970 to 1989. The best models are in the bold box.

a: Geese banded in 1970, 1971, 1973 and 1974, south of the 74°N.

b: Geese banded in 1971, 1972 and 1973, north of the 74°N.

c: Geese banded from 1970 to 1974 (sexes pooled), south and north of the 74°N.

S: survival rate; *f*: recovery rate; g: group-dependent; s: sex-dependent; t: time-dependent (see text).

P_{GoF} = *P*-value of the Goodness-of-Fit test; AIC: Akaike's Information Criterion.

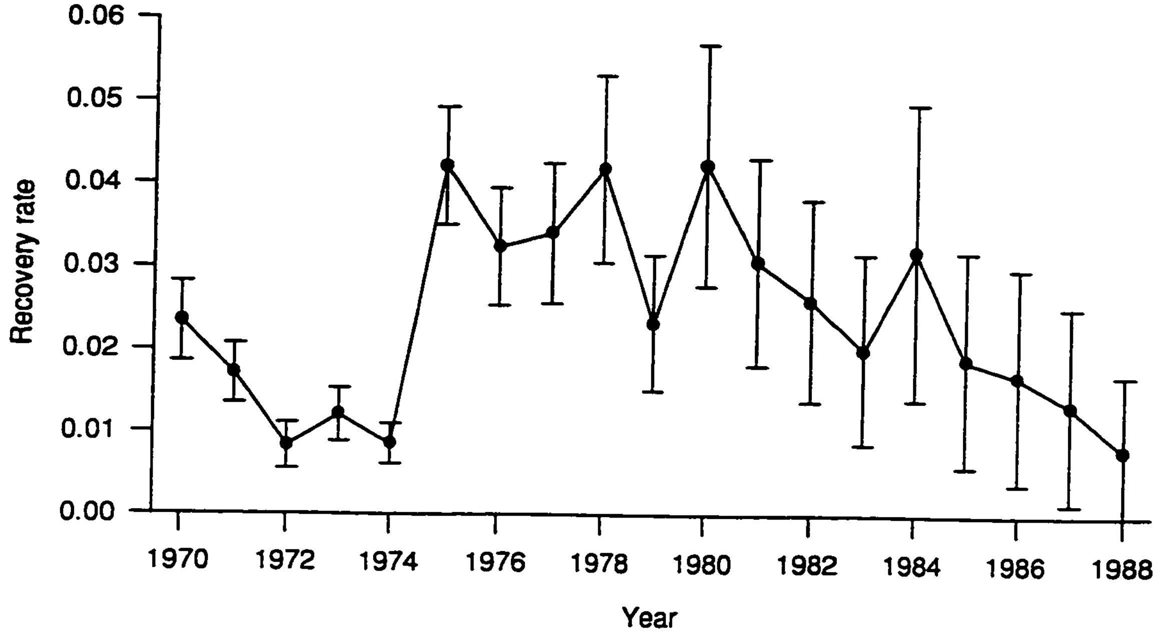


Fig. 4. Annual recovery rates (mean ± SE) of Greater Snow Geese banded in the Arctic (1970-74), under the model *S ft*.

keep maximum power for the tests involving the survival rates. Based on the previous results(chapter 3), we first tested the hypothesis of equality of direct and indirect recovery rates between the two groups of adult females (legbanded only, lb vs. neckbanded, nb, Ho: $f^{*}_{nb} = f^{*}_{lb}$ and Ho: $f_{lb} = f_{nb}$ respectively; Fig. 5). The first hypothesis was strongly rejected by the LRT, indicating that neckbanded geese had a higher direct recovery rates than legbanded ones. However, the hypothesis of equal indirect recovery rate hypothesis was not rejected. Thus, indirect recovery rates were set similar between legbanded and neckbanded females (model ($S\text{nast}\, f\text{ast}\, f^{*}\text{nt}$)). The hypothesis of equality between direct recovery rates of legbanded only adult females and indirect recovery rates was also accepted, leaving a different direct recovery rate only for the neckbanded females (model ($S\text{nast}\, f\text{ast}\, f^{*n}\text{t}$)). The effect of sex on the recovery rates of young was not significant (model ($S\text{nast}\, f\text{as't}\, f^{*n}\text{t}$); Fig. 5). Other attempts to further reduce the number of parameters associated with recovery rate failed. Recovery rates of adults were about half of those for young (0.028 vs. 0.065 on average, respectively) except for direct recovery rates of neckbanded females (0.065) which was twice as high as those for legbanded females (Fig. 6).

From this model, we then tested effects on survival rates. The effect of neck bands on survival was not significant (model ($S\text{ast}\, f\text{as't}\, f^{*n}\text{t}$)); Fig. 5). The effect of sex was marginally significant for adults ($P = 0.04$, model ($S\text{as*t}\, f\text{as't}\, f^{*n}\text{t}$)) but based on the AIC, the reduced model was accepted, suggesting that sex differences were weak. The effect of sex was strongly significant in young but this was solely due to the 1991 cohort. A model with equal survival rates in young males and females except for the 1991 cohort was accepted (model ($S\text{as}_{91}\text{t}\, f\text{as't}\, f^{*n}\text{t}$)). Furthermore, the effect of time on adult survival rate was not significant but was significant for young. The selected model ($S\text{as}_{91}\text{t*}\, f\text{as't}\, f^{*n}\text{t}$) had the lowest AIC (Fig. 5). It yielded a constant annual survival rate of 0.79 (SE = 0.03) for adults. The survival rate of juvenile was about half of that for adults but varied among years (mean $S = 0.35$ (0.11); Fig. 6).

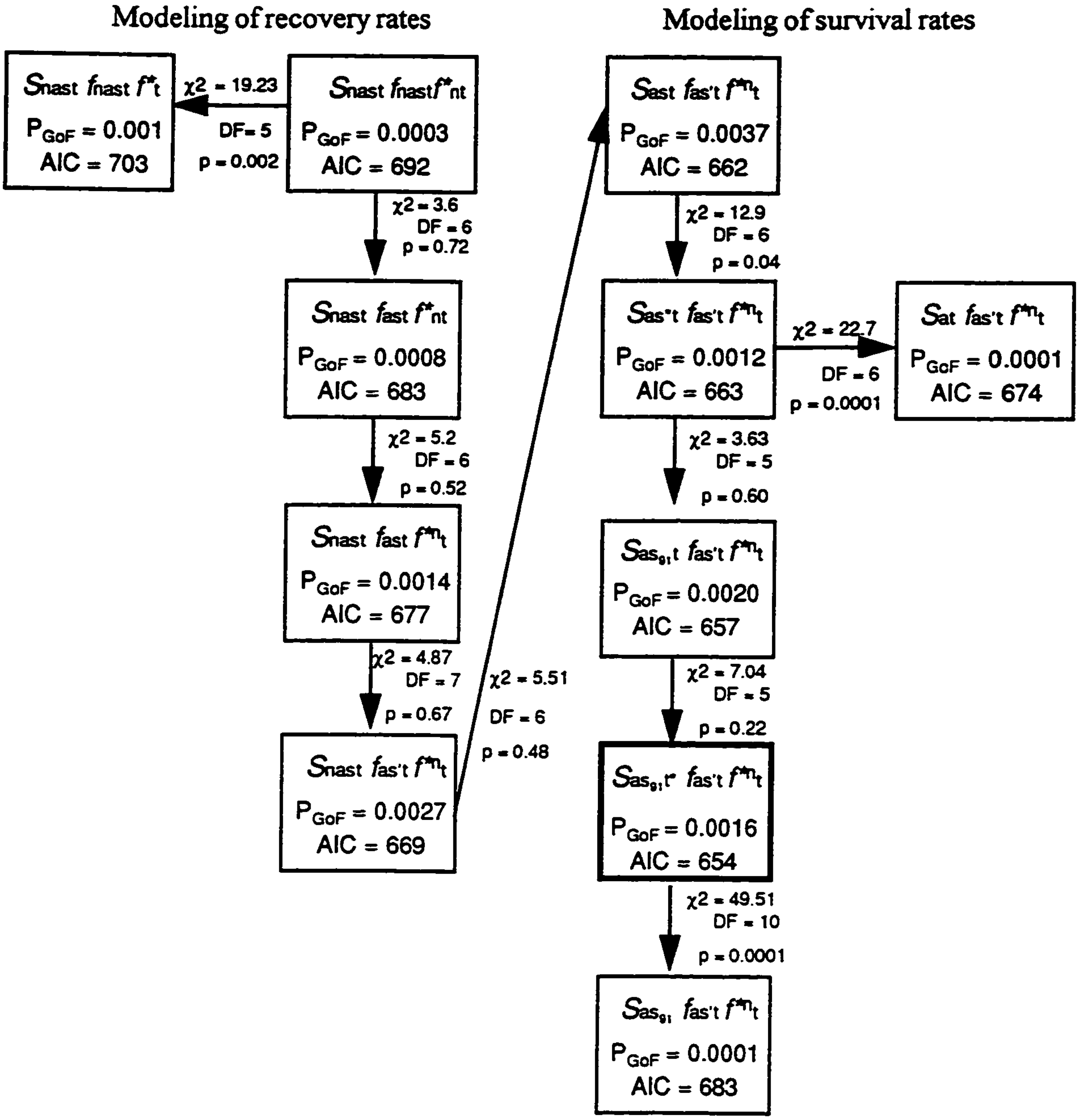


Fig. 5. Modeling of survival and recovery rates for greater snow geese banded on Bylot Island during the late period with SURVIV. Banding and recovery years are from 1990 to 1996. The best model is in the bold box.

S: survival rate; *f*: recovery rate.

P_{GoF} = *P*-value of the Goodness-of-Fit. AIC: Akaike's Information Criterion.

t: time-dependent
t*: time-dependent for the young only
s : sex-dependent
s*: sex-dependent for the young only
s_{91}: sex-dependent for the 1991 cohort of young only
s': sex-dependent for the adults only

f^* : specific direct recovery rate
f^{*n} : specific direct recovery rate for neckbanded females only
a: age-dependent
n: neck band-dependent

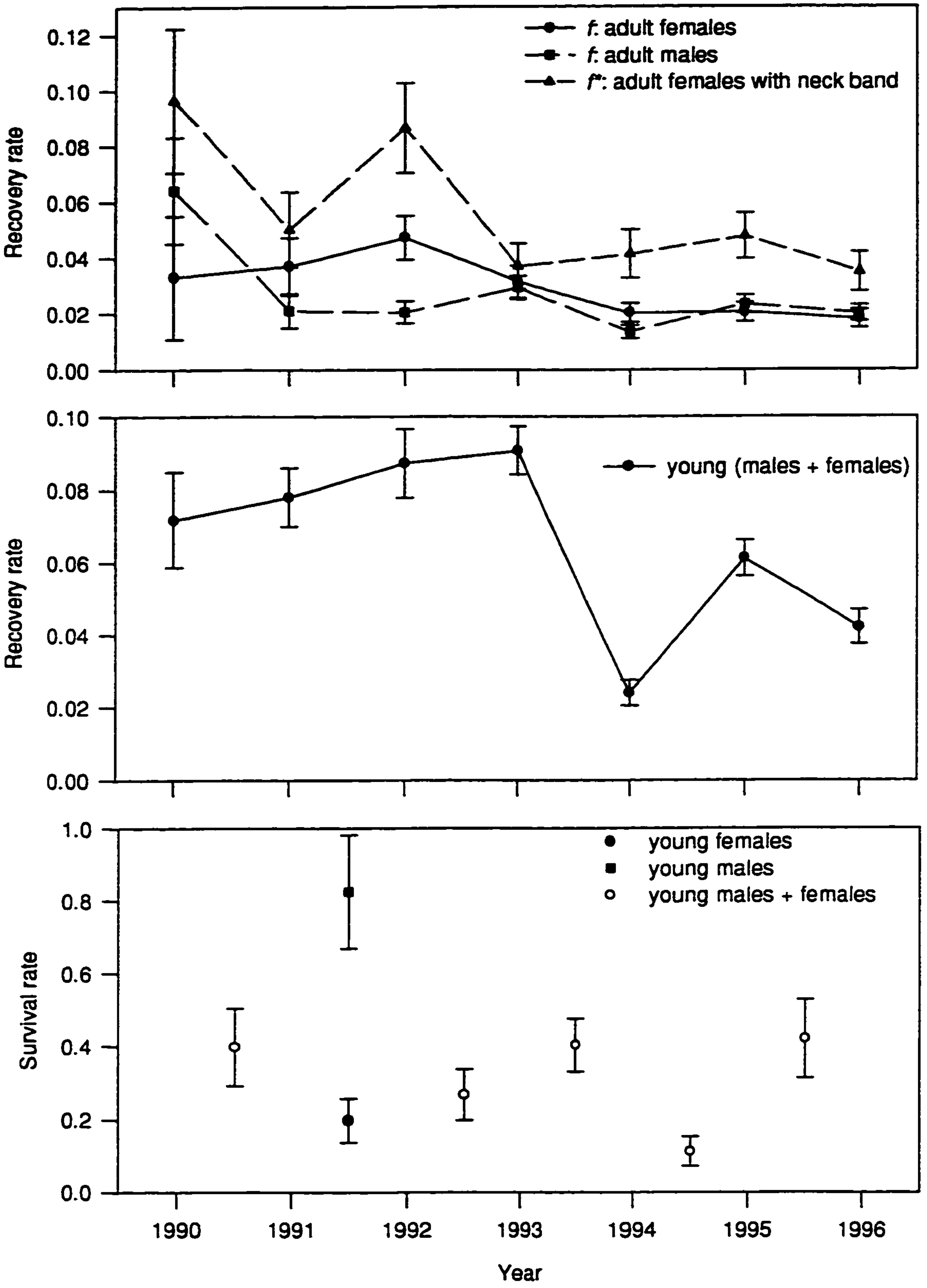


Fig. 6. Annual recovery and survival rates (mean ± SE) of Greater Snow Geese banded on Bylot Island, under the model $Sas_{91}t^{*}fas'tf^{*n}t$, for the late period (1990-1996).

S: survival rate; f: recovery rate; f^{*n}: specific direct recovery rate for neckbanded females only; a: age-dependent; s_{91}: sex-dependent for the 1991 cohort of young only; t*: time-dependent for the young only; s': sex-dependent for the adults only; t: time-dependent.

Harvest rate

The estimated total legal harvest increased significantly from 1970 to 1995 ($R^2 = 0.38$, $P = 0.001$) but annual variations were considerable (Fig. 7a). Annual variation in harvest can be largely explained by annual variations in proportion of young in the fall flock as harvest is much larger in years of high recruitment ($R^2 = 0.30$, $P = 0.003$; Fig. 7b). This is because young are much more vulnerable to hunting than adults

Harvest rates estimated by the two methods were similar (Fig. 8). Over the entire period (1970-1996), the mean harvest rate was 0.08 ± 0.01 for adults, but more than 6 times higher for young (0.52 ± 0.06). However, temporal trends were similar between the 2 age classes and there were large annual variations for both adults and young. The harvest rate showed a sharp increase with the re-opening of the US hunt in 1975, especially in adults, and until 1983 remained 2 to 3 times higher than during the early interval (from 1970 to 1974). After 1984, it declined abruptly to stabilize at a level 1.5 to 2 times lower than during the previous period (Table 1). Temporal trends in harvest rates determined with the national surveys were consistent with those estimated with band recovery data (Table 1 and Fig. 4).

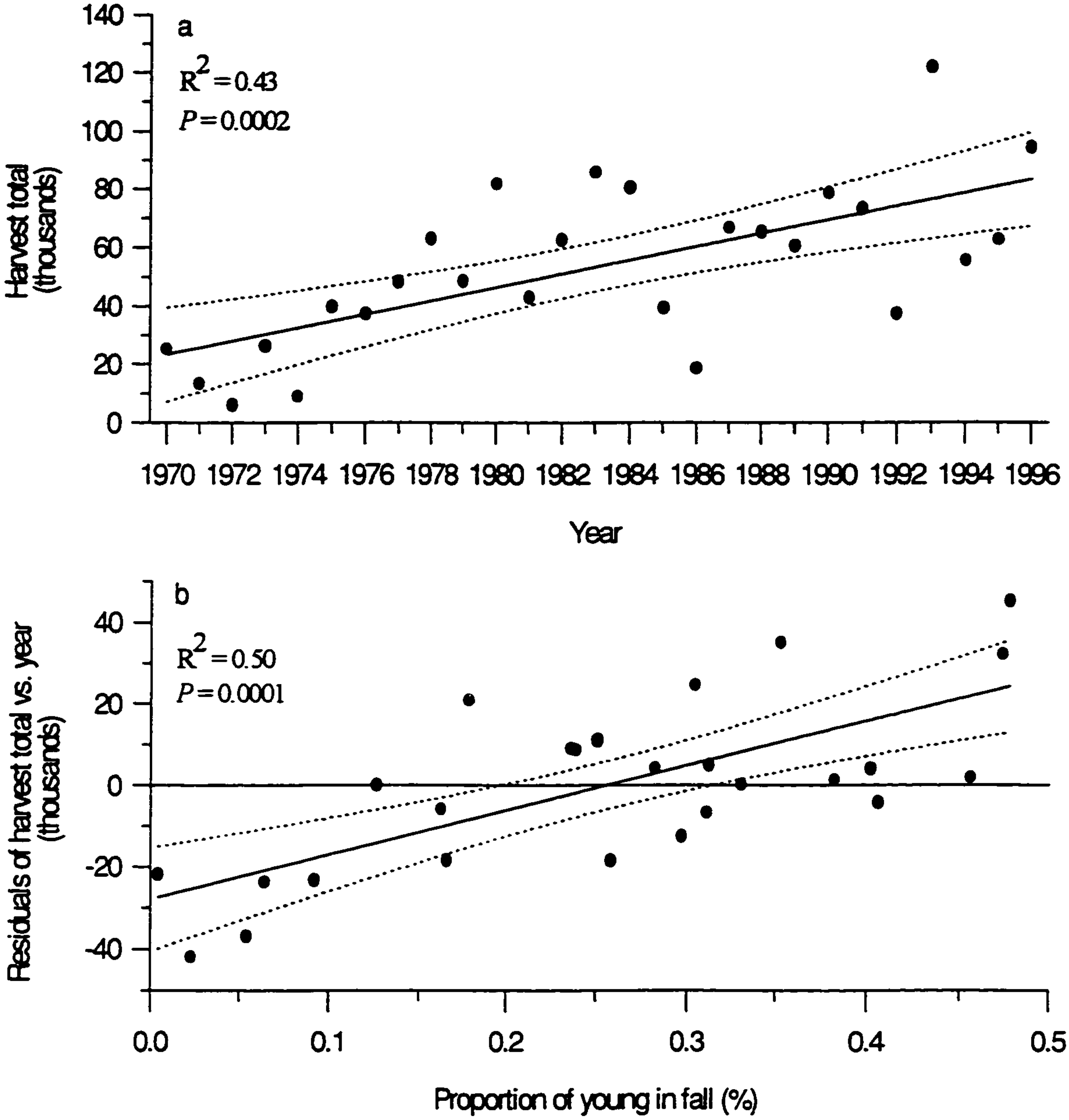


Fig. 7. Total harvest estimated annually (a) and residuals from the linear relationship between total harvest and year in relation to proportion of young in the fall (b), for the Greater Snow Goose population. The solid lines represents the linear regression model and the dashed ones, the 95% confidence interval.

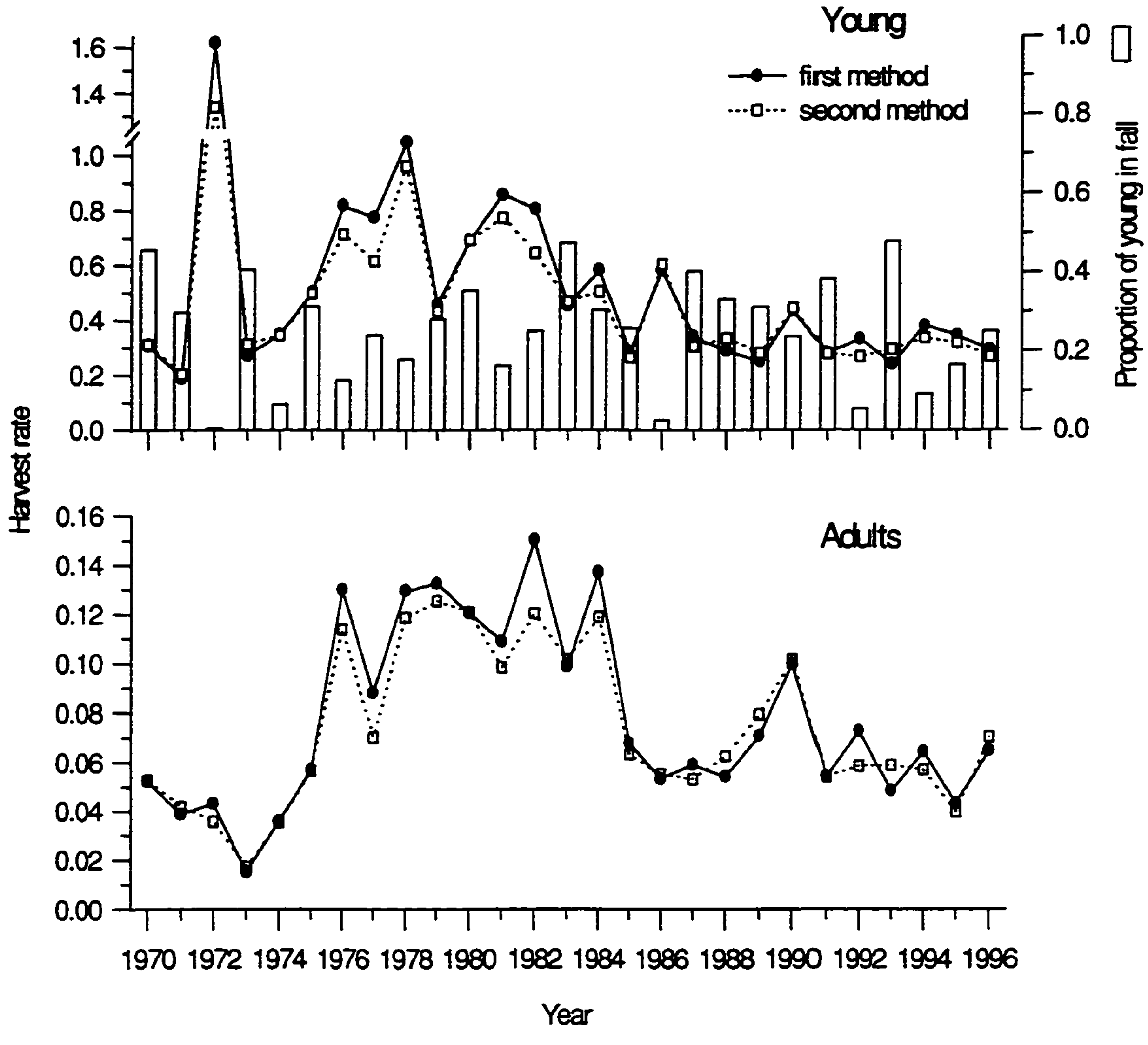


Fig. 8. Harvest rates for young and adult Greater Snow Geese, from 1970 to 1996. The first method used a fall population calculated with the preceding spring population, corrected by the oversummer survival rate. The second method used a fall population calculated as the following spring population + the harvest total (see methods).

DISCUSSION

Population size and recruitment

Despite the ten-fold increase in population size between 1970 and 1996, the growth of the Greater Snow Goose population showed no sign of levelling-off during the late period. Furthermore, there was no evidence of a density-dependent effect on recruitment despite this large population growth. Proportion of juveniles and mean brood size measured in fall are affected by the mortality of young occurring from fledging to fall staging (chapter 5). This could explain, in part, annual variations in these parameters, as well as in annual survival of young. We observed a similar pattern of variation in fall migration survival of young over a 3-year period using a comparable data set (see chapter 5), suggesting that a large part of the annual variations could be due to variations in fall migration survival.

In earlier studies on Greater Snow Geese (Reed 1990, Reed and Plante 1997), it was also shown that fecundity was not affected by density, but the latter study concluded that a long term decline in body size, mass and condition of juvenile birds was associated with increasing densities on the brood rearing areas. Several studies have reported density-dependent effect on fecundity or recruitment (clutch size, growth and survival of young) in other goose populations which are increasing (Cooch et al. 1989 and 1991, Owen and Black 1989, Francis et al. 1992b).

Factors affecting survival rates

Estimated annual survival rates for Greater Snow Geese were similar to values estimated for other hunted goose populations in North America (e.g. Rexstad 1992, Francis et al. 1992b, Hestbeck 1994, Ward et al. 1997). We detected no sex-specific variation in adult survival, which is consistent with the pattern found in Canada geese (*Branta canadensis*; Samuel et al. 1990, Rexstad 1992), Lesser Snow Geese (Francis et al. 1992b) and Brant (*Branta bernicla*; Ward et al. 1997). Except for the 1991 cohort, young survival rate was also unrelated to sex. Because of the slight sexual dimorphism in geese, no difference in survival between sex were expected. Although in a portion of the St. Lawrence estuary, Giroux and Bédard (1986) found a higher hunting mortality of adult female Greater

Snow Geese, compared to males, under some circumstances, this difference could have been local and not applicable to the overall population.

Adult survival rates were constant within each period (early and late). Short-term temporal variations might have been too small to be detected given the duration and sample sizes of this study. Temporal variations in survival rate between 1975 and 1989 could not be estimated because banding stopped during this period. Although recoveries continued to accumulate, annual variations in survival rate could no longer be estimated without making the unrealistic assumption of constant recovery rate.

There was no difference in survival rates between the early and late period, despite the ten-fold increase in population size. This also suggests that no natural density-dependent factors have affected adult survival yet. This study and others (Owen and Black 1989, Ebbinge 1991, Francis et al. 1992b) suggest that goose populations are rarely exposed to natural density-dependent regulation factors even at high density.

There was no significant difference between adult survival with respect to the breeding latitude. However, the sample size was small, both in terms of number of banding years and marked birds, reducing the power of the analysis. If variations exist with latitude, they could be due to differential costs of reproduction and/or migration, but could be too small to have been detected with the available sample size.

Hunting, survival and population growth

The Greater Snow Goose population was generally stable during an 8-year period from 1975 to 1982. During this time, recruitment did not change compared to the period before or after when population was growing rapidly. Adult survival rates were also similar between the early and late periods when the population was growing rapidly but, unfortunately, we have no survival estimate during the period when growth stopped because no banding was conducted. However, there was a clear increase in harvest rates with the re-opening of the US hunt in 1975. The doubling of harvest rate during this period compared to the early and late periods suggests that this factor was responsible for the stabilization of the population. This does not, however, provide proof that the increase in harvest rates directly caused a decline in survival as other unknown factors could have affected survival independently at the same time.

Recovery rates are often used as an index of hunting mortality but changes in recovery rates could be due either to changes in reporting rate, to changes in harvest rate, or a combination of the two. Variations in recovery rates of adult birds during the three periods were similar to those of the harvest rate which provides further evidence that hunting mortality increased considerably for a short period after 1975. Estimations of recovery rates between 1975 and 1989 requires the assumption of a constant adult survival rate during the early and mid period and this was likely not met. Survival may have decreased during this period because of high harvest rates and possible senescence toward the end of the time interval (Rockwell et al. 1996). However, a decrease in survival during this period would have biased low recovery probabilities compared to the assumption of constant survival. Therefore, our conclusion of an increase in recovery rate and hunting mortality after 1974 is conservative.

As outlined by Nichols et al. (1984), Anderson et al. (1987) and Nichols (1991), a direct test of the relationship between hunting and survival requires large-scale experimentation involving the manipulation of hunting regulations according to some *a priori* design. However, our results provide indirect evidence which suggest a causal relationship between survival and hunting pressure in geese. Nonhunted populations also have higher mean adult survival rates than hunted ones (i.e. Barnacle geese *Branta bernicla*, Owen and Black 1989) and, for some hunted populations, a negative relationship between survival rate and hunting pressure has been found (Ebbinge 1991, Francis et al. 1992b, Hestbeck 1994, Ward et al. 1997).

Possible bias in harvest rate estimates

Our harvest rates depend on the accuracy of spring population counts, estimated total harvest and, for one method, estimates of the adult survival rate. Several biases could affect these parameters. The area used by geese in spring is relatively small and well-defined, allowing good coverage and limiting the probability of missing segments of the population during survey (Reed et al. 1998).

Because hunting areas of Greater Snow Geese are geographically restricted in both Canada and the USA, kill estimates obtained by CWS and USFWS surveys are believed to be less accurate than for other species (Boyd and Finney 1978). This could explain unrealistically high estimated harvest rates of juveniles in 1972 and 1978. Precision of harvest estimate probably increased over time with more data resulting from increasing harvest. However, temporal trends should not be strongly affected by this problem.

Another assumption made to estimate harvest rates was that survival was constant throughout the entire period (from 1970 to 1996). We have suggested that the increased hunting pressure during the period of no population growth reduced adult survival rates. However, as no hunting occurs from spring to fall, the adult oversummer survival rates should have been less affected. With the second method of estimating harvest rates, our assumption of no natural mortality occurred during fall and winter may not have been met, which could have led to an over-estimation of harvest rates. Overall, because the two methods gave similar results, this suggests that biases, if any, were not severe.

Factors affecting harvest rates

Annual variations in the harvest are likely the result of several factors. A major one is the proportion of young in fall, but weather conditions, number of hunters, bag-limits and length of hunting season also contribute to variation in harvest. The sudden increase in the harvest rates following 1975 was undoubtedly due to the re-opening of hunting in the USA. However, the harvest rate suddenly declined in the mid-eighties and had remained low despite increase in the length of hunting season and bag limit. Explanations for this decline are mainly speculative. One or a few poor hunting seasons combined with a high production of young could have triggered the population growth, by reducing hunting mortality, leading to a run-away process. During the same period, geese started to expand their range during the fall migration and winter (Reed et al. 1998). They are now more dispersed, especially in agricultural fields, where hunting may be less efficient than in the "traditional" marshes (pers. obs., Giroux and Bédard 1986).

CONCLUSION

Annual survival of Greater Snow Geese was affected by age, but not by sex and breeding locations, and did not differ between two periods of population growth. Our study provided evidence of a causal relationship between hunting mortality and population dynamics in Greater Snow Geese. We showed that the population became essentially stable during a period of high level of hunting, which presumably reduced adult survival rates. However, it was not clear why harvest rates dropped and the population started to grow again after the early 1980s. This emphasizes the need for long-term monitoring to accurately estimate changes in population growth, harvest rates and survival rates, especially for management purposes.

Appendix

Estimation of harvest rates of the Greater Snow Goose

Variables used:

Measured:

Ns_i : spring population in year i

PF_i^y : proportion of young in fall in year i

H_i : harvest total in year i (H_i^Q : in Québec; H_i^U : in the USA)

AR_i : harvest age-ratio in year i (proportion of young in the harvest; AR_i^Q : in Québec; AR_i^U : in the USA)

Calculated:

NF_i : fall population in year i (NF_i^a : of adults; NF_i^y : of young)

HR_i : harvest rate in year i (HR_i^a : of adults; HR_i^y : of young)

S_{su} : oversummer survival

Estimation of young and adult fall flocks:

First method:

$NF_i^a = Ns_i * S_{su}$

$NF_i^y = NF_i^a * PF_i^y / (1 - PF_i^y)$

Second method:

$NF_i = Ns_{i+1} + H_i$

$NF_i^a = NF_i * (1 - PF_i^y)$

$NF_i^y = NF_i * P_i^y$

Estimation of harvest rate:

$$HR_i^a = (H_i^Q * (1 - AR_i^Q) + H_i^U * (1 - AR_i^U)) / NF_i^a$$

$$HR_i^y = (H_i^Q * AR_i^Q + H_i^U * AR_i^U) / NF_i^y$$

CHAPITRE 5

SURVIVAL OF YOUNG GREATER SNOW GEESE DURING THE FALL MIGRATION.

RÉSUMÉ

Le vol migratoire est l'une des parties les plus critiques du cycle vital des oiseaux migrateurs et peux affecter négativement leur survie. Nous avons estimé la survie pendant la plus importante partie de la migration automnale de jeunes de la Grande Oie des neiges (*Chen caerulescens atlantica*) en utilisant des individus marqués pendant l'été à l'île Bylot (T.N.O., Canada) et l'automne à la Réserve Nationale de Faune du Cap Tourmente (Québec, Canada). Les retours de bagues ont été analysés avec le logiciel SURVIV, l'utilisation de deux périodes de baguage (avant et après la migration) permettant l'estimation du taux de survie pendant la migration. Des observations de familles dont la femelle adulte avait reçu un collier durant l'été, pendant la première partie - la plus importante - de la migration, ont aussi permis d'estimer ce paramètre. De grandes variations inter-annuelles de la survie pendant la migration ont été mises en évidence, principalement reliées aux variations des conditions des cohortes avant l'envol: une masse corporelle élevée à la fin de l'été et une date d'envol hâtive influençaient positivement et de façon indépendante la survie. La survie des jeunes pendant la migration automnale la plus élevée s'est produite en 1993 et 1995 avec plus de la moitié des jeunes survivant à la migration alors que seulement 10% environ en 1994 complétaient le voyage. Les observations ont permis également de conclure à une certaine indépendance des jeunes d'une même famille face au risque de mortalité pendant la migration. La concordance relative des résultats selon les différentes méthodes a permis d'augmenter la confiance dans les résultats.

ABSTRACT

The migratory flight is one of the most hazardous stages of the life cycle of migratory birds and could affect negatively their survival. Survival of young Greater Snow Geese (*Chen caerulescens atlantica*) during the first and major portion of fall migration was estimated using marked individuals banded during summer on Bylot Island (N.W.T., Canada) and fall at the Cap Tourmente National Wildlife Area (Québec, Canada). The two-seasons (before and after the main portion of the migratory flight) banding allowed to estimate fall migration survival, using recovery data and SURVIV program. Observations before and after the main portion of the migratory flight of families with adult females neckbanded during summer were also used to estimate this parameter. Large inter-annual variations in fall migration survival occurred, and were linked to variations in cohort conditions: high body mass at the end of the summer and early fledging date had, independently, a positive effect on survival. The highest survival occurred in 1993 and 1995 with more than half of the young surviving the migration, while only 10% in 1994 completed the journey. Brood mates appeared to be relatively independent in regard to the risk of mortality during migration. Similarity among estimations given by the different methods increased our confidence in results.

INTRODUCTION

The migratory flight is one of the most hazardous stages of the life cycle of migratory birds. Long-distance flights, unpredictable and often harsh weather conditions, and the crossing of ecological "barriers" such as deserts, large bodies of open water or high mountains all increase mortality risk during migration (Alerstam 1990, Gwinner 1990). Pienkowski and Evans (1985) reported that shorebirds with shorter migratory flights had better survival than populations with longer ones. Owen and Black (1991), who reviewed the importance of migration mortality in non-passerine birds, reached the same conclusion: mortality is especially high in species which undertake long journeys particularly for young birds. However, reliable estimates of migratory mortality are rare because it is rarely possible to measure losses incurred during the journey between nesting and wintering areas. Yet, post-fledging survival is an important component of the life cycle and could be an important factor determining recruitment into the population, especially for long-distance migrants (Owen and Black 1991).

In a population of Barnacle Geese (*Branta leucopsis*) breeding in Svalbard and wintering in Scotland, gosling survival rate during migration was estimated at 65%, compared to 96% for full grown birds (Owen and Black 1989). Gosling survival was also positively related to their age at banding and body mass. For the mid-continent population of Lesser Snow Geese (*Chen caerulescens caerulescens*), Francis et al. (1992a) showed that newly fledged geese had lower survival rates than adults, and suggested that much of the mortality occurred before geese left the breeding areas or during the first stage of migration, although they gave no direct estimate of mortality. Gosling survival also varied annually, suggesting that conditions experienced by various cohorts influenced their survival (Francis et al. 1992b).

In arctic-nesting herbivorous birds such as geese, young have little time to complete their growth and acquire the fat reserves required for the southward migration (Lesage and Gauthier 1997). Inter-annual variations in breeding date and growth conditions during the summer will therefore affect the body condition of each cohort at fledging (Lepage et al. 1998). Weather conditions (especially wind, a major factor affecting migration; Butler et al. 1997, Richardson 1990) and food availability on staging areas during fall migration could also vary among years and affect survival.

The Greater Snow Goose (*Chen caerulescens atlantica*) is a long-distant migrant nesting in the High Arctic. This species migrates along a relatively narrow path, which provides a unique opportunity to capture and resight marked birds along the way. Our objectives were to 1) compare estimates of survival of young Greater Snow Geese obtained with several independent methods using marked birds, 2) determine annual variations in fall migration survival, 3) examine to what extent mortality among brood mates is independent and 4) examine how variations in fledging conditions of cohorts can explain inter-annual variations in migration survival.

METHODS

Study species and chronology of migration

The Greater Snow Goose is the northernmost breeding species of geese in North America, nesting throughout the eastern Canadian Arctic Archipelago and Northwest Greenland (Bellrose 1980). The largest breeding colony is located on the south plain of Bylot Island (N.W.T, 73°N 80°W), with > 27,000 nesting pairs in 1993 (Reed et al. 1992. Gauthier et al. 1996). This population migrates 4,000 km from Bylot Island to the wintering grounds situated on the mid-Atlantic coast of the United States. Chronology of migration and use of staging areas in the Arctic and sub-Arctic are poorly known. Departures from Bylot Island occur at the end of August (J.F. Giroux, unpub. data). About five weeks later, geese arrive in the upper estuary of the St. Lawrence River (Québec, 47°N 70°W), a major staging area, 3,000 km farther south. This confined staging area is used from late September to early November (Maisonneuve and Bédard 1992, pers. obs.). Large arrivals of geese usually occur in the first half of October, typically in 2 or 3 "waves" (pers. obs., J.F. Giroux, unpub. data). Departures of geese occur throughout October and are more gradual. From the St. Lawrence estuary, the geese migrate the additional 1,000 km to their wintering grounds along the Atlantic coast from New Jersey to North Carolina.

Banding method and recoveries

From 1990 to 1996, goose families were captured annually in a glacial valley on Bylot Island for banding during a 7-day period in early-August when the adults were molting and before the young could fly (see Hughes et al. 1994 for a description of the study area). Birds were classified as adults (> one year old) or young based upon plumage, and their sex was determined by cloacal eversion. Banding occurred after non-breeders (including yearlings), who molt earlier, had regained flight abilities. Therefore, virtually all adults captured were breeders and were at least two years old since snow geese do not breed as yearlings (Cooke et al. 1995). All birds received a metal US Fish and Wildlife Service leg band and many adult females received plastic neck bands. Neck bands were yellow with black, 4-digit alphanumeric codes (2 letters and 2 numbers). Since 1993, female goslings also received a colored plastic legband with a different color every year (Table 3 in appendix A). The culmen, head, tarsus and ninth primary of all the goslings were measured (see Lepage et al. 1998 for details). They were weighted to the nearest 25g (nearest g since 1995). All goslings were carefully checked for the presence of web-tags put on during the hatching period in the study area (Lepage et al. 1998).

From 1993 to 1996, banding was also done during the fall at Cap Tourmente National Wildlife Area (NWA, Québec, 47°04'N 72°47'W), a major staging area in the upper estuary of the St. Lawrence River. Geese were captured in agricultural fields with baited cannon-nets between 5 and 31 October (see Morez 1996 for details). Measurements described above were conducted, but only standard metal leg bands were used.

Recoveries occurred during the fall and winter hunting, which is concentrated in southern Québec and the eastern United States of America, and came mostly from the Bird Banding Laboratory. In the upper estuary of the St. Lawrence River, outfitters were also solicited by letters or personal contact to report bands directly to our laboratory. We used recoveries for the period 1993 to 1995 (Table 3 in appendix A).

Observation of neckbanded geese

Brood size of neckbanded females was determined by visual observations using 60x spotting scopes before and after migration. On Bylot Island, observations of neckbanded geese were made by 2-3 observers on 15-19 August in 1994 and on 10-21 August in 1995 and 1996. Post-migration observations were made in the St. Lawrence estuary from late September to early November in the same years, covering the full staging period of geese. Each year, 3 to 4 people made daily observations at the sites most heavily used by geese: one or two people at Cap Tourmente NWA, one in Iles-aux-Grues/Iles-aux-Oies islands and one at bird sanctuaries scattered on the south shore of the St. Lawrence between Quebec city and La Pocatière (see Appendix E).

The following information was recorded: neck band code, number of young with the female (brood size) and presence or absence of mate. Young geese usually stay with their parents until they are nearly one year old (Prevett and MacInnes 1980, Owen 1980). On Bylot Island, geese occurred in discrete families or in small flocks and goslings stayed close to their parents, facilitating accurate recording of family status. On the staging areas, however, flocks were large (often > 1,000) and the resulting high density complicated status determination. At both sites, behavior was used to determine the status and brood size of neckbanded geese: walking or feeding with young and an adult in close contact, aggressive interactions by the adults against other birds while young stay close to them or by young against other young, and simultaneous take-off or landing. Presence of legbands on the young (metal or colored plastic bands) and the male was also used to ascertain the status.

Survival analyses

Band recovery analyses were conducted following the procedures and notations of Brownie et al. (1985) using the computer program SURVIV (White 1983) to test several models. Use of two banding periods (pre- and post-migration) allowed an estimation of the fall migration survival, which, otherwise, is confounded with the direct recovery rate. This requires the assumption that the direct recovery rate of birds banded on Bylot Island and at Cap Tourmente are the same. Even though fall banding occurred at the beginning of the hunting season, we removed recoveries occurring north of Cap Tourmente or before the first day of banding at Cap Tourmente (excluding 19.3% of the recoveries) to ensure that recovery rates were similar between summer and fall banded birds. The following notations were used in the models. M_i and N_i represented the number of adult Greater Snow Geese banded before (summer) and after (fall) migration, respectively, in the *ith* year of the study and M'_i and N'_i were the same for young. S_i^*, S_i' and f_i' represented the fall migration survival rate, the annual survival rate and the recovery rate, respectively, for young in the *ith* year of the study. S_i and f_i represented the same parameters for adults (Table 4 in appendix A). Because survival of adults during fall migration is known to be close to 1 (see chapter 2), the fall migration survival rate of adults was not paramaterized in the model. Neck-banded females were not included in the analysis because they have higher recovery rates than those without (see chapter 3). These procedures reduced the number of parameters to be estimated and thus increased the precision of the parameters of primary interest. The most general model included the effects of age (a; two age classes: young and adults), sex (s) and time (t) on both survival and recovery rates. A hierarchy of models sequentially constraining some parameters was tested to determine the most parsimonious list of parameters needed to model the data. Likelihood ratio tests (Brownie et al. 1985) between models and the Akaike Information Criterion (AIC; Burnham et al. 1995) were used to select the best model among subsets of the general one.

With visual observations, we could estimate survival of young during the migration from two independent data sets. The first one included all families that were observed both before migration on Bylot Island and after it, on the staging areas (hereafter called the double-observed families). As the fate of each family was known, the fall migration survival rate of these young was estimated by:

$$S^* = \text{Brood size in the estuary} / \text{Brood size on Bylot Island}$$

The second data set consisted of the marked families observed only once, either on Bylot Island or on the staging areas (the single-observed families). If we assumed that observed birds on each site were a random sample of the same population at two different times, survival of young could be estimated by comparing the average brood size of families observed before and after migration. Because of our marking procedure, newly-marked adults were largely successful breeders. On the contrary, previously-marked adults included an unknown proportion of failed or non-breeders which often dispersed away from the study area before the late summer observation period (J. Bêty, unp. data), leading to heterogeneity in the probability of re-observation. Therefore, to insure homogeneity in the data set, only newly-marked birds were used in this analysis. For this data set, survival of juveniles during the fall migration was estimated by the change in number of young per family between Bylot Island (1) and the St. Lawrence estuary (2):

$$S^* \approx \frac{p_2}{p_1} \qquad \mathrm{SE} = SE\left[\frac{p_2}{p_1}\right]$$

and $p = \frac{Ny}{Nf}$ *Ny*: number of young; *Nf*: number of family.

Effect of hunting

Based on recoveries, some hunting occurred before arrival of geese in the St. Lawrence staging areas, but its impact was negligible (0.03% of all recoveries of birds banded on Bylot Island). On the contrary, the sites where fall observations took place were heavily hunted. This could bias the migration survival estimates as families were exposed to hunting mortality between the time they arrived at the staging areas and the time they were observed. Because most geese arrive in the first two weeks of October on the staging areas, a family observed late in the fall season was likely to have been exposed to hunting mortality for a longer period of time than one which was observed early in the season. To evaluate this bias on survival estimates based on the observations of neckbanded families, we calculated migration survival as above but using only the first 50% or 70% of all neck bands observed in the fall. The small number of double-observed families precluded this calculation for this data set.

To further evaluate the impact of hunting, we used families for which the status was determined more than once during fall (ca. 60% of observed families in 1995 and 1996). We estimated a daily survival of young during their stay on the staging areas with the Mayfield method (Mayfield 1975, Johnson 1979). Each young within a brood was treated independently, with respect to its hunting vulnerability. Because hunting pressure was not evenly distributed throughout the season, we divided the season into 4 equal periods each year and calculated a Mayfield estimate for each to better meet the assumption of constant mortality risk.

Independence of fate

We tested the hypothesis of independence of young within broods for migration mortality. To do so, we estimated the probabilities of observing each possible family size after migration for each family size observed before migration, based on average migration survival estimates and assuming independence of fate among siblings. For example, a family of two young before migration could lose 0, 1 or 2 young during migration, each young having the same probability of survival regardless of what happened to its brood mates. For each year, the expected distribution of family size after migration was weighed by the proportion of each family size observed before migration, both for single- and double-observed families. For the single-observed families, we compared expected and observed distributions of presence or absence of young after migration, using the 70% data set to minimize the hunting bias. The absence of young after migration implies a total brood loss or no young before migration and presence of young implies no loss or partial brood loss, which could not be separated in this case. The known fate of each double-observed families allowed us to estimate both total and partial brood loss. The expected and observed distributions of no, partial and total brood loss were then compared for 1995 and 1996 (1994 was excluded because of the small sample size).

Cohort paramaters

A cohort is here defined as a group of individuals born during the same time interval (year). As Greater Snow Goose is a single-brooded species, the cohort of 1994, for example, referred to young born during the breeding season of 1994. We were interested in mean age and mass at fledging of each cohort. Age of all captured goslings was determined from their ninth primary length and mass was standardized at age of 35 days while controlling for seasonal effects on growth (see details in chapter 6 and Lepage et al. 1998). Age at banding allowed us to estimate the mean fledging date of each cohort (fledging age = 43 days; Lesage and Gauthier 1997).

RESULTS

Annual variations in fall migration survival

Overall, survival estimated by the 3 independent methods gave similar results. Although values differed slightly between methods, magnitude and trends among years were consistent (Fig. 1). The largest discrepancy occurred for the 1994 survival estimate obtained with the data set of double-observed families which was much lower compared to the other two. However, the former estimate was based on a very small sample size (N = 5). The general agreement between methods suggests that our survival estimates are reliable.

With band recovery data, the preferred model was $(S_{as't}.f_{at})$(Fig. 2). In this model, survival and recovery rates were age- and time-dependent. No effect of sex on the survival and recovery rates was found, except for adult survival. Fall migration survival rates for the young ranged from 0.17 (SE = 0.06) in 1994 to 0.77 (0.18) in 1995 (Table 1), which represented significant annual variation in first-year survival rates (χ^2 = 13.85, df = 2, P = 0.001).

Visual observations reduced the population sampled to neckbanded birds and their families but yielded more details on the occurrence of mortality during migration. Depending on the year, 26 to 39% of the neckbanded geese observed with young at Bylot Island were resighted again on the staging areas. Migration survival of young was 0% in 1994 as the 5 observed families lost all their young. In 1995, the survival was much better as 20 young out of 39 (51%) were seen again after the migration (N = 19 families). In 1996, only 18 young out of 46 completed the migration, a survival rate of 39% (N = 24 families).

Many more marked birds were observed only once, either on Bylot Island or on the staging areas, than double-observed families (Table 2). Marked birds were more likely to be observed on the fall staging areas than on Bylot Island (about three times more) because of the higher density and easier access at the former site. This data set also showed that fall migration survival of young was low in 1994, 0.12 (SE = 0.06), high in 1995, 0.57 (0.09) and intermediate in 1996, 0.38 (0.07) (Table 2).

All three methods point to a large inter-annual variation in fall migration survival rate of young. The highest survival rate occurred in 1993 and 1995, with more than half of the

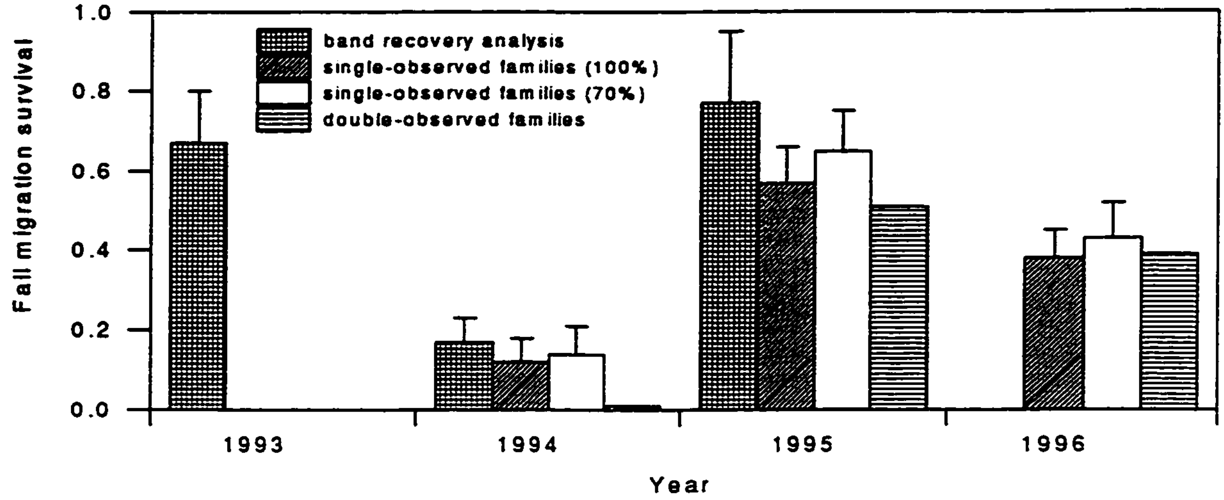


Fig. 1. Estimate (mean ± SE) of fall migration survival of young Greater Snow Geese, using band recovery analysis or family resightings. Family resightings involve neckbanded birds observed on Bylot Island and/or on the St. Lawrence estuary (at only one site: single-observed; at both site: double-observed). For the single-observed families, different proportions of neckbanded birds observed on the estuary could be used (the first 70% or 100%; see methods and results).

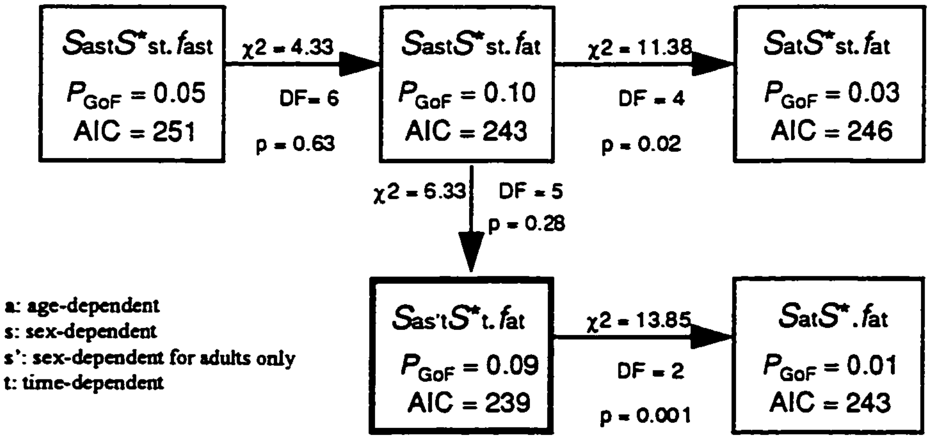


Fig. 2. Modeling of survival and recovery rates for Greater Snow Geese banded at Bylot Island and Cap Tourmente with SURVIV. Banding and recovery years are from 1993 to 1995. The best model is in the bold box.

S: survival rate; *S**: migration survival rate for young; *f*: recovery rate; PGoF: P-value of Goodness-of-Fit; AIC: Akaike's Information Criterion.

Table 1. Annual survival and recovery rates (mean ± SE) and migration survival rates of Greater Snow Geese banded at Bylot Island and Cap Tourmente, 1993-95, under the model (Sas't S* fat).

	Adults						Young					
	Recovery		Survival				Recovery		Survival		Migration survival	
			females		males							
	f	SE	*S*	SE	*S*	SE	*f*	SE	*S*	SE	*S*	SE
1993	0.025	0.005					0.113	0.020			0.670	0.130
1994	0.019	0.003	0.140	0.140	0.580	0.139	0.082	0.021	0.382	0.085	0.175	0.056
1995	0.022	0.003	0.540	0.164	0.772	0.186	0.067	0.015	0.155	0.063	0.772	0.184

Table 2. Family size (mean ± SE) of newly neckbanded females observed on Bylot Island before the migration and in the St. Lawrence estuary after the migration. Numbers in brackets are families observed in both places.

	Number of family					
	1994		1995		1996	
No. of young	Bylot	Estuary	Bylot	Estuary	Bylot	Estuary
0	33 (10)	143 (14)	17 (3)	95 (9)	36 (13)	206 (22)
1	4 (3)	7	11 (6)	70 (7)	14 (6)	35 (2)
2	5 (1)		14 (6)	34 (5)	21 (6)	20 (4)
3	1		18 (7)	17 (1)	10 (3)	9 (1)
4	1		5	6	3 (1)	
5			1			1
Total	44 (14)	150 (14)	66 (22)	222 (22)	84 (29)	271 (29)
% with young	25%	5%	74%	57%	57%	24%
Mean brood size[a]	1.91±0.28	1.00±0.00	2.41±0.14	1.68±0.08	2.04±0.13	1.65±0.10
Fall survival	0.12 ± 0.06		0.57 ± 0.09		0.38 ± 0.07	

a: mean brood size = number of young / number of families with young.

young completing their migration, whereas in 1994 only ca. 10% of young survived the migration.

Effect of hunting on survival estimates

Analysis of the temporal distribution of first observations of neckbands in fall showed that a greater proportion of marked families were observed in the first half of the staging period than in the second half: depending on the year, it took 26 to 46% of the total length of the staging period to observe 50% of all neckbanded birds, and 35 to 58% of the staging period to observe 70% of them (Table 3). Restricting the survival analysis to the first 50% or 70% of the birds observed tended to increase slightly the survival estimate in 1995 and 1996, but almost doubled it in 1994 (Table 3). Inter-annual differences, however, remained unchanged with the highest survival in 1995 and the lowest in 1994. The large increase in 1994 could be due in part to the small sample size of families with young (N = 7) that year.

The fall staging survival rate (i.e. Mayfield estimate) could not be estimated in 1994 because of too few families with young with multiple resightings. In 1995 and 1996, status of 38% (N = 71) and 28% (N = 36) of the families observed at least twice during the fall changed, respectively. By period, the daily survival estimate was relatively high but variable, presumably reflecting variability in hunting pressure and/or vulnerability. The daily estimate ranged from 0.990 ± 0.010 to 0.943 ± 0.014 in 1995 and from 1.00 ± 0.00 to 0.944 ± 0.020 in 1996 (Fig. 3). In both years, the highest rate occurred in the first period, when 22% and 50% of neckbands were observed in 1995 and 1996, respectively. For the entire duration of neckband observation, the daily survival rate was estimated at 0.96 ± 0.01 in 1995 and 0.97 ± 0.01 in 1996.

Independence of fate

Because siblings share characteristics known to affect migration survival (hatching date, body mass at fledging; see chapter 6) and are exposed to the same events during migration, we tested the hypothesis of independence of siblings with respect to mortality during migration. If mortality of siblings was partially dependent, no and total brood loss would occur more than expected under the assumption of independence. Conversely, if

Table 3. Estimation of fall migration survival of young Greater Snow Geese in newly marked families using various proportions of the total neck bands observed during the fall staging period. N = number of neck bands observed in the fall.

		Proportion of total neck bands observed in the fall		
		50%	70%	100%
Duration of observation period [a] (%)	1994	42%	58%	100%
	1995	46%	54%	100%
	1996	26%	35%	100%
Survival	1994	0.21 ± 0.12	0.14 ± 0.07	0.12 ± 0.06
	1995	0.68 ± 0.11	0.65 ± 0.10	0.57 ± 0.09
	1996	0.45 ± 0.11	0.43 ± 0.09	0.38 ± 0.07
N	1994	73	102	146
	1995	101	142	203
	1996	127	178	255

a: This percentage represents the time required from the beginning of the staging period to observe 50%, 70% or 100% of the total neck bands seen during the whole staging period.

siblings were completely dependent for mortality, no partial brood loss would occur. For both single- and double-observed families, there was no significant difference between the observed and expected distributions in 1994 and in 1995, suggesting independence among young (Figs. 5 and 6). However, in 1996, more families without young were observed than expected for the single-observed families and more total and no brood loss occurred than expected for the double-observed families (Figs. 4 and 5).

Mortality of young during migration seems to be widespread among families, as few of them were not affected by it: only 26% and 31% of double-observed family in 1995 and 1996 had no loss of young (1994 was excluded because of small sample size).

Effect of cohort conditions

Average conditions of cohorts and the timing of fledging varied considerably among years. Mean body mass at fledging was lowest in 1994 and highest in 1996: 75% of young in 1996 had a higher mass than young in 1994 (Fig. 6). Mean fledging date was similar in 1994 and 1995 (19 August) but slightly earlier in 1993 (17 August) and later in 1996 (22 August). Consequently, by the time 80% of the young had reached fledging age in 1993, only 50% had reached this stage on the same date in 1994 and 1995 and 10% in 1996 (Fig. 7).

The lowest migration survival occurred in 1994, a year where time of fledging was near average but body mass of young was the lowest at fledging. Although mean body mass in 1994 was 88% of the 1995 value, fall migration survival in 1994 was 5 times lower than in 1995, suggesting an important effect of body mass on migration survival. However, although body mass was highest in 1996, survival was lower than in 1993 and 1995, possibly due to the late fledging date that year. The earlier fledging date in 1993 did not result in a higher survival compared to 1995. The low mass at fledging in 1993 could have canceled the advantage of early fledging in 1993.

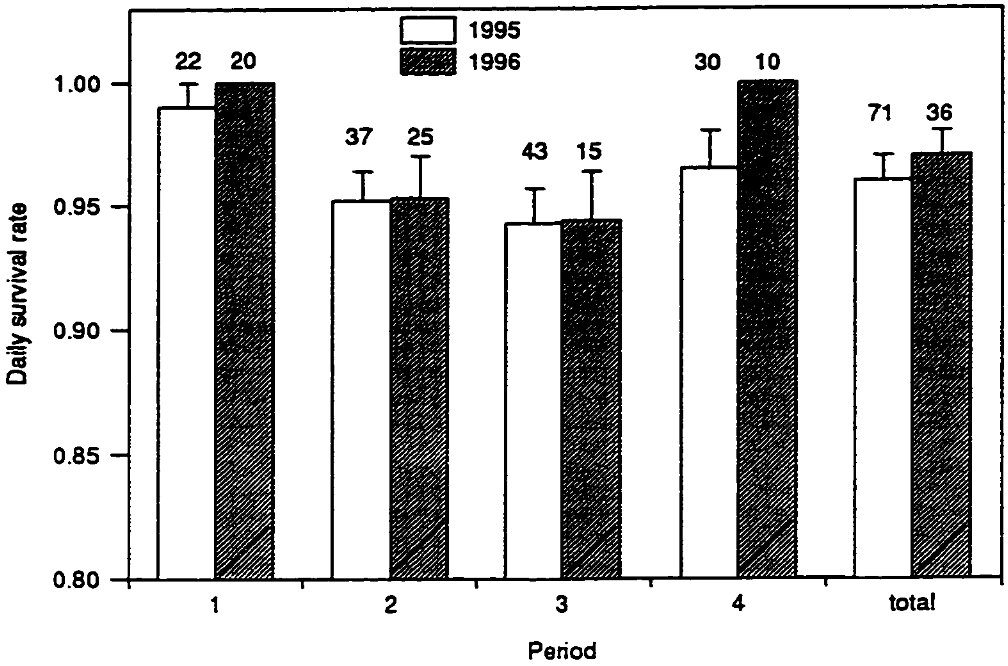


Fig. 3. Daily survival rate estimates (Mayfield estimates) in 1995 and 1996 for young Greater Snow Geese during the fall staging period, using multiple-sighted families. Periods are of 8 and 6 days in 1995 and 1996, respectively. Numbers of observed families for each period are given on top of the bars. A family can be observed in more than one period.

N.B.: 50% of families were observed in the first period in 1996. After the first half of the second period, 50% of families in 1995 and 70% in 1996 had been observed. At the end of the second period, 70% of families had been observed in 1995.

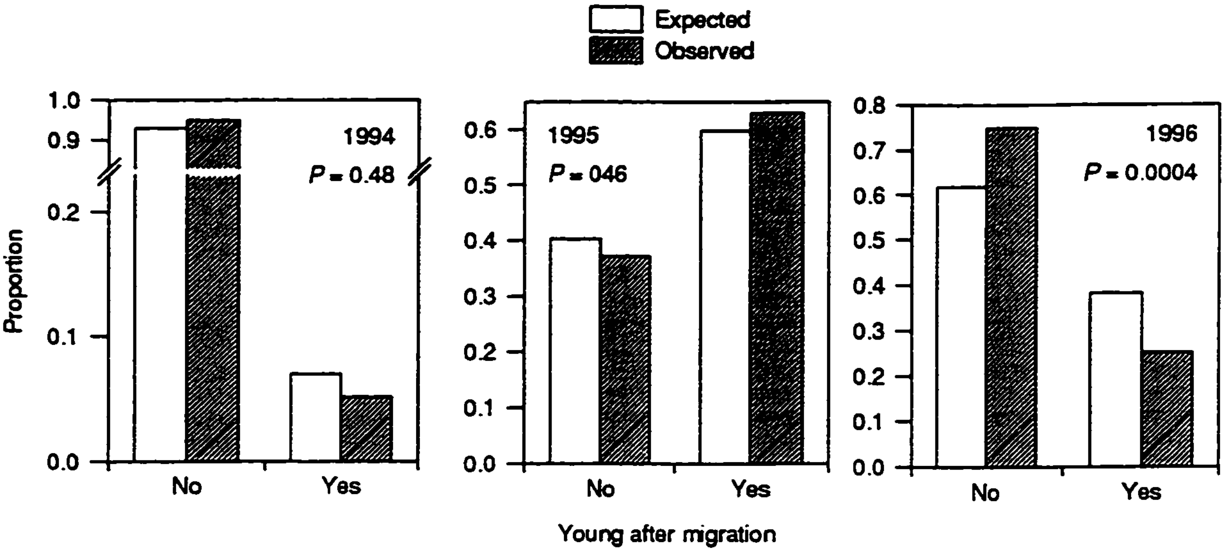


Fig. 4. Observed and expected distributions of presence of young after migration for single-observed families. The observed distributions use the first 70% observed neck bands in the fall, while the expected distributions were calculated assuming independence of siblings for migration mortality. The *P*-value of chi-square tests are given.

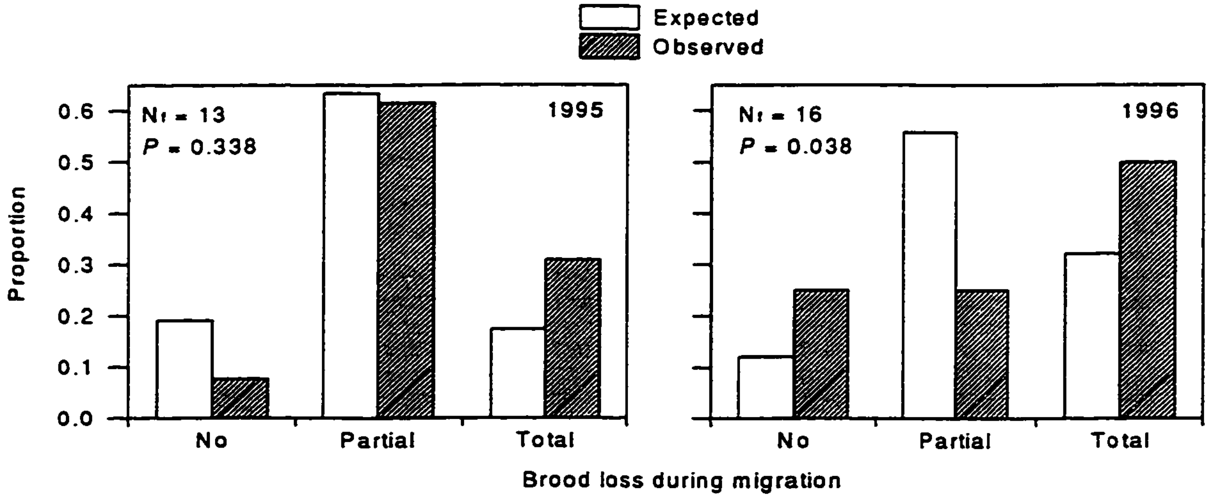


Fig. 5. Observed and expected distributions of brood loss for double-observed families with more than one young in 1995 and 1996. The expected distributions were calculated assuming independence of siblings for migration mortality (see methods).
N_t = number of families.

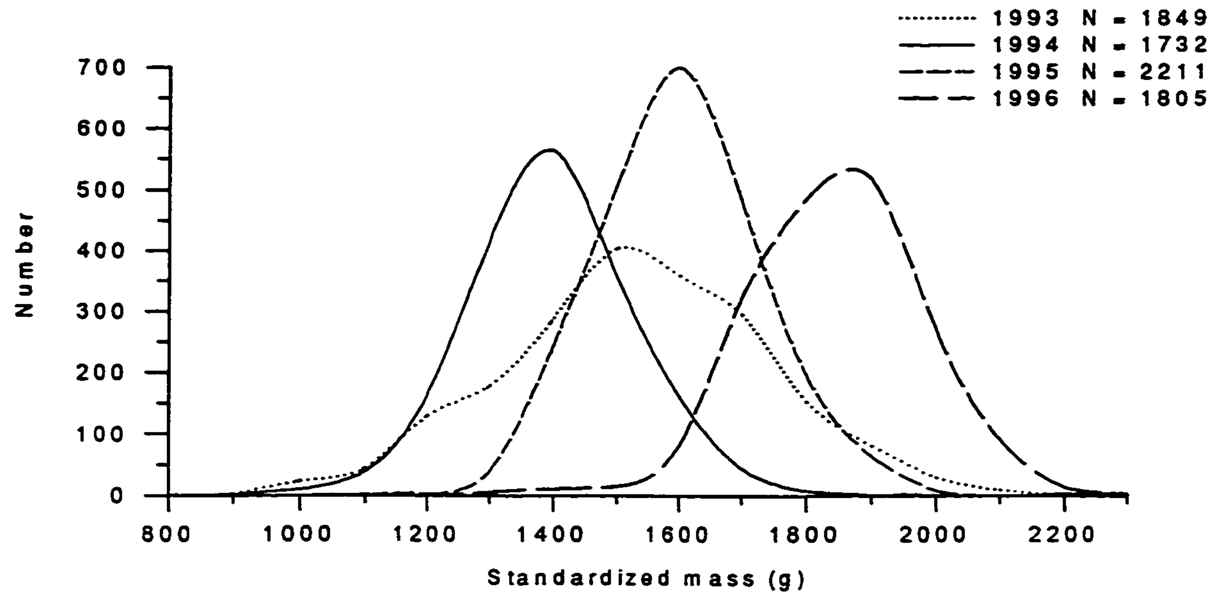


Fig. 6. Body mass of Greater Snow Goose goslings captured at banding on Bylot Island, by cohorts. Mass is standardized at 35 days with a multilinear regression (see methods).

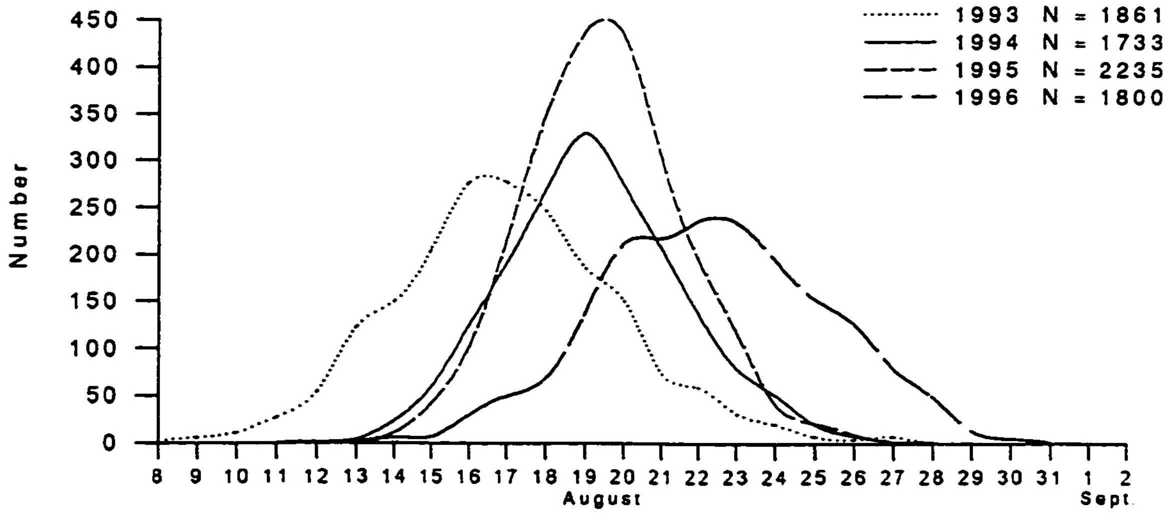


Fig. 7. Estimated fledging date of Greater Snow Goose goslings captured at banding on Bylot Island, by cohorts (see methods).

DISCUSSION

A large inter-annual variation in migration survival of young Greater Snow Geese occurred, with a 5-fold difference between the highest and lowest survival estimates. However, for any year, the survival of juvenile Greater Snow Geese was lower than for adults (estimated at 93%; see chapter 2). Data on the extent of young migration mortality among and within broods is sparse in the literature because it is rarely possible to follow individual families throughout the migration. Here, marked families observed before and after migration allowed us to estimate the extent of brood loss and the independence of fate among siblings. The relative low proportion of families with no loss of young suggests that mortality of young during migration is widespread among families. However, within broods, we found evidence that mortality among siblings during migration was relatively independent.

Migration survival varied greatly among years, suggesting strong effects of cohort and environmental conditions. We have shown elsewhere that fall migration survival of a young is positively related to its mass at the end of the summer and negatively to its relative hatching date (i.e. the earlier its fledging date, the better its migration survival; chapter 6). Therefore, inter-annual variations in cohort conditions could explain, at least partially, annual variations in fall migration survival. Our analysis suggests that both body mass and fledging date can independently influence gosling survival during fall migration, as cohorts with the lowest mass or later fledging date had the poorest survival. The very low survival of the 1994 cohort compared to other years despite a moderate difference in body mass suggests a threshold effect of body mass on survival. Differences in survival among the 1993, 1995 and 1996 cohorts were comparatively small. Among those, the lower survival of the 1996 cohort, despite a higher mass prior to migration, clearly shows the importance of early fledging. Therefore, the effect of fledging date on fall migration survival could be especially important in years of late breeding and have only a minor impact in early-breeding ones.

Other critical factors possibly acting on the fall migration survival are the weather conditions encountered en route as well as the quality of the staging areas used between the breeding grounds and the estuary of the St. Lawrence river. Because there is no fat accumulation before fledging, goslings starting the migratory flight will need to stop frequently, at least in the first part of the migration, to accumulate fat stores (Lesage and Gauthier 1997). Much of the migration mortality could thus happen during this period, especially if goslings encountered bad weather and poor food availability.

Potential biases

Fall migration survival rate was estimated from the breeding grounds to the staging areas of the St. Lawrence estuary, leaving out the final migratory leg to the wintering grounds. We believe that this should have a negligible effect on our estimate for several reasons: The part considered is the first and lengthiest part of the migratory journey (ca. 3,000 of 4,000 km) and certainly the most difficult (flights over sea, harsh arctic and sub-arctic lands). High quality feeding habitats in the staging areas of southern Québec should enable geese to replenish their fat reserves and leave for the final migratory flight in good condition. Moreover, because geese are exposed to hunting mortality from their arrival in the upper estuary, subsequent survival estimates would be a combination of natural and hunting mortality.

Reliable estimates of migration survival are difficult to obtain because it is rarely possible to either directly measure losses incurred during the journey between nesting and wintering areas or to separate annual survival into seasonal estimates. Confidence in our fall migration survival estimate can be assessed by comparing methods and by examining sources of potential bias. By using 3 independent methods, we were able to identify possible problems in estimations. These methods yielded relatively similar estimates and all of them showed identical trends between years. Estimates based on band recoveries were higher than estimates from neck bands observations, but their confidence intervals were large. A critical assumption of the two banding periods model is that direct recovery rates are identical for the two banding samples. Although we controlled this bias to some extent by deleting recoveries occurring before Cap Tourmente, the second banding occurred at a heavily hunted site and this could have introduced some bias.

Estimates from neck band observation could also be biased if: (1) neck bands affect survival and behavior of the marked birds, (2) banding induce immediate mortality and disrupt family cohesion, (3) adoption occurs during migration and at staging areas or (4) a large proportion of mortality on the staging areas is due to hunting. We have shown elsewhere that neck bands did not affect survival and behavior (chapter 2 and 3) and that immediate post-banding mortality was small (chapter 1). In Lesser Snow Geese, family groups reunited rapidly after banding and brood-mixing and adoption were rare (Prevett and MacInness 1980, Williams et al. 1995). Using different proportions of neck bands observed during the fall allowed us to partially control hunting bias in the fall migration survival estimates. The increase in survival estimates when using a decreasing proportion of total neck bands observed (i.e. those observed the earliest and thus less exposed to hunting mortality) suggests a certain impact of hunting on our survival estimate. To minimize this bias, exposure to hunting risk should be minimized by using the shortest duration of observation period after arrival of the birds while retaining an adequate sample size. We suggest that this trade-off is best achieved by using 70% of all neck bands observed. Analysis of weekly survival rates during staging also shows that impact of hunting was not as large during the first part of the staging as later on.

CHAPITRE 6

SEASONAL EFFECTS ON POST-FLEDGING SURVIVAL OF GREATER SNOW GOOSE YOUNG.

RÉSUMÉ

Nous avons évalué l'effet respectif de la chronologie de la nidification et de la masse corporelle sur les variations intra- et inter-annuelles de la survie après l'envol des jeunes de la Grande Oie des neiges (*Chen caerulescens atlantica*). Le baguage réalisé à la fin de l'été à l'île Bylot (T.N.O., Canada) a permis d'estimer les caractéristiques individuelles des oisons (masse corporelle et date d'éclosion relative). Les récupérations subséquentes de bagues ont été utilisées comme indice de survie et modélisées selon la régression logistique pour évaluer simultanément l'effet de plusieurs variables (masse corporelle, date d'éclosion relative, date médiane d'éclosion, année) et leurs interactions sur la survie après l'envol. Un oison éclos plus tôt que la moyenne avait une probabilité significativement plus élevée de survie après l'envol, surtout lors des années de nidification tardive. La masse corporelle (corrigée pour les effets de l'âge et les effets saisonniers) avait aussi un effet significatif et indépendant, les oisons les plus gros ayant une meilleure probabilité de survie après l'envol. Cet avantage était aussi accentué les années de nidification tardive. Par contre, la masse corporelle n'avait pas d'effet sur la survie après l'envol pour les oisons éclos tôt contrairement aux oisons éclos durant ou après le pic d'éclosion. Une analyse éliminant les oisons potentiellement d'une même famille a conduit aux mêmes conclusions. De plus, il n'y avait pas de preuve de croissance compensatoire pendant la migration automnale, suggérant que les différences de tailles mesurées à la fin de l'été persistent jusque l'âge adulte.

ABSTRACT

We studied the relative effect of timing of nesting and body mass on intra- and inter-annual variations in the post-fledging survival of Greater Snow Goose young (*Chen caerulescens atlantica*). Banding done at the end of the summer on Bylot Island (N.W.T., Canada) allowed the estimation of individual goslings parameters (body mass and relative hatching date). Band recoveries were taken as an index of post-fledging survival and used in a logistic regression procedure to evaluate simultaneously the effect of several variables (body mass, relative hatching date, median hatching date, year) and their interactions on post-fledging survival. Hatching early had a positive effect on the post-fledging survival probability, and this effect was accentuated in late breeding years. Mass at banding also affected post-fledging survival independently, as the heaviest goslings (for a given age and once the seasonal effects are controlled for) survived better. This advantage was also greater in late breeding years. However, body mass had no effect on survival of early-hatched birds, contrary to mid- and late-hatched ones. Deleting apparent siblings did not change conclusions of the analysis. Furthermore, there was no evidence of compensatory growth during the fall migration, suggesting that differences in body size at the end of the summer persist until adulthood.

INTRODUCTION

Seasonal variations in reproductive success are a general feature of many populations of birds. Several components of reproductive success decline during the breeding season. In general, there is a tendency for young which hatch late in the season to grow more slowly (Cooch et al. 1991, Sedinger and Flint 1991, Lindholm et al. 1994, Lepage et al. 1998) and have lower survival (Owen and Black 1989, Daan et al. 1990, Norris 1993, Sedinger et al. 1995) and recruitment rates (Cooke et al. 1984) than early-hatched young. The seasonal decline in reproductive value is partly due to decreasing post-fledging survival of offsprings with increasing hatching date (reviewed by Daan et al. 1989 and Rohwer 1992). However, a correlation between hatching date and post-fledging survival does not mean that date itself causes difference in survival. For instance, because the growth rate of young may vary with hatching date (i.e. for the same age, early-hatched young are heavier than late-hatched ones), seasonal variations in post-fledging survival could be causally related to differences in growth rate. Several studies have indeed shown that fledglings with a relatively small body mass (or size) have low post-fledging survival (e.g. Owen and Black 1989, Tinbergen and Boerlijst 1990, Magrath 1991).

Effects of growth rate on post-fledging survival could be especially important in long-distance migrants because of the high energetic demand of migration. Effects of body condition at fledging could be amplified in large arctic-nesting birds because the limited amount of time between hatching and departure for fall migration may not allow completion of growth of all body components before migration (Lesage and Gauthier 1997). The short arctic growing season may therefore confound even more the effect of hatching date and body mass on post-fledging survival. Owen and Black (1989) found that age at banding and pre-fledging body mass of Barnacle geese (*Branta leucopsis*) were positively related to fall migration survival of juveniles, as was first-year survival in Lesser Snow Geese (*Chen caerulescens caerulescens*, Francis et al. 1992b). Survival of young Emperor Geese (*Chen canagicus*) between fledging and arrival on fall staging areas was also affected by pre-fledging body mass (Schmutz 1993).

Greater Snow Geese (*Chen caerulescens atlantica*) are the northernmost breeding geese in North America, nesting throughout the eastern Canadian Arctic Archipelago and

Northwest Greenland (Bellrose 1980). They nest in a highly seasonal environment characterized by short summers and variable breeding conditions, especially among years. Previous studies showed a continuous decline of pre-fledging components of reproductive success throughout the season (Lepage 1997). A faster growth for early-hatched goslings, resulting in a larger size and an heavier mass at the end of the summer, was also reported for some years (Lepage et al. 1998). In contrast to the predictable decline in breeding conditions within season, between year variations tend to be much less predictable (e.g. Lepage et al. 1996). These variations provided the opportunity to study the relative effect of hatching date and body mass on post-fledging survival of young under contrasting annual conditions. Our objective was thus to separate the effect of timing of nesting and body mass on intra- and inter-annual variations in the post-fledging survival, an important fitness component.

METHODS

Study area and banding method

This study was conducted on Bylot Island (NWT 73°N 80°W), Northwest Territories, Canada. Southern Bylot Island is the most important breeding site for Greater Snow Geese, with > 27,000 nesting pairs in 1993 (Reed et al. 1992, Gauthier et al. 1996). Geese nest in a semi-colonial fashion on different parts of the island and generally use different sites for nesting and brood-rearing (Hughes et al. 1994, Lepage et al. 1998). From 1991 to 1996, a sample of nests were visited daily during the hatching period to tag all newly-hatched gosling (sometimes in pipped eggs, Alliston 1975) with an individually numbered web-tag. Shortly before fledging (i.e. about 5 weeks after hatch), goose families were captured in mass banding drives during a 7-day period in early-August when the adults were molting and before the young could fly. Goslings were sexed by cloacal eversion, measured (culmen, head, tarsus and 9th primary length), weighed to the nearest 25 g (to the nearest gram in 1995 and 1996) and checked for the presence of web-tags. Each individual received a metal US Fish and Wildlife Service band. Banded geese found dead at the banding sites within a few days were not included in the data (see chapter 1).

Recoveries of banded birds by hunters occurred during the fall and winter hunting seasons in southern Québec and the eastern United-States of America, and came from the Bird Banding Laboratory. In the upper estuary of the Saint Lawrence river (Québec, 47°N 72°W), outfitters were also solicited by letters or personal contact to report bands directly to our laboratory. We used recoveries from 1991 to 1996. Goslings recaptured on Bylot Island during subsequent banding drives were also included in the data.

Gosling parameters

There were 2 groups of goslings captured during banding: unmarked goslings, and those originally marked at hatch with a web-tag (i.e. those of known age at capture). We estimated the age of unmarked goslings from year-specific linear relationship between age of marked goslings and length of their ninth primary (see appendix B and details in Lepage et al. 1998). Hatching date of goslings was then estimated with:

$$\text{hatching date} = \text{banding date} - \text{age at banding}$$

Mass at banding may be affected by the age, the relative hatching date (hatching date transformed to relative date with respect to the median annual hatching date), the year and the interactions between these variables (Lepage et al. 1998). To allow inter-annual comparisons, mass were corrected for these effects by using general linear models (Table 1). Residuals from this model, where age and seasonal effects on body mass were controlled for, were then used in subsequent analyses (hereafter called residual mass).

Table 1. Factors affecting the mass of goslings (N = 9705) near fledging. *F* and *P* values are shown for the complete model and for each independent variables in the model.

Source	df	F Value	Pr > F
Model ($R^2 = 0.64$)	23	757.9	0.0001
Year	5	202.6	0.0001
Age	1	260.6	0.0001
Age * Year	5	226.5	0.0001
Hatch date	1	88.4	0.0001
Hatch date * Year	5	2.9	0.0114
Age * Hatch date	1	42.4	0.0001
Age * Hatch date * Year	5	2.6	0.0224

Data analysis

Let θ_j denote the probability that individual j from a banded sample is recovered during the hunting season. The recovery probability, θ_j, is a function of two parameters:

$$\theta_j = \phi_j * p_j$$

where ϕ_j is the probability that a young banded goose survives from banding until the subsequent hunting seasons (i.e. survived at least its first fall migration) and p_j is the probability that a young alive at the end of its first fall migration is shot and recovered. As ϕ and p could not be estimated separately, absolute survival probabilities for any given variables can not be computed. Thus, θ_j was used as an index of survival. There is no evidence that hunting vulnerability is related to body condition in Greater Snow Geese (Morez 1996), so we assumed that p_j did not depend on the body mass at the time it was shot. A test of the null hypothesis that θ_j was not related to an external variable, x_j (i.e. hatching date, mass at banding), therefore, tested whether ϕ_j (post-fledging survival) was related to this external variable.

As recovery data are binary (i.e. a banded young is either recovered or not; recovered birds were scored as 1 and unrecovered as 0), we used logistic regression procedure to evaluate simultaneously the effect of several variables (relative hatching date, median annual hatching date, residual mass, sex, banding year) and their interactions on post-fledging survival (Cox 1970, Trexler and Travis 1993). We used a backward model selection procedure (LOGISTIC procedure of SAS; SAS Institute Inc. 1988) and likelihood ratio tests (LRT; Hosmer and Lemeshow 1989) and the Akaike Information Criterion (AIC; Burnham et al. 1995) to select the best model.

Independence of fate

In our analysis, each young was treated as an independent observation. However, because young stay with their family for up to a year (Prevett and MacInness 1980, variations in probability of death could be greater between broods than within broods, which violates the assumption of independence. For instance, if a family comes within the range of hunters, all young in the family are likely to have an increased risk of mortality at the same time. Even though the banding procedure did not allow us to know the brood affiliation, recoveries were examined for potential siblings, which were defined as birds killed the same day and at the same site, that were banded in the same catch and with a difference in banding age of ≤ 2 days (the confidence range in determining age with the 9th primary length; Lepage 1997). We randomly chose only one of these "apparent siblings" and computed again the logistic regression analyses.

Compensatory growth

Some young geese measured and banded on Bylot Island during summer and killed at Cap Tourmente National Wildlife Area the following fall were measured again. It allowed us to test for compensatory growth which could have occurred during the month and a half of fall migration. We used principal components analysis to calculate the first principal component (PC1) score for each individual based on the correlation matrix of measurements (culmen, head and tarsus lengths). We estimated PC1 scores in birds measured in late summer and fall, and related them with a linear regression. We then tested the hypotheses that the slope of the relationship was equal to 0 (full compensation) or 1 (no compensation).

RESULTS

The logistic analysis included 9,596 banded young, of which 613 were recovered (80% recovered in the first fall hunting season) and 47 were recaptured on Bylot Island during subsequent banding drives (Table 2). There was no difference between sexes in the probability of being recovered ($\chi^2 = 0.32$, $df = 1$, $P = 0.57$). Sex ($P = 0.14$), median hatching date ($P = 0.22$) and interactions not significant ($P > 0.1$) in the general model were removed and a reduced model was selected based on AIC and LRT (Table 3). Although the relative hatching date and its interaction with median hatching date were not quite significant in the selected model, removing them one at a time did not improve the AIC and the LRT was almost significant (Table 4). Removing both variables considerably increased the AIC and the LRT was highly significant (Table 4). This indicated that both variables contributed to the explanatory power of the model and they were thus retained. In this model, variation in the probability of being recovered (θ_j) was related to banding year, relative hatching date, residual mass and several interactions (Table 3).

The effect of banding year on θ_j could result both from inter-annual variations in p, the probability of being shot and recovered, which could vary greatly from year to year depending on hunting success, and in ϕ_j, the post-fledging survival as large inter-annual variations in fall migration survival can also occur (chapter 5). This means that even though θ_j differed significantly among cohorts (i.e. banding years), no strong inferences on these differences could be drawn with respect to annual variations in post-fledging survival. In contrast, because p was assumed not to be related to the other variables (relative hatching date and residual mass; see methods and discussion), variations in θ_j in relation to these variables corresponded to variations in ϕ_j, the post-fledging survival. There was an interaction between relative and median hatching date because, although the survival index declined progressively with hatching date in all years, the slope differed depending on median annual hatching date (Fig. 1a). The steepest slopes were found in years where median hatching date was latest (10-16 July) which suggests that the positive effect of early hatching on post-fledging survival was accentuated in a late breeding year. However, the advantage of hatching early persisted even in early breeding years.

Table 2. Number of young Greater Snow Geese banded in summer on Bylot Island and subsequently recovered by hunters or recaptured, and mean cohort parameters at banding.

	Number			Median	Cohort parameters at banding			
Year	Banded	Recovered[a]	%	hatch date [b]	age [c]	SE	mass [d]	SE
1991	1118	152	13.6	10 July (191)	36.3	3.1	1718	6
1992	892	97	10.9	16 July (198)	28.9	2.4	1645	16
1993	1849	207	11.2	4 July (186)	38.4	2.8	1569	6
1994	1731	53	3.1	7 July (188)	35.8	2.4	1440	4
1995	2206	158	7.2	7 July (188)	35.2	2.3	1637	3
1996	1800	93	5.2	10 July (192)	31.5	3.2	1881	5
All years	9596	760	7.9					

a: Direct and indirect recoveries. Also included a few live recaptures.

b: 1992 and 1996 are leap years, which means that actual median hatch date is a day later than for the other years (Julian dates are in brackets).

c: in day.

d: Least square means of a multilinear relationship between mass at banding (in g) and banding year, banding age, relative hatching date and their interactions.

Table 3. Logistic regression model and parameter estimates for the probability of being recovered after the first fall migration for young Greater Snow Geese banded in summer on Bylot Island.

Parameter	Coefficients	SE	χ^2	df	*P*
Constant	18.25	2.2	69.92	1	0.0001
Relative hatching date (rhd)	1.37	0.76	3.24	1	0.0717
Residual mass (rmass)	-0.03	0.01	5.55	1	0.0185
Banding year	-0.22	0.02	89.71	1	0.0001
rhd*mhd [a]	-7.78e-3	4.00e-3	3.79	1	0.0515
rmass*mhd	2.49e-4	0.99e-4	6.34	1	0.0118
rmass*rhd	1.8e-4	0.75e-4	5.78	1	0.0162

a: mhd: median hatching date.

Table 4. Effects of relative hatching date and its interaction with median hatching date on the logistic regression models. For each model, the Akaike Information Criterion (AIC) and the deviance (DEV) are given. Boldface denotes the AIC value for the selected model.

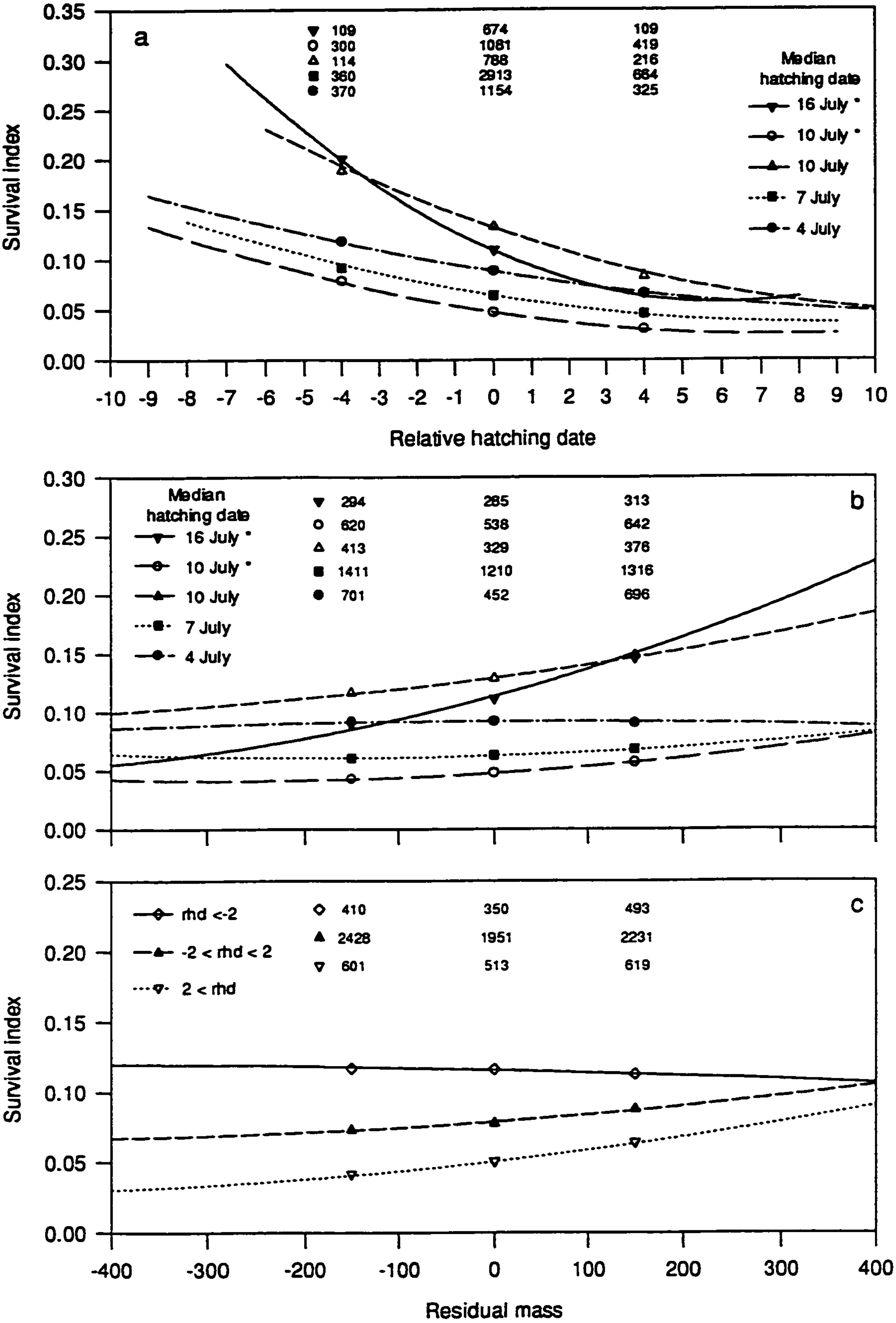
	Model	AIC	DEV	Tests between models
(1)	rhd + rmass + b_yr + rhd*mhd + rmass*mhd + mass*rhd	**5160.5**	5146.5	
(2)	rmass + b_yr + rhd*mhd + rmass*mhd + mass*rhd	5161.8	5149.8	rhd removed (2) vs. (1): $\chi^2_1 = 3.3$, $P = 0.07$
(3)	rhd + rmass + b_yr + rmass*mhd + mass*rhd	5162.3	5150.3	rhd*mhd removed (3) vs. (1): $\chi^2_1 = 3.8$, $P = 0.05$
(4)	rmass + b_yr + rmass*mhd + mass*rhd	5214.0	5204.0	rhd and rhd*mhd removed (4) vs. (2): $\chi^2_1 = 54.3$, $P < 0.001$ (4) vs. (3): $\chi^2_1 = 54.8$, $P < 0.001$

rhd: relative hatching date.
rmass: residual mass.
b_yr: banding year.
mhd: median hatching date.
* : interaction between two variables.

Mass at banding also affected post-fledging survival independently of date, as the heaviest goslings (for a given age and once the seasonal effects are controlled for) survived better. However, the interaction between residual mass and median hatching date indicated that the effect of mass was also dependent on the chronology of nesting. As with hatching date, the effect of mass was accentuated in late breeding years (10-16 July; Fig. 1b). For all cohorts combined, the effect of residual mass on the survival index was also dependent on relative hatching date (significant interaction of residual mass and relative hatching date). Mass appeared to have no effect for the early-group (rhd < -2, $N = 1253$), as opposed to the mid- ($-2 \leq$ rhd ≤ 2, $N = 6610$) and late-hatched group (rhd > 2, $N = 2832$) where mass had a positive effect on survival, with a more accentuated effect for the late-hatched group (Fig. 1c). In summary, small, late-hatched young had a low post-fledging survival, especially in year of late breeding.

Apparent siblings

So far, all banded young have been included in the analysis and this might have biased the results if young within a brood have more similar hunting vulnerability than young between broods. Under this hypothesis, some broods would contribute relatively more data, which is undesirable because siblings have similar parameters (hatching date and mass). We therefore refitted the selected model in Table 3 to a reduced data set where "apparent siblings" (see methods) were represented by a single, randomly chosen young. We found 40 cases of "apparent siblings" affecting 94 young (out of 760 recovered young). Using this reduced data set, all variables and interactions present in the original model remained significant and changes in the variables coefficients were minor (see appendix C).


a
Survival index
0.35
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0.25
0.20
0.15
0.10
0.05
0.00
▼ 109
○ 300
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■ 360
● 370
674
1081
788
2913
1154
109
419
216
664
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Median hatching date
16 July *
10 July *
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7 July
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-10 -9 -8 -7 -6 -5 -4 -3 -2 -1 0 1 2 3 4 5 6 7 8 9 10
Relative hatching date
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Median hatching date
16 July *
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7 July
4 July
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○ 620
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1316
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rhd <-2
-2 < rhd < 2
2 < rhd
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▲ 2428
▽ 601
350
1951
513
493
2231
619
-400
-300
-200
-100
0
100
200
300
400
Residual mass

Fig. 1. Relationship between post-fledging survival index (*θ*, see methods) and (a) relative hatching date (*rhd*) by median hatching date, (b) residual mass (*rmass*) by median hatching date and (c) residual mass by relative hatching date in young Greater Snow Geese. The lines give the best fit of the predicted values calculated according to the selected model of the logistic regression analysis. The symbols represent mean survival estimates on grouped data in relation with (a) mean *rhd* or (b and c) *rmass* of each group. For (a), the 3 groups are: *rhd* < -2; -2 ≤ *rhd* ≤ 2; *rhd* > 2; For (b) and (c), the 3 groups are: *rmass* < -50; -50 ≤ *rmass* ≤ 50; *rmass* > 50. Sample sizes of groups are given at the top of the graphs. The * indicates leap years. (preceding page)

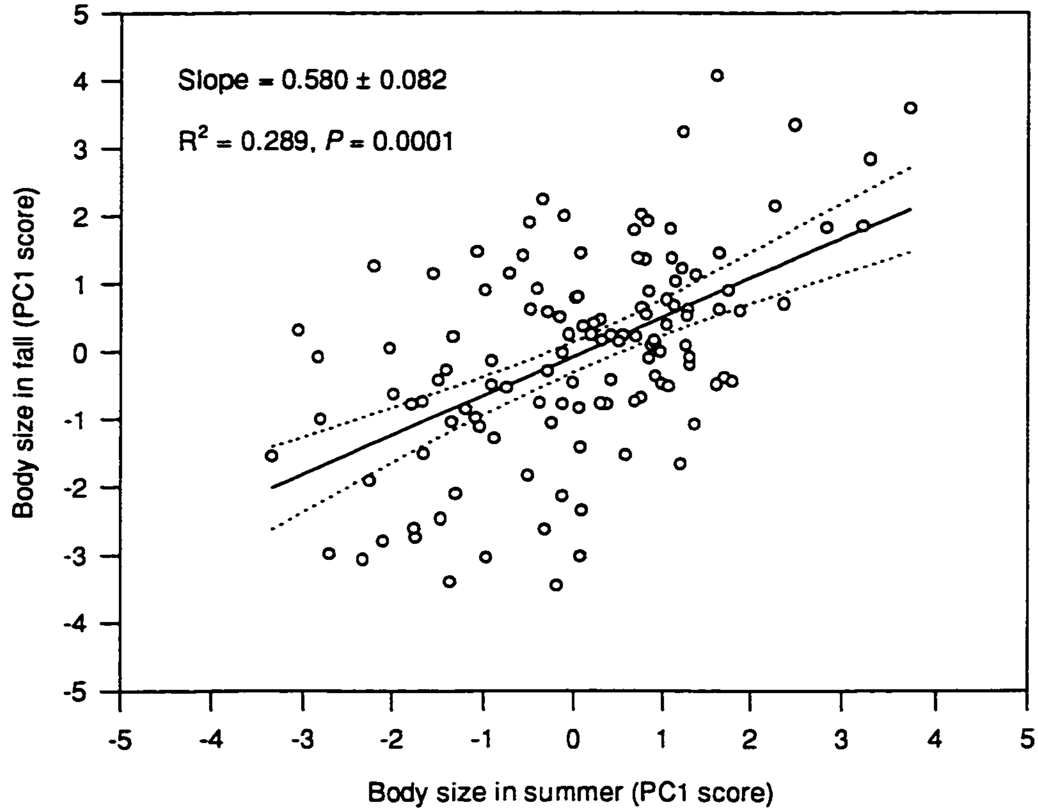


Fig. 2. Linear relationship between body size in fall and in late summer for 130 young Greater Snow Geese banded during summer on Bylot Island (N.W.T.) and recovered the following fall in the St. Lawrence estuary (Québec). The first principal component (PC1) score for each individual measured at the two locations was based on culmen, head and tarsus lengths. The solid line represents the linear relationship and the dotted lines the 95% confidence limits for the regression.

Compensatory growth

Of the 613 recovered birds, 130 were measured again in the fall following the banding period (i.e. ca. 3 months of age). There was a significant linear relationship between fall and late summer PC1 scores ($R^2 = 0.29$, $P = 0.0001$). The hypothesis of full compensatory growth during fall migration was therefore rejected (i.e. the slope was different from 0). The hypothesis of no compensatory growth (slope = 1) was also rejected ($P < 0.001$), suggesting that some level of compensatory growth occurred (Fig. 2). Therefore, differences observed among individuals at the end of the summer persisted at least throughout the following fall, but were somewhat attenuated.

DISCUSSION

Like most pre-fledging components of reproductive success (Lepage 1997), post-fledging migration survival of young Greater Snow Geese showed a steady decline with hatching date. Seasonal decline in post-fledging survival in relation with hatching date is a well-known phenomenon and has been shown in several bird populations (Cooke et al. 1984, Daan et al. 1989, Magrath 1991, Rohwer 1992, Norris 1993, Spear and Nur 1994, Sedinger et al. 1995, Brinkhof et al. 1997). However, most of these studies used recaptures or resightings of marked individuals at study sites (usually breeding sites) the following year (sometimes up to several years after marking). Thus, they cannot rule out the possibility that some of the observed differences are due to dispersal rather than mortality. They also provide few insights on the timing of mortality after fledging. In contrary, our data came primarily from band recoveries by hunters (93%), which removed the problem of dispersal. and most of the bands (80%) were recovered during the first hunting season following marking. The documented effects on post-fledging survival therefore occurred mostly during the first fall migration.

In our population, advantages of hatching early included more time before the onset of migration to complete growth, especially breast muscles, and to accumulate fat. Fat accumulation and breast muscle development start at a late stage of growth in geese: At fledging (43 days), there was virtually no fat accumulation (1% of body mass) and breast muscles had reached only 41% of asymptotic mass in Greater Snow Geese (Lesage and Gauthier 1997). However, growth rate of breast muscles was rapid at fledging: a difference of only a few days may result in large difference in breast muscle development (Lesage and Gauthier 1997). Advantages of being early-hatch *within* season are amplified in late-breeding seasons, as time to complete growth is even shorter then. Therefore, length of growing season has a substantial effect on post-fledging survival in large birds like geese, with early-hatched young being in better condition on average than late-hatched ones for fall migration. The small fat scores of goslings at the onset of migration, combined with the late development of breast muscles, suggest that most of the fall migration mortality probably occurs during the first stage of migration.

The relationship between survival and hatching date could also be accentuated by possible differential departure dates for migration between early- and late-hatched young. If late-hatched young have to delay their departure in order to complete growth, this may increase the likelihood of migrating under poor weather conditions and using staging areas of rapidly declining quality, resulting in a greater risk of mortality (chapter 5, Richardson 1990, Butler et al. 1997). Unfortunately, chronology of migration is still poorly known in this population. Data from satellite transmitters fitted on adults (6 females in 1993 and 7 males in 1995) indicated that departures from Bylot Island occurred around 24 August in 1993 (range 20 to 28 August) and 30 August in 1995 (range 28 August to 3 September), less than 10 days after the first goslings had been observed to fly (Giroux, unp. data). It suggests that families leave Bylot Island rapidly after the young can fly, but the small sample size precluded the assessment of differences in departure dates between families with early- or late-hatched young.

Post-fledging survival was also independently affected by body mass, regardless of age and seasonal effects on growth. The positive effect of mass on survival was accentuated in late breeding season, as for the effect of relative hatching date. However, while post-fledging survival of early-hatched young was essentially independent of mass, mid- and late-hatched young with low body mass survived poorly. Therefore, the disadvantage of being hatched late could be partly attenuated for some goslings if they had a better growth than average, either because of particular genetic traits or of good conditions experienced during brood-rearing.

Few studies have directly investigated the relationship between post-fledging survival and individual parameters in Arctic-nesting birds. A positive effect of mass on fall migration survival was also found for emperor goose young, despite a relatively short migratory flight (600 - 750 km; Schmutz 1993). Although Schmutz (1993) did not relate hatching date to survival, he did not dismiss this parameter as a contributing factor to pre-fledging body mass. Owen and Black (1989) showed that fall migration survival of young barnacle geese of a population breeding in Svalbard was strongly related to gosling body mass, and to a lesser extent to their age at banding. Other studies gave an estimate for recruitment or post-fledging survival but without separating the fall migration component: in general, first-year survival and recruitment is higher for early-hatched birds and/or for heavier ones (Cooke et al. 1984, Francis et al. 1992, Sedinger et al. 1995). Our results strongly suggest that seasonal effects on post-fledging survival occur shortly after fledging.

Some critical assumptions

An important assumption in our study was that p (the probability that a young is shot and recovered) was not related to hatching date and body mass for young Greater Snow Geese. Morez (1996) showed that hunting vulnerability of young did not depend on their mass or size when shot. It was especially important to test this assumption because compensatory growth during migration was weak, indicating that differences in mass observed at the end of the summer persisted through fall. Difference in hunting vulnerability related to hatching date could still occur if large variations in arrival dates in the fall staging areas existed between families with early- or late-hatched young. Geese arriving earlier could experience a higher hunting risk, thereby increasing their probability of being recovered. Even though we cannot rule out entirely this possibility, we found no evidence of large differences in arrival dates for families in the fall staging areas (chapter 5). Thus, we conclude that there was no relationship between p and hatching date and that relationships between θ and external variables were largely dependent of the effect these variables on post-fledging survival.

Another critical assumption was the independence of fate of young: siblings (i.e. young of the same brood) could experience more similar hunting mortality risk. Although we could not test this assumption directly, eliminating the "apparent siblings" did not change the results. Furthermore, we found evidence that mortality of young during fall migration is relatively independent within broods (chapter 5). We thus conclude that young were largely independent individuals with respect to post-fledging survival and probability of being recovered.

Other factors affecting post-fledging survival

Several studies have shown that families with large broods were dominant over smaller families (Boyd 1953, Raveling 1970, Black and Owen 1987, 1989, Lepage et al. 1998 but see Mulder et al. 1995). Thus, early-hatched young, which tend to be associated with larger families (Lepage 1997), may be more likely to be in dominant families and hence have greater access to the best food patches (Prop et al. 1984, Prop and Deerenberg 1991). If use of stopovers during the first part of the migratory flight is critical for fat accumulation, early-hatched young in large families would then have an additional advantage over late-hatched ones, accentuating the differential survival.

Young males are slightly heavier than young females at the end of the summer (6% difference for body mass; Lesage and Gauthier 1997) but growth rates are similar between sexes (Lepage 1997, Lesage and Gauthier 1997). We found no evidence of an effect of sex on post-fledging survival. Differences between sexes might be too small to induce differential survival during migration. However, because nutrient requirements are higher in males (due to their slightly larger body size), differential survival in disfavor of males could arise under deteriorating feeding conditions. In a population of lesser snow geese, there was evidence of a decline in sexual size dimorphism and increase in pre-fledging mortality of male goslings over the years and within seasons (Cooch et al. 1996 and 1997). These variations resulted in a sex-ratio change and were associated with parental age and a long-term decline in brood-rearing habitat quality. However, consequences on post-fledging survival and population dynamics are unclear (Cooch et al. 1997). The absence of sex effect on post-fledging survival in our study suggests that either these effects are not widespread in geese, or that feeding conditions in our study area did not deteriorate to the point of inducing sex-specific effects on survival.

CONCLUSION

Durant ma recherche, je me suis attardé aux nombreux problèmes reliés à une estimation rigoureuse de la survie chez une population aviaire migratrice, à l'identification des facteurs naturels et humains pouvant l'affecter, et au rôle joué par ce paramètre dans la dynamique d'une population animale exploitée. Une évaluation rigoureuse des taux de survie d'une population animale exige de capturer et de marquer de manière unique un grand nombre d'individus.

Comme les techniques de marquage pourraient provoquer des modifications importantes des comportements et de la survie des individus nouvellement marqués, il est apparu essentiel de vérifier l'impact du marquage sur la mesure principale à l'étude, la survie, avant de répondre plus spécifiquement à des hypothèses biologiques généralisables à l'ensemble de la population.

Effets du marquage sur la survie

Les techniques et marqueurs utilisés lors de la présente étude sont communément employés depuis plusieurs décennies, notamment en Amérique du Nord. Malgré cela, une évaluation détaillée de leurs effets sur la survie des oiseaux ainsi marqués a rarement été réalisée. Plusieurs effets peuvent être distingués. En premier lieu, la capture en elle-même peut avoir une influence directe sur la survie, en raison du stress, de l'incapacité à s'alimenter pendant plusieurs heures, voire du piétinement induit par le confinement dans un espace restreint de plusieurs dizaines ou centaines d'individus. Dans ce cas, il s'agit principalement d'un effet direct mais à court terme: après leur libération, les oiseaux devraient retrouver rapidement leur comportement et les taux de survie d'avant capture. Dans la population de Grande Oie des neiges à l'étude, l'impact immédiat de la capture, en termes de mortalité, était minime et affectait principalement les individus qui présentaient la plus faible probabilité de survie lors de la migration (chapitre 1 et 6). Néanmoins, les analyses ont permis de préciser plus rigoureusement les conditions à respecter lors des captures, pour ce qui est du nombre d'oiseaux capturés, de la période et de l'emplacement du site de capture.

Des effets à plus long terme de la capture peuvent se produire, notamment si les marqueurs utilisés sont susceptibles d'entraîner une gêne conséquente par leur taille et/ou leur poids. Certains auteurs ont souligné ce problème potentiel, sans toujours apporter une démonstration formelle de l'impact réel du marqueur (Greenwood and Blair 1974, Craven 1979, Samuel et al. 1990, Castelli and Trost 1996). Chez les oiseaux, les bagues posées à la patte sont considérées comme n'ayant aucune conséquence sur la survie subséquente, après l'éventuel impact de la capture proprement dite. Au contraire des bagues, les marqueurs plus volumineux, comme les colliers, présentent une plus grande probabilité d'effets néfastes sur la survie. Ces effets peuvent s'avérer transitoires: après une période d'adaptation, pendant laquelle une certaine mortalité pourrait avoir lieu, il n'y aurait ensuite plus de différence entre les oiseaux marqués ou non. En revanche, l'effet pourrait perdurer de manière constante sur une longue période, entraînant alors une baisse significative de la survie des oiseaux ainsi marqués.

Pour notre étude, un certain nombre de femelles adultes recevaient un collier en plastique, en plus d'une bague. Pour déterminer l'effet transitoire du collier (du baguage à la fin de l'été jusqu'à l'automne suivant), la survie des individus nouvellement marqués avec un collier a été comparée avec celle des individus anciennement marqués, également porteurs d'un collier (chapitre 2). Les résultats n'indiquaient pas de différences significatives entre les deux groupes, permettant de conclure que le collier ne provoque pas d'effets négatifs transitoires sur la survie.

Au chapitre 3, nous avons testé, cette fois, un effet permanent du collier, en comparant la survie des femelles adultes avec colliers à celle des femelles adultes avec bagues uniquement. Les probabilités de survie ont été estimées par modélisations mathématiques utilisant des données de récupérations de bagues, des réobservations de colliers et des recaptures d'individus marqués lors du baguage. L'utilisation de ces 3 méthodes indépendantes a permis, d'une part, d'augmenter la confiance dans les résultats obtenus, et d'autre part, de dégager des conclusions et des interrogations qui n'auraient pas été décelées avec une seule méthode. En définitive, le collier ne semblait pas avoir d'effet négatif à long terme sur la survie. En revanche, les analyses ont clairement démontré la pertinence d'utiliser un ensemble de méthodes indépendantes pour la modélisation des probabilités de survie, afin de mettre en évidence les limitations et les biais possibles de chacune. Ainsi, il apparaît essentiel de poursuivre l'étude de l'impact du marquage et du marqueur, notamment sur des aspects démographiques autres que la survie susceptibles d'être affectés (propension à nicher, par exemple), et sur les phénomènes de "mémoire de capture", comme l'évitement des sites de capture par des oiseaux anciennement marqués, notamment ceux porteurs de collier.

Survie et dynamique de population

Comprendre les mécanismes régissant la croissance d'une population est particulièrement important dans le cas d'une population exploitée, afin de réaliser une gestion rigoureuse de la ressource. Un suivi à long terme de la population de la Grande Oie des neiges a permis d'évaluer le rôle respectif des différents processus naturels et de l'exploitation par la chasse dans sa dynamique (chapitre 4). Nos résultats indiquent que la survie des adultes ne semble pas encore affectée par des phénomènes dépendants de la densité, même si la taille de la population a été multipliée par 10 pendant la période considérée. Trois phases de croissance de la population ont été identifiées, qui correspondaient à des niveaux différents de pression de chasse, alors que la production de jeunes restait similaire entre ces périodes. La population à l'étude étant fermée (pas d'immigration ou d'émigration), cela suggère que la chasse a eu un impact négatif sur la survie, et, en conséquence, qu'elle a contrôlé, dans une certaine mesure, la dynamique de la population pendant une certaine période. Cependant, la croissance continue de la population depuis le milieu des années 1980 malgré l'augmentation de la durée de saison de chasse et des limites de prises quotidiennes et de possession indique un relâchement de l'impact de la chasse sur la croissance. Un retour à une situation de contrôle de la dynamique de population par la chasse nécessiterait une augmentation importante de la pression de chasse. Cependant, il est évident que les possibilités de régulation par la chasse de la population de la Grande Oie des neiges dépendent également de facteurs sociaux, économiques et politiques qui peuvent s'avérer contraignants dans la mise en place de plans d'aménagement. À mon sens, les résultats présentés dans ce chapitre fournissent les bases pour une modélisation précise de la dynamique de la population de la Grande Oie des neiges, étape indispensable dans l'élaboration d'un programme de gestion de cette ressource renouvelable.

Il ouvre aussi la voie à d'autres études afin de mieux comprendre la dynamique et les conséquences de la croissance de cette population. Des paramètres démographiques autres que la survie des adultes sont-ils affectés par des phénomènes dépendants de la densité ? Comment l'augmentation de la population modifie-t-elle les stratégies migratoires (utilisations spatio-temporelles des haltes migratoires, par exemple) ? Quels facteurs influencent le succès de chasse ? Pour répondre à de telles questions, il apparaît indispensable de poursuivre le suivi à long terme, que ce soit le recensement de la population ou le programme de marquage et d'observation.

Les effets saisonniers sur la survie après l'envol

La survie après l'envol (*post-fledging survival*) des jeunes est un paramètre important du fitness, bien qu'il soit rarement mesuré à cause de contraintes pratiques. Le marquage (colliers et bagues) et l'utilisation d'un corridor de migration relativement étroit par la population de la Grande Oie des neiges ont fourni l'opportunité d'estimer la survie des jeunes pendant la migration automnale et d'identifier les facteurs qui l'affectent. Dans le chapitre 5, nous avons principalement cherché à estimer la survie des jeunes pendant la migration automnale, au niveau de la cohorte, encore une fois en utilisant plusieurs méthodes indépendantes afin de réduire au mieux les biais éventuels. L'observation de familles marquées, avant et après la migration, et la modélisation des récupérations de bagues posées également avant et après la migration ont permis de mettre en évidence de grandes variations inter-annuelles de la survie pendant la migration, qui constituent une part majeure de la variabilité de la survie annuelle des jeunes (voir chapitre 4). Nos résultats ont clairement démontré l'importance considérable, bien que variable, de la mortalité pendant la migration sur les jeunes oies, et donc sur le recrutement futur des différentes cohortes. Les observations de familles marquées ont montré également que les jeunes d'une même famille, même s'ils possèdent des caractéristiques communes (comme la date d'éclosion et la masse corporelle), semblent relativement indépendants face à la mortalité pendant la migration. Les variations inter-annuelles de la survie pendant la migration automnale ont été reliées aux conditions des cohortes avant l'envol: une survie inférieure d'une cohorte, par rapport aux autres, pouvait s'expliquer par une masse corporelle moyenne à la fin de l'été inférieure et/ou une date d'envol moyenne plus tardive. Au chapitre 6, nous avons identifié plus précisément, au niveau individuel, l'influence des effets saisonniers sur la survie post-envol. La date relative d'éclosion, ainsi que la masse corporelle, influencent directement et de manière indépendante la probabilité de survivre à la migration automnale: les oisons éclos tôt et/ou ayant atteint une masse corporelle plus élevée à la fin de l'été ont une probabilité de survie post-envol plus grande. Ces effets sont d'autant plus marqués lors des années de nidification tardive. Ceci n'implique pas, toutefois, que seuls ces paramètres influencent la survie après l'envol. D'autres facteurs, comme les conditions météorologiques durant la migration et la qualité des haltes migratoires pourraient également affecter la survie, mais ils restent à étudier en détail.

En conclusion, ce travail a permis, d'une part, d'évaluer les conséquences à court et long terme du marquage sur la population à l'étude et d'autre part, de mieux comprendre la dynamique de cette population. 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'en corriger les effets négatifs, si besoin est. Il souligne les différents facteurs naturels et humains qui affectent les taux de survie de différentes classes d'âge et de sexe, pour différentes périodes temporelles. Il ouvre ainsi la voie à des études futures qui pourront estimer plus en détail certains mécanismes démographiques, comme le recrutement, l'effet de la reproduction sur la survie subséquente, et examiner les conséquences d'une croissance démographique sur ces mécanismes.

Références

Aebischer, N.J., and J.C. Coulson. 1990. Survival of the Kittiwake in relation to sex, year, breeding experience and position in the colony. Journal of Animal Ecology 59: 1063-1071.

Alerstam, T. 1990. Bird migration. Cambridge University Press. Cambridge.

Alisauskas, R.T. 1996. Effect of neckbands on survival of arctic-nesting geese. Canadian Wildlife Service Progress Report. 9 Pages.

Alliston, W.G. 1975. Web-tagging duckling in pipped eggs. Journal of Wildlife Management 39: 625-628.

Anderson, D.R., K.P. Burnham, J.D. Nichols, and M.J. Conroy. 1987. The need for experiments to understand population dynamics of American black ducks. Wildlife Society Bulletin 15: 282-284.

Ankney, C.D. 1975. Neck bands contribute to starvation in female lesser snow geese. Journal of Wildlife Management 39: 825-826.

Ballou, R.M., and F.W. Martin. 1964. Rigid plastic collars for marking geese. Journal of Wildlife Management 28: 846-847.

Bellrose, F.C. 1980. Ducks, Geese and Swans of North America. Stackpole Books.

Black, J.M., and M. Owen 1987. Determinants of social rank in goose flocks: acquisition of social rank in young geese. Behaviour 102: 129-146.

Black, J.M., and M. Owen 1989. Agonistic behaviour in barnacle goose flocks: assessment, investment and reproductive success. Animal Behaviour 37: 199-209.

Boyd, H. 1953. On encounters between white-fronted geese in winter flocks. Behaviour 5: 85-129.

Boyd, H., and G.H. Finney. 1978. Migratory game bird hunters and hunting in Canada. Canada Wildlife Service. Ottawa. Rep. No. 43. 127 Pages.

Boyd, I.L., J.P. Croxall, N.J. Lunn, and K. Reid.1995. Population demography of Antarctic fur seals: the costs of reproduction and implications for life-histories. Journal of Animal Ecology 64: 505-518.

Breitwisch, R. 1989. Mortality patterns, sex ratios, and parental investment in monogamous birds. Pages 1-50 *in* Current Ornithology. Volume 6. (D.M. Power, ed.) Academic Press, New York, New York, USA.

Brinkhof, M.W.G., A.J. Cavé, and A.C. Perdeck. 1997. The seasonal decline in the first-year survival of juvenile coots: an experimental approach. Journal of Animal Ecology 66: 73-82.

Brownie, C., D.R. Anderson, K.P. Burnham, and D.S. Robson. 1985. Statistical inference from a band recovery data - a handbook. Second ed. U.S. Fish and Wildl. Serv. Res. Pub. 156. 305 Pages.

Burnham, K.P., D.R. Anderson, G.C. White, C. Brownie and K.H. Pollock. 1987. Design and analysis methods for fish survival experiments based on release-recapture. American Fisheries Society Monograph 5. Bethesda, Maryland, USA.

Burnham, K.P, G.C. White, and D.R Anderson. 1995. Model selection strategy in the analysis of capture-recapture data. Biometrics 51: 888-898.

Butler, R.W., T.D. Williams, N. Warnock, and M.A. Bishop. 1997. Wind assistance: a requirement for migration of shorebirds. Auk 114: 456-466.

Castelli, P.M., and R.E. Trost. 1996. Neck bands reduce survival of Canada geese in New Jersey. Journal of Wildlife Management 60: 891-898.

Cézilly, F., A. Viallefont, V. Boyd, and A.R. Johnson. 1996. Annual variation in survival and breeding probability in Greater Flamingos. Ecology 77: 1143-1150.

Clobert, J. 1995. Capture-recapture and evolutionary ecology: a difficult wedding? Journal of Applied Statistics 22: 989-1008.

Cooch, E.G., D.B. Lank, R.F. Rockwell, and F. Cooke. 1989. Long-term decline in fecundity in a snow goose population: evidence for density-dependence? Journal of Animal Ecology 58: 711-726.

Cooch, E.G., D.B. Lank, A. Dzubin, R.F. Rockwell, and F. Cooke. 1991a. Body size variation in lesser snow geese: environmental plasticity in gosling growth rates. Ecology 72: 503-512.

Cooch, E.G., D.B. Lank, R.F. Rockwell, and F. Cooke. 1991b. Long-term decline in body size in a snow goose population: evidence of environmental degradation? Journal of Animal Ecology 60: 483-496.

Cooch, E.G., D.B. Lank, and F. Cooke. 1996. Intraseasonal variation in the development of sexual size dimorphism in a precocial bird: evidence from the lesser snow goose. Journal of Animal Ecology 65: 439-450.

Cooch, E.G., D.B. Lank, R. Robertson, and F. Cooke. 1997. Effects of parental age and environmental change on offspring sex ratio in a precocial bird. Journal of Animal Ecology 66: 189-202.

Cooch, G. 1953. Techniques for mass capture of flightless blue and lesser snow geese. Journal of Wildlife Management 17: 460-465.

Cooke, F., and D.S. Sulzbach. 1978. Mortality, emigration and separation of mated snow geese. Journal of Wildlife Management 42: 271-280.

Cooke, F., C.S. Findlay, and R.F. Rockwell. 1984. Recruitment and timing of reproduction in lesser snow geese (*Chen caerulescens caerulescens*). Auk 101: 451-458.

Cooke, F., R.F. Rockwell, and D.B. Lank. 1995. The snow geese of La Pérouse Bay. Oxford University Press, Oxford.

Cormack, R.M. 1964. Estimates of survival from the sighting of marked animals. Biometrika 51: 429-438.

Cox, D.R. 1970. The analysis of binary data. Methuen, London England.

Craven, S.R. 1979. Some problems with Canada goose neckbands. Wildlife Society Bulletin 7: 268-273.

Croxall, J.P., P. Rothery, S.P.C. Pickering, and P.A. Prince. 1990. Reproductive performance, recruitment and survival of wandering albatrosses *Diomeda exultans* at Bird Island, South Georgia. Journal of Animal Ecology 59: 775-796.

Daan, S., C. Dijkstra, and J.M. Tinbergen. 1990. Family planning in the kestrel (*Falco tinnunculus*): the ultimate control of covariation of laying date and clutch size. Behaviour 114: 83-116.

Daan, S., C. Dijkstra, R. Drent, and T. Meijer. 1989. Food supply and the annual timing of avian reproduction. Acta Congressus Internationalis Ornithologici 19: 392-407.

Darwin, C. 1859. The origin of species by means of natural selection, or the preservation of favoured races in the struggle for life. First edition. John Murray, London.

Doak, D.F. 1995. Source-sink models and the problem of habitat degradation: general models and applications to the Yellowstone grizzly. Conservation Biology 9: 1370-1379.

Dzubin, and Cooch. 1992. Measurements of geese: General field methods. California Waterfowl Association. Sacramento.

Ebbinge, B.S. 1991. The impact of hunting on mortality rates and spatial distribution of geese, wintering in the western palearctic. Ardea 79: 197-209.

Francis, C.M., M.H. Richards, F. Cooke, and R.F. Rockwell. 1992a. Changes in survival rates of lesser snow geese with age and breeding status. Auk 109: 731-742.

Francis, C.M., M.H. Richards, F. Cooke, and R.F. Rockwell. 1992b. Long-term changes in survival rates of lesser snow geese. Ecology 73: 1346-1362.

Gaillard, J.-M., D. Frontier, J.D. Lebreton, J. Trouvilliez, and J. Clobert. 1989. An analysis of demographic tactics in birds and mammals. Oikos 56: 59-76.

Gaillard, J.-M., D. Delorme, J.M. Boutin, G. Van Laere, B. Noisaubert, and R. Pradel. 1993. Roe deer survival patterns: a comparative analysis of contrasting populations. Journal of Animal Ecology 62: 778-791.

Gauthier, G., and J. Tardif. 1991. Female feeding and male vigilance during nesting in Greater Snow Geese. Condor 93: 701-712.

Gauthier, G., J-F. Giroux, and J. Bédard. 1992. Dynamics of fat and protein reserves during winter and spring migration in greater snow geese. Canadian Journal of Zoology 70: 2077-2087.

Gauthier, G., L. Rochefort, and A. Reed. 1996. The exploitation of wetland ecosystems by herbivores on Bylot Island. Geoscience Canada 23: 253-259.

Gauthier, G., and S. Menu. 1997. The use of capture-recapture models in greater snow geese: Is there a transient effect of capture and marking on survival? Proceedings of the Survey Methods Section, Statistical Society of Canada Annual Meeting.

Gauvin, J., and A. Reed. 1987. A simulation model for the Greater Snow Goose population. Canadian Wildlife Service, Occasional Paper No. 64, 26 Pages.

Gessaman, J.A., and K.A. Nagy. 1988. Transmitter loads affect the flight speed and metabolism of homing pigeons. Condor. 90: 662-668.

Giroux, J.F., and J. Bédard. 1986. Sex-specific hunting mortality of greater snow geese along firing lines in Quebec. Journal of Wildlife Management 50: 416-419.

Greenwood, R.J., and W.C. Blair. 1974. Ice on waterfowl markers. Wildlife Society Bulletin 2: 130-134.

Gwinner, E. (Ed.). 1990. Bird Migration. Physiology and Ecophysiology. Springer-Verlag, Berlin.

Haramis, G.M., J.D. Nichols, K.H. Pollock, and J.E. Hines. 1986. The relationship between body mass and survival of wintering canvasbacks. Auk 103: 506-514.

Harris, M.P., S.T. Buckland, S.M. Russel, and S. Wandless. 1994. Year- and age-related variation in the survival of adult European Shags over a 24-year period. Condor 96: 600-605.

Hepp, G.R, R.J. Blohm, R.E. Reynolds, J.E. Hines, and J.D. Nichols. 1986. Physiological condition of autumn-banded mallards and its relationship to hunting vulnerability. Journal of Wildlife Management 50: 177-183.

Hestbeck, J.B. 1994. Survival of Canada geese banded in winter in the Atlantic flyway. Journal of Wildlife Management 58: 748-756.

Hestbeck, J.B., and R.A. Malecki. 1989. Estimated survival rates of Canada geese within the Atlantic Flyway. Journal of Wildlife Management 53: 90-96.

Hestbeck, J.B., D.H. Rusch, and R.A. Malecki. 1990. Estimating population parameters for geese from band-recovery and mark-recapture data. Trans. North Am. Wildl. Nat. Ressour. Conf. 55 : 350-373.

Holmes, D.J., and S.N. Austad. 1995. The evolution of avian senescence patterns: Implications for understanding primary aging processes. American Zoologist 35: 307-317.

Hosmer, D.W., Jr., and S. Lemeshow. 1989. Applied logistic regression. John Wiley & Sons, New York, New York, USA.

Hughes, R.J., A. Reed, and G. Gauthier. 1994. Space and habitat use by greater snow goose broods on Bylot Island, Northwest Territories. Journal of Wildlife Management 58: 536-545.

Johnson, D.H. 1979. Estimating nest success: the Mayfield method and alternative. Auk 06: 651-661.

Jolly, G.M. 1965. Explicit estimates from capture-recapture data with both death and immigration-stochastic model. Biometrika 52: 225-247.

Kanyamibwa, S., A. Schierer, R. Pradel, and J.D. Lebreton. 1990. Changes in adult survival rates in a western European population of the White Stork *Ciconia ciconia*. Ibis 132: 27-35.

Lebreton, J.D., and J. Clobert. 1991. Bird population dynamics, management and conservation: The role of mathematical modeling. Pages 105-125 *in* Bird Population Studies (C.M. Perrins, J.D. Lebreton, G.J.M. Hirons, Eds.). Oxford University Press. Oxford.

Lebreton, J.D., K.P. Burnham, J. Clobert, and D.R Anderson. 1992. Modeling survival and testing biological hypotheses using marked animals: a unified approach with case studies. Ecological Monographs 62: 67-118.

Lebreton, J.D., R. Pradel, and J. Clobert. 1993. The statistical analysis of survival in animal populations. TREE 8: 91-95.

Lemieux, L. 1959. The breeding biology of the greater snow goose on Bylot Island, Northwest Territories. The Canadian Field-Naturalist 73: 117-128.

Lepage, D. 1997. Variation saisonnière du succès reproducteur chez la Grande Oie des neiges (*Chen careulescens atlantica*). Ph.D thesis, Université Laval, Sainte-Foy, Québec.

Lepage, D., G. Gauthier, and A. Desrochers. 1998. Larger clutch size increases fledging succes and offspring quality in a precocial species. Journal of Animal Ecology 67: 210-216.

Lepage, D., G. Gauthier, and A. Reed. 1998. Seasonal variation in growth of greater snow goose goslings: the role of food supply. Oecologia 114: 226-235.

Lepage, D., G. Gauthier, and A. Reed. 1996. Breeding-site infidelity in greater snow geese: a consequence of constraints on laying date? Canadian Journal of Zoology 74: 1866-1875.

Lesage, L., and G. Gauthier. 1997. Growth and organ development in greater snow goose goslings. Auk 114: 229-241.

Lindholm, A, G. Gauthier, and A. Desrochers. 1994. Effects of hatch date and food supply on gosling growth in arctic-nesting greater snow geese. Condor 96: 898-908.

MacInnes, C.D. 1966. Population behavior of eastern Arctic Canada geese. Journal of Wildlife Management 30: 536-553.

Magrath, R.D. 1991. Nestling weight and juvenile survival in the blackbird, *Turdus merula*. Journal of Animal Ecology 60: 335-351.

Maisonneuve, C., and J. Bedard. 1992. Chronology of autumn migration by greater snow geese. Journal of Wildlife Management 56: 55-62.

Maisonneuve, C., and J. Bédard. 1993. Distribution and movements of greater snow geese, *Chen caerulescens atlantica*, during fall staging in the St. Lawrence estuary, Québec. The Canadian Field-Naturalist 107: 305-313.

Marti, C.D. 1997. Lifetime reproductive success in Barn Owls near the limit of the species range. Auk 114: 581-592.

Mayfield, H. 1975. Suggestions for calculating nest success. Wilson Bulletin 87: 456-466.

Morez, V. 1996. L'effet de la condition physique de la grande oie blanche sur sa vulnérabilité à la chasse et à la capture. M.Sc. thesis, Université Laval, Sainte-Foy, Québec.

Mulder, R.S., T.D. Williams and F. Cooke. 1995. Dominance, brood size and foraging behavior during brood-rearing in the lesser snow goose: an experimental study. Condor 97: 99-106.

Newton, I. 1989. Lifetime reproduction in birds. Academic Press, London.

Newton, I., P. Rothery and I. Wyllie. 1993. Annual survival of Sparrowhawks *Accipiter nisus* breeding in three areas of Britain. Ibis 135: 49-60.

Newton, I., P. Rothery and I. Wyllie. 1997. Age-related survival in female Sparrowhawks *Accipiter nisus*. Ibis 139: 25-30.

Nichols, J.D. 1991. Responses of North American duck populations to exploitation. Pages 498-525 *in* Bird Population Studies (C.M. Perrins, J.D. Lebreton, G.J.M. Hirons, Eds.). Oxford University Press. Oxford.

Nichols, J.D., M.J. Conroy, D.R. Anderson, and K.P. Burnham. 1984. Compensatory mortality in waterfowl populations: a review of the evidence and implications for research and management. Trans. North Am. Wildl. Nat. Ressour. Conf. 49: 535-554.

Norris, K. 1993. Seasonal variation in the reproductive success of blue tits: an experimental study. Journal of Animal Ecology 62: 287-294.

Owen, M., and J.M. Black. 1989. Factors affecting the survival of barnacle geese on migration from the breeding grounds. Journal of Animal Ecology 58: 603-617.

Owen, M., and J.M. Black. 1991. The importance of migration mortality in non-passerine birds. Pages 360-372 in Bird Population Studies (C.M. Perrins, J.D. Lebreton and G.J.M. Hirons Eds.). Oxford University Press. Oxford.

Owen, M. 1980. Wild geese of the world. Batsford. London.

Pianka, E.R. 1970. On r and K selection. American Naturalist 104: 592-597.

Pienkowski, M.W., and P.R. Evans. 1985. The role of migration in the population dynamics of birds. Pages 331-352 *in* Behavioural ecology: ecological consequences of adaptative behaviour (R.M. Sibly and R.H. Smith Eds.). Blackwell Scientific Publications, Oxford.

Pollock, K.H., J.D. Nichols, C. Brownie, and J.E. Hines. 1990. Statistical inference for capture-recapture experiments. Wildl. Monogr. 107. The Wildlife Society, Bethesda, Md. 97 Pages.

Pons, J-M., and P. Migot. 1995. Life-history strategy of the herring gull: changes in survival and fecundity in a population subjected to various feeding conditions. Journal of Animal Ecology 64: 592-599.

Pradel, R., and J-D. Lebreton. 1993. User's guide to program SURGE, Version 4.2. Document polycopié. CEFE/CNRS, Montpellier, France.

Pradel, R., E. Cooch, and F. Cooke. 1995. Transient animals in a resident population of snow geese: local emigration or heterogeneity? Journal of Applied Statistics. 22: 695-710.

Prevett, J.P. and C.D. MacInnes. 1980. Family and other social groups in snow geese. Wildlife Monographs 71:1-46.

Prop, J., and C. Deerenberg. 1991. Spring staging in brent geese Branta bernicla leucopsis: feeding constraints and the impact of diet on the accumulation of body reserves. Oecologia 87: 19-28.

Prop, J., M.R. van Eerden and R.H. Drent. 1984. Reproductive success of the barnacle goose *Branta leucopsis* in relation to food exploitation on the breeding grounds, western Spitsbergen. Norks Polarinstitutt Skrifter 181: 87-117.

Raveling, D.G. 1970. Dominance relationships and agnostic behavior of Canada geese in winter. Behaviour 37: 291-319.

Raveling, D.G. 1976. Do neck bands contribute to starvation of female lesser snow geese? Journal of Wildlife Management 40: 571-572.

Raveling, D.G. 1977. Canada geese of the Churchill River Basin in north-central Manitoba. Journal of Wildlife Management 41: 35-47.

Raveling, D.G., J.D. Nichols, J.E. Hines, D.S. Zezulak, J.G. Silveria, J.C.Johnson, R.W. Aldrich, and J.A. Weldon. 1992. Survival of cackling Canada geese, 1982-88. Journal of Wildlife Management 56: 63-73.

Reed, A., J.F. Giroux, and G. Gauthier. 1998. Population size, productivity, harvest and distribution. Pages ?-? *in* The Greater Snow Goose: Population, ecosystem concerns, agricultural impacts and recommendations for future management. (B.D.J. Batt, Ed.) *in press.*

Reed, A., H. Boyd, P.Chagnon, and J. Hawkings. 1992. The number and distribution of Greater Snow Geese on Bylot Island and near Jungersen Bay, Baffin Island, in 1988 and 1993. Arctic 45: 115-119.

Rexstad, E.A. 1992. Effect of hunting on annual survival of Canada Geese in Utah. Journal of Wildlife Management 56: 297-305.

Richardson, W.J. 1990. Timing of bird migration in relation to weather. Pages 78-101 *in* Bird migration: Physiology and ecophysiology (E. Gwinner, Ed.). Springer-Verlag, Berlin.

Rockwell, F.C., E. Cooch, and S. Brault. 1996. Dynamics of the mid-continent population of Lesser Snow Geese - Projected impacts of reductions in survival and fertility on population growth rates. *in* Arctic ecosystems in peril.

Rohwer, F.C. 1992. The evolution of reproductive patterns in waterfowl. Pages 486-539 *in* Ecology and Management of Breeding Waterfowl (B.D.J. Batt et al. Eds.). University of Minessota Press. Minneapolis. USA.

Rusch, D.H., S.R. Craven, R.E. Trost, J.R. Cary, R.L. Drieslein, J.W. Ellis, and J.Wetzel. 1985. Evaluation of efforts to redistribute Canada geese. Trans. North Am. Wildl. Resour. Conf. 50: 506-524.

Samuel, M.D., D.H. Rusch, and S.R. Craven. 1990. Influence of neck bands on recovery and survival rates of Canada geese. Journal of Wildlife Management 54: 45-54.

Sarrazin, F., C. Bagnolini, J-L. Pinna, E. Danchin, and J. Clobert. 1994. High survival estimates of Griffon Vultures (*Gyps fulvus fulvus*) in a reintroduced population. Auk 111: 853-862.

SAS Institute Inc. 1988. SAS/STAT user's guide. Release 6.03. Cary, North Carolina.

Schmutz, J.A. 1993. Survival and pre-fledging body mass in juvenile emperor geese. Condor 95: 222-225.

Schmutz, J.A., S.E. Cantor, and M.R. Peterson. 1994. Seasonal and annual survival of emperor geese. Journal of Wildlife Management 58: 525-535.

Seber, G.A.F. 1965. A note on the multiple-recapture census. Biometrika 52: 249-259.

Sedinger, J.S., and P.L. Flint. 1991. Growth rate is negatively correlated with hatch date in black brant. Ecology 72: 496-502.

Sedinger, J.S., P.L. Flint, and M.S. Lindberg. 1995. Environmental influence on life-history traits: growth, survival, and fecundity in black brant (*Branta bernicla*). Ecology 76: 2404-2414.

Sedinger, J.S., M.S. Lindberg, E.A. Rexstad, N. Chelgren, and D.H. Ward. 1997. Testing for handling bias in survival estimation for black brant. Journal of Wildlife Management 61: 782-791.

Spear, L., and N. Nur. 1994. Brood size, hatching order and hatching date: effects on four life-history stages from hatching to recruitment in western gulls. Journal of Animal Ecology 63: 283-298.

Stearns, S.C. 1992. The Evolution of Life Histories. Oxford.

Tinbergen, J.M., and M.C. Boerlijst. 1990. Nestling weight and survival in individual great tits (*Parus major*). Journal of Animal Ecology 59: 1113-1127.

Tremblay, J.-P., G. Gauthier, D. Lepage, and A. Desrochers. 1997. Factors affecting nesting success in greater snow geese: effects of habitat and association with snowy owls. Wilson Bulletin 109: 449-461.

Trexler, J.C., and J. Travis. 1993. Nontraditional regression analysis. Ecology 74: 1629-1637

Ward, D.H., E.A. Rexstad, J.S. Sedinger, M.S. Lindberg, and N.K.Dawe. 1997. Seasonal and annual survival of adult Pacific Brant. Journal of Wildlife Management 61: 773-781.

White, G.C 1983. Numerical estimation of survival rates from band-recovery and biotelemetry data. Journal of Wildlife Management 47: 716-728.

Williams, T.D., F. Cooke, E.G. Cooch, and R.F. Rockwell. 1993. Body condition and gosling survival in mass-banded lesser snow geese. Journal of Wildlife Management 57: 555-562.

Weimerskirch, H. 1990. Reproductive effort in long-lived birds: age-specific patterns of condition, reproduction and survival in the wandering albatross. Oikos 64: 464-473.

Zicus, M.C., E.D. Michael, and J.I. Cromer. 1983. Population dynamics and harvest of Canada geese in West Virginia. Northeast Wildl. 50: 111-117.

Annexe A

Matrices de récupération des bagues de la Grande Oie des neiges

- baguage dans l'Arctique de 1970 à 1974
- baguage à l'île Bylot (T.N.O.) de 1990 à 1996
- baguage à l'île Bylot (T.N.O.) et au Cap Tourmente (Québec) de 1993 à 1995

Modélisation des récupérations attendues de bagues avec 2 périodes de baguage, avant (Ile Bylot) et après la migration (Cap Tourmente)

Table 1. Banding and recovery matrix of adult greater snow geese banded in the Arctic from 1970 to 1974.

South of the 74°N of latitude

		Recoveries																				
Year	No. banded	70	71	72	73	74	75	76	77	78	79	80	81	82	83	84	85	86	87	88	89	Total
70	981	23	9	5	8	2	20	11	12	8	8	9	7	4	1	1	0	0	0	1	0	**129**
71	462		13	4	4	5	7	7	8	4	2	2	2	1	2	1	1	0	1	0	1	**65**
73	320				3	3	9	6	3	6	1	6	4	1	1	1	0	2	0	0	0	**46**
74	484					3	18	11	8	14	4	6	1	4	2	5	3	1	1	0	0	**81**
Total	**2247**	**23**	**22**	**9**	**15**	**13**	**54**	**35**	**31**	**32**	**15**	**23**	**14**	**10**	**6**	**8**	**4**	**3**	**2**	**1**	**1**	**321**

North of the 74°N of latitude

		Recoveries																			
Year	No. banded	71	72	73	74	75	76	77	78	79	80	81	82	83	84	85	86	87	88	89	Total
71	1329	26	29	10	5	20	20	9	11	9	10	5	3	0	2	3	3	1	0	0	**166**
72	254		4	1	0	5	0	1	4	2	1	2	0	0	1	0	0	1	0	0	**22**
73	795			4	8	17	13	9	14	7	9	6	1	0	6	2	1	0	1	0	**98**
Total	**2378**	**26**	**33**	**15**	**13**	**42**	**33**	**19**	**29**	**18**	**20**	**13**	**4**	**0**	**9**	**5**	**4**	**2**	**1**	**0**	**286**

Total

		Recoveries																				
Year	No. banded	70	71	72	73	74	75	76	77	78	79	80	81	82	83	84	85	86	87	88	89	Total
70	981	23	9	5	8	2	20	11	12	8	8	9	7	4	1	1	0	0	0	1	0	**129**
71	1791	0	39	33	14	10	27	27	17	15	11	12	7	4	2	3	4	3	2	0	1	**231**
73	574	0	0	4	4	3	14	6	4	10	3	7	6	1	1	2	0	2	1	0	0	**68**
74	1279	0	0	0	4	11	35	24	17	28	11	15	7	5	2	11	5	2	1	1	0	**179**
Total	**4625**	**23**	**48**	**42**	**30**	**26**	**96**	**68**	**50**	**61**	**33**	**43**	**27**	**14**	**6**	**17**	**9**	**7**	**4**	**2**	**1**	**607**

Table 2. Banding and recovery matrix of greater snow geese banded on Bylot Island (N W.T) from 1990 to1996.

Age Sex	Collar	Year	No. banded	Recoveries							
				1990	1991	1992	1993	1994	1995	1996	Total
Adult Female	No	1990	65	2	1	2	4	1	0	2	**12**
		1991	126		2	3	3	0	2	2	**12**
		1992	249			10	1	4	3	2	**20**
		1993	103				6	1	0	2	**9**
		1994	395					6	5	4	**15**
		1995	169						5	3	**8**
		1996	176							4	**4**
		Total	**1257**	**2**	**3**	**15**	**14**	**12**	**15**	**19**	**76**
Adult Female	Yes	1990	108	12	7	4	1	0	1	2	**29**
		1991	262		13	12	5	2	4	1	**37**
		1992	303			27	6	1	0	1	**35**
		1993	525				19	10	13	9	**51**
		1994	527					22	8	4	**34**
		1995	686						33	8	**41**
		1996	761							24	**24**
		Total	**3192**	**14**	**20**	**43**	**31**	**35**	**53**	**16**	**251**
Adult Male	No	1990	165	11	1	2	0	1	0	0	**15**
		1991	360		10	4	6	5	1	3	**29**
		1992	550			10	16	2	4	7	**39**
		1993	613				17	5	11	5	**38**
		1994	923					12	17	14	**43**
		1995	834						26	9	**35**
		1996	956							22	**22**
		Total	**4401**	**11**	**11**	**16**	**39**	**25**	**59**	**60**	**221**
Young Female	No	1990	191	11	3	4	1	1	0	0	**20**
		1991	550		40	5	4	1	1	0	**51**
		1992	416			34	4	0	0	3	**41**
		1993	929				81	17	2	3	**103**
		1994	911					27	5	0	**32**
		1995	1126						72	12	**84**
		1996	898							32	**32**
		Total	**5021**	**11**	**43**	**43**	**90**	**46**	**80**	**50**	**363**
Young Male	No	1990	199	15	1	1	3	0	0	1	**21**
		1991	591		49	12	5	5	6	6	**83**
		1992	478			43	6	1	2	0	**52**
		1993	989				86	8	5	2	**101**
		1994	962					18	2	1	**21**
		1995	1161						68	8	**76**
		1996	928							45	**45**
		Total	**5308**	**15**	**50**	**56**	**100**	**32**	**83**	**63**	**399**
Adults + young		Total	**19179**	**53**	**127**	**172**	**271**	**150**	**296**	**241**	**1310**

Table 3. Recoveries of greater snow geese banded on Bylot Island (BI) in late summer and Cap Tourmente (CT) in fall from 1993 to 1995.

					Recovery year		
Age	Sex	Banding year	Site	No.banded	1993	1994	1995
Adult	Female[a]	1993	BI	103	3	0	0
			CT	132	5	0	1
		1994	BI	395		3	5
			CT	434		12	7
		1995	BI	169			3
			CT	358			7
Adult	Male	1993	BI	613	15	5	8
			CT	164	2	1	4
		1994	BI	923		9	13
			CT	337		13	5
		1995	BI	834			21
			CT	352			8
Young	Female	1993	BI	929	74	11	2
			CT	121	12	2	0
		1994	BI	911		17	5
			CT	83		8	1
		1995	BI	1126			61
			CT	134			11
Young	Male	1993	BI	989	71	6	3
			CT	128	16	2	0
		1994	BI	962		10	1
			CT	87		6	0
		1995	BI	1161			58
			CT	148			8

a: Only adult females without neck bands.

N.B.: Recoveries occurring north or before the banding period of Cap Tourmente are excluded.

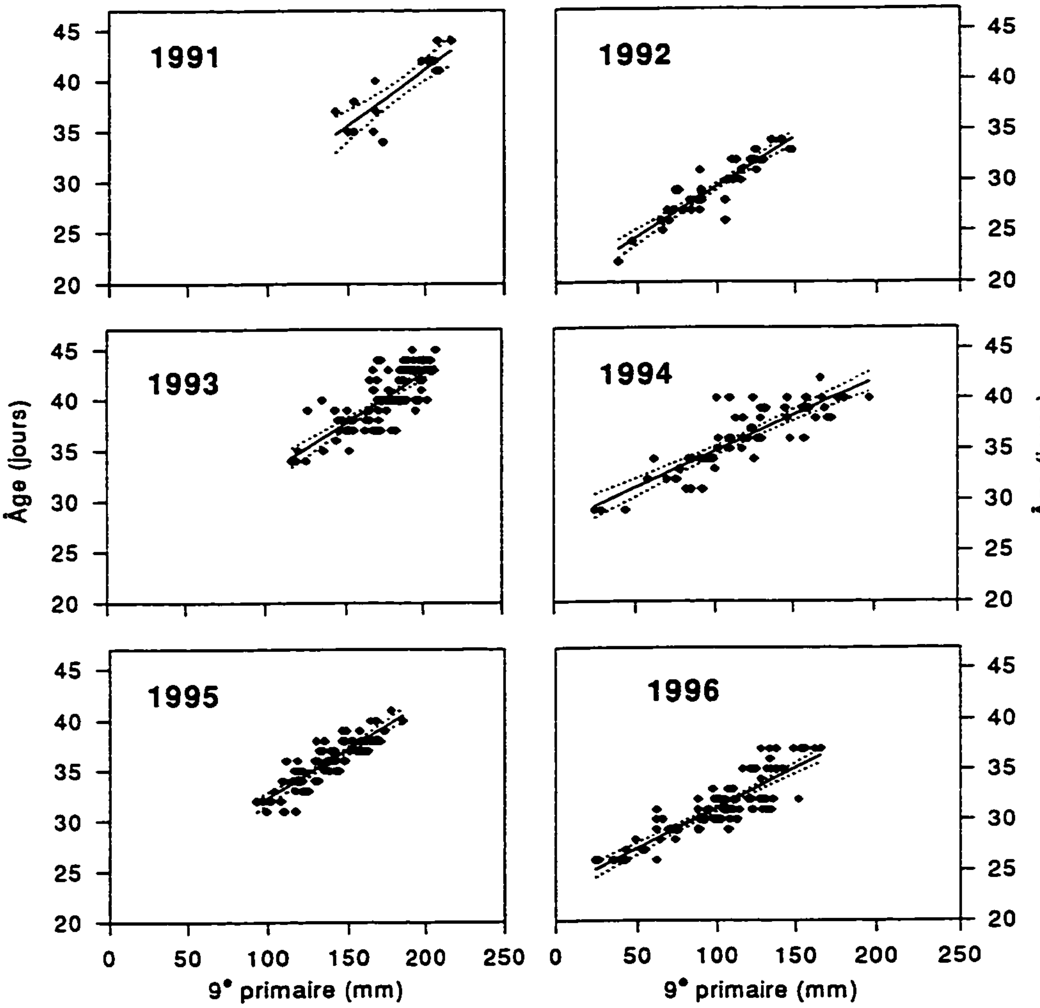
Table 4. Expected number of band recoveries with 2 periods of banding, before the migration (Bylot Island) and after the migration (Cap Tourmente). The model includes time-specific recovery rates (f_i), fall migration survival rates (S_i*), and annual survival rates (S_i). For the sake of simplicity, sexes were pooled.

				Recovery year		
Age	Year	Banding period	No. banded	1993	1994	1995
Adults	1993	Before	M_1	M_1f_1	$M_1S_1f_2$	$M_1S_1S_2f_3$
		After	N_1	N_1f_1	$N_1S_1f_2$	$N_1S_1S_2f_3$
	1994	Before	M_2		M_1f_2	$M_1S_2f_3$
		After	N_2		N_1f_2	$N_1S_2f_3$
	1995	Before	M_3			M_1f_3
		After	N_3			N_1f_3
Young	1993	Before	M'_1	$M'_1S_1^*f_1'$	$M'_1S_1^*S_1'f_2$	$M'_1S_1^*S_1'S_2f_3$
		After	N'_1	N'_1f_1'	$N'_1S_1'f_2$	$N'_1S_1'S_2f_3$
	1994	Before	M'_2		$M'_1S_2^*f_2'$	$M'_1S_2^*S_2'f_3$
		After	N'_2		N'_1f_2'	$N'_1S_2'f_3$
	1995	Before	M'_3			$M'_1S_3^*f_3'$
		After	N'_3			N'_1f_3'

Annexe B

Estimation de l'âge par la 9^e rémige primaire

Cette figure illustre la relation, basée sur les individus marqués à l'éclosion et capturés à la fin de l'été (donc d'âge connu), entre l'âge des jeunes et la longueur de leur 9^e primaire. Ces relations ont été utilisées dans les chapitres 5 et 6 pour estimer l'âge des jeunes non marqués à l'éclosion et capturés durant le baguage à la fin de l'été. Les traits pleins représentent le modèle linéaire de régression et les traits pointillés l'intervalle de confiance à 95% de la régression.



Annexe C

Modèle de régression logistique

Un biais potentiel dans la régression logistique utilisée au chapitre 6 est la possibilité d'une non-indépendance entre oisons d'une même famille face aux risques de mortalité dues à la chasse. Les variations de la probabilité d'être tué à la chasse pourraient être plus grande entre les familles qu'à l'intérieur des familles. Par exemple, si une famille d'oies passe à portée de chasseurs, tous les jeunes de la famille sont plus susceptibles d'avoir un risque accru de mortalité. Pour contrôler ce biais potentiel, nous avons examiné les données de récupération pour des "frères et soeurs apparents", c'est à dire des oisons tués le même jour au même endroit et qui avaient été bagués lors de la même capture et avec une différence d'âge inférieure à 2 jours. Nous avons trouvé 40 cas répondant à ces critères, affectant 94 jeunes (sur 760 récupérés). Un jeune choisi au hasard parmi les "frères et soeurs apparents" était utilisé dans une nouvelle analyse de régression logistique utilisant le modèle sélectionné lors de l'analyse avec l'ensemble des données. Avec cette nouvelle analyse, toutes les variables et interactions présentes dans l'analyse originale sont restées significatives et les changements des coefficients étaient mineurs (Tableau 1).

Tableau 1. Modèle de régression logistique et estimés des paramètres pour la probabilité de récupération de bagues pour les jeunes de la Grande Oie des neiges bagués pendant l'été à l'île Bylot, éliminant les "frères et soeurs apparents" (voir chapitre 6).

Paramètre	Coefficient	SE	χ^2	df	*P*
Constante	17.18	2.3	57.17	1	0.0001
Date d'éclosion relative (*dér*)	1.32	0.79	2.77	1	0.0960
Masse résiduelle (*massr*)	-0.03	0.01	4.19	1	0.0407
Année de baguage	-0.21	0.02	75.77	1	0.0001
*dér*dém*	-7.48e-3	4.17e-3	3.22	1	0.0727
*massr*dém*	2.39e-4	1.02e-4	5.64	1	0.0195
*massr*dér*	1.6e-4	0.78e-4	4.38	1	0.0364

dém: date d'éclosion médiane.

Annexe D

Estimation des probabilités de survie saisonnière avec les réobservations de colliers

OBJECTIF

Afin d'estimer la taille de la population automnale de la Grande Oie des neiges (*Chen caerulescens atlantica*) à partir des décomptes réalisés lors des inventaires printaniers, nous voulions déterminer une probabilité saisonnière de survie du printemps à l'automne.

METHODES

Baguage et observations des oies porteuses de colliers

De 1990 à 1996, des familles d'oies ont été capturées durant l'été à l'île Bylot (T.N.O., Canada). Un collier de plastique jaune à code alphanumérique unique était posé sur la plupart des femelles adultes (voir détails au chapitre 3).

Les réobservations étaient réalisées tout au long de l'année à plusieurs endroits, de l'automne 1990 à l'automne 1997. Aux printemps et automnes, les réobservations avaient lieu le long du fleuve St-Laurent (Québec, 47°N 72°W), qui constitue les haltes migratoires printanière et automnale de la Grande Oie des neiges. Afin d'estimer les probabilités de survie saisonnières du printemps à l'automne et de l'automne au printemps, nous avons utilisé la première réobservation d'un collier au cours de l'automne ou du printemps suivant l'été du marquage comme étant le marquage initial. Ainsi étaient constitués deux groupes d'oiseaux "marqués". D'une part, les individus dont la première observation a eut lieu l'automne immédiatement après le marquage estival forment le groupe des oiseaux "marqués" à l'automne. D'autre part, les oiseaux qui n'ont pas été observés lors de l'automne suivant leur marquage estival, mais le printemps suivant, forment le groupe des oiseaux "marqués" au printemps. Les deux périodes discrètes d'observation annuelles, le printemps et l'automne, permettent donc l'estimation des probabilités de survie saisonnière. Sur la base de la date médiane d'observation par période, les périodes de survie se découpent comme suit: hiver (de l'automne au printemps) = 16 Octobre - 5 Mai, été (du printemps à l'automne) = 6 Mai - 15 Octobre. Comme les deux périodes sont de durée inégale, nous avons calculé des estimés de survie mensuelle afin de rendre les estimés comparables entre eux.

Analyses des données

Les probabilités de survie des femelles adultes ont été estimées avec les réobservations de colliers, en utilisant les modèles de capture-recapture de Cormack-Jolly-Seber (Cormack 1964, Jolly 1965, Seber 1965) et les logiciels RELEASE (Burnham et al., 1987) et SURGE (Lebreton et al., 1992). Le modèle le plus général testé incluait l'effet de la saison (s) et de l'année (a) sur, à la fois, les probabilités de survie (ϕ) et de réobservation (p) et l'effet du groupe ("marqués" au printemps ou à l'automne) sur les probabilités de réobservation. Afin de faciliter la notation des différents modèles, p^f a été utilisé pour les probabilités de réobservation des oiseaux "marqués" à l'automne et p^p pour celles des oiseaux "marqués" au printemps. Cette notation présentait l'avantage de couvrir des modèles avec des structures différentes de probabilités de réobservation entre les 2 groupes. La concordance des données (GOF) au modèle CJS a été testée avec RELEASE, qui teste l'hétérogénéité permanente et temporaire des réobservations pour chaque cohorte. RELEASE a été appliqué pour les deux groupes séparément et aussi pour les données groupées. Un ensemble hiérarchique de modèles contraignant certains paramètres a été déterminé par la méthode de maximum de vraisemblance, avec le logiciel SURGE. Pour déterminer la liste la plus réduite des paramètres nécessaire à la modélisation des données, la valeur significative des différents effets a été testée avec des tests de rapport de vraisemblance (likelihood ratio tests, LRT) et le modèle préféré a été sélectionné avec le Critère d'Information d'Akaike (Akaike's information criterion, AIC; Lebreton et al. 1992, Burnham et al. 1995).

RESULTATS

Tests préliminaires

Les résultats des tests de GOF (obtenus avec RELEASE) n'indiquaient pas de présence d'hétérogénéité, que ce soit pour chacun des groupes ou les données groupées (Tableau 1). Cependant, un examen attentif des tableaux de contingence 3.Sm pour les données groupées a révélée une tendance, non significative au total, dans le patron de réobservations selon la période de "marquage". Les oiseaux "marqués" au printemps étaient plus réobservés lors des printemps suivants par rapport aux nombres attendus, et moins réobservés pendant les automnes suivants. Il n'y avait pas de tendance claire pour les oiseaux "marqués" à l'automne. Ces résultats suggèrent la nécessité de partir d'un modèle général prenant en compte les possibles différences pour les probabilités de réobservation des deux groupes.

Sélection des modèles

Nous avons commencé par réduire autant que possible le nombre de paramètres associés aux probabilités de réobservation, afin de garder le maximum de puissance statistique pour les tests impliquant les probabilités de survie (Tableau 2). L'effet du groupe pour les probabilités de réobservation lors des occasions de printemps n'était pas significatif (df = 4, $P = 0.9$). En revanche, il était très significatif pour les probabilités de réobservation lors des occasions d'automne (df = 6, $P < 0.0001$), indiquant qu'en moyenne, les oiseaux "marqués" au printemps avaient une probabilité d'être observés durant l'automne inférieure aux oiseaux observés pour la première fois durant l'automne (Fig. 1). Une tendance à l'augmentation des probabilités de réobservation suivie d'une stagnation se dégage, ce qui reflète, à la fois, les variations de pression d'observation et les changements récents du comportement migratoire des oies.

Ni l'effet de l'année (df = 8, $P = 0.15$), ni celui de la saison (df = 1, $P = 0.19$) sur la probabilité de survie n'étaient significatifs. Ainsi, le meilleur modèle réduit était $(\phi p^{sp}{}_{f*y}\, p^{f}{}_{f*y}\, p_{sp*y})$.

Tableau 1. Tests de concordance des données du modèle de Cormack-Jolly-Seber Pour les données de réobservations des grandes oies des neiges marquées avec un collier (programme RELEASE).

Groupe de l'automne

	$\chi 2$	df	*P*
Test 3.SR	3.89	4	0.42
Test 3.Sm	14.55	13	0.34
Test 3.S (SR + Sm)	18.44	17	0.36
Test 2.Ct	8.28	8	0.41
Test 2.Cm	18.53	13	0.14
Test 2.C (Ct + Cm)	26.81	21	0.14
Test 2 + 3	45.25	38	0.19

Groupe du printemps

	$\chi 2$	df	*P*
Test 3.SR	6.91	3	0.07
Test 3.Sm	5.39	4	0.25
Test 3.S (SR + Sm)	12.30	7	0.09
Test 2.Ct	5.89	6	0.43
Test 2.Cm	0.86	8	0.99
Test 2.C (Ct + Cm)	6.75	14	0.94
Test 2 + 3	19.05	21	0.58

Groupes de l'automne et du printemps

	$\chi 2$	df	*P*
Test 3.SR	7.06	9	0.63
Test 3.Sm	38.99	27	0.06
Test 3.S (SR + Sm)	46.05	36	0.12
Test 2.Ct	9.35	8	0.31
Test 2.Cm	27.29	21	0.16
Test 2.C (Ct + Cm)	36.64	29	0.15
Test 2 + 3	82.70	65	0.07

Tableau 2. Modélisation avec SURGE des taux de survie et de réobservation des grandes oies des neiges marquées avec un collier. Pour chaque modèle est donné le nombre de paramètres identifiables (*np*), la déviance (DEV), et le Akaike Information Criterion (AIC). L'AIC en gras correspond au modèle sélectionné.

Modèle	*np*	DEV	AIC	Tests entre modèles
(1) $(\phi_{s*y} p^{sp}_{s*y} p^{f}_{s*y})$	29	6755	6813.4	
(2) $(\phi_{s*y} p^{sp}_{f*y} p^{f}_{f*y} p_{sp*y})$	25	6756	6806.2	Effet du groupe sur le taux de réobservation du printemps (2) vs. (1): $\chi^2_4 = 0.77, P = 0.94$
(3) $(\phi_{s*y} p_{s*y})$	19	6793	6831.1	Effet du groupe sur le taux de réobservation de l'automne (3) vs. (2): $\chi^2_6 = 36.9, P = 0.00$
(4) $(\phi_{s} p^{sp}_{f*y} p^{f}_{f*y} p_{sp*y})$	17	6768	6802.3	Effet de l'année sur le taux de survie (4) vs. (2): $\chi^2_8 = 12.06, P = 0.15$
(5) $(\phi p^{sp}_{f*y} p^{f}_{f*y} p_{sp*y})$	16	6770	**6802.0**	Effet de la saison sur le taux de survie (5) vs. (4): $\chi^2_1 = 1.71, P = 0.19$

p^{sp} = probabilité de réobservation pour le groupe "marqué" au printemps.
p^{f} = probabilité de réobservation pour le groupe "marqué" l'automne.
s = saison.
y = année.

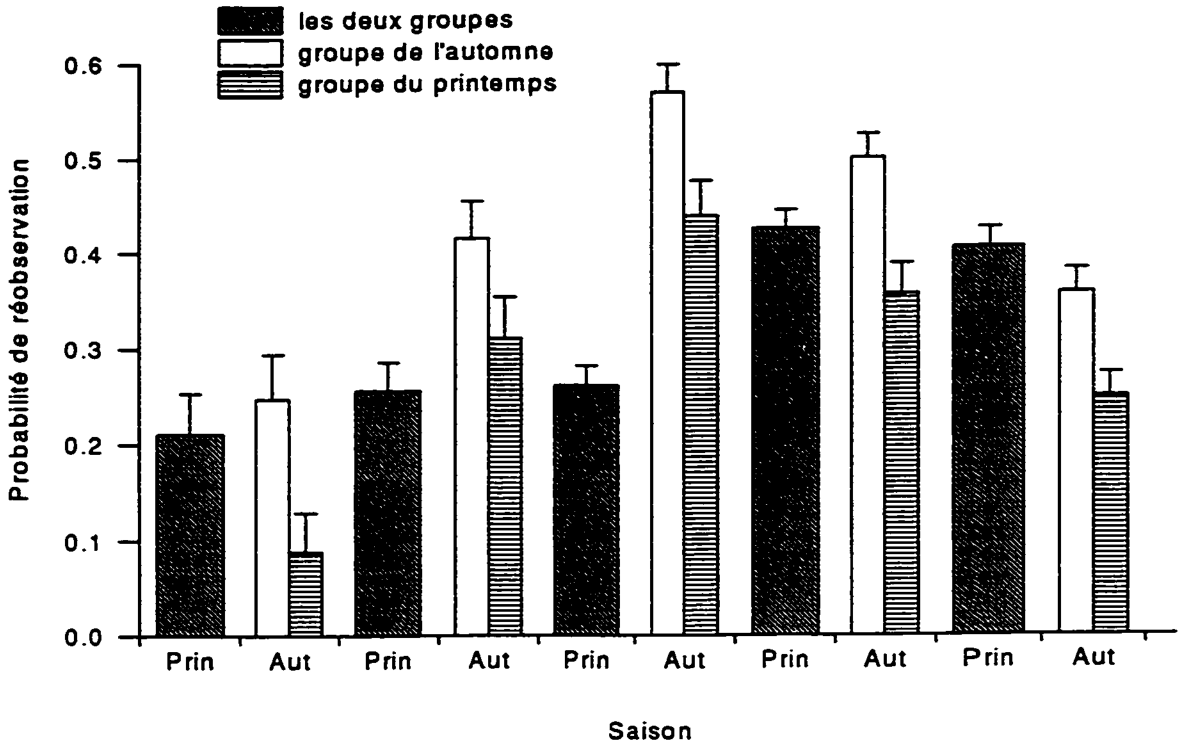


Fig. 1. Probabilités de réobservations saisonnières (moyenne ± SE) d'oies des neiges avec collier en fonction du groupe (oiseaux "marqués" au printemps ou à l'automne), du printemps 1993 à l'automne 1997, sous le modèle $(\phi\, p^{sp}{}_{f*y}\, p^{f}{}_{f*y}\, p_{sp*y})$. La probabilité de réobservation au printemps est identiques pour les deux groupes.
Prin: printemps; Aut: automne.

Selon le modèle sélectionné, la survie saisonnière était estimée à 0.85 (SE = 0.08). La survie mensuelle pour la période de l'automne au printemps (7 mois) était légèrement supérieure (0.976 (0.024)) à celle pour la période printemps-automne (0.967 (0.021)). La probabilité composite de survie annuelle (produit des probabilités saisonnières, corrigée pour un taux de rétention de collier de 0.97 (0.01); voir chapitre 3) était de 0.74 (0.02).

DISCUSSION

Estimés saisonniers de la probabilité de survie

Les probabilités saisonnières de survie ne différaient pas significativement entre elles et ne présentaient pas de variations annuelles. Sur une base mensuelle, une probabilité de survie pendant l'hiver (de l'automne au printemps) supérieure à celle de l'été (du printemps à l'automne), est quelque peu surprenante, bien que la différence soit faible (voir chapitre 2 pour une discussion plus approfondie).

La probabilité composite de survie annuelle est relativement basse, comparée aux estimés obtenus pour la même population marquée, avec d'autres méthodes ou d'autres ensembles de données (chapitre 2, 3 et 4). Il est possible que d'autres sources d'hétérogénéité non identifiées existent pour les deux groupes considérés, ce qui pourrait biaiser les estimés. De plus, une chasse importante est effectuée durant l'automne, en même temps que les réobservations. Ainsi, la prémisse de non-mortalité (ou mortalité négligeable) durant l'échantillonnage n'est pas respectée (cette prémisse découle de la condition d'échantillonnage instantané). Cependant, cela ne devrait pas entraîner des biais systématiques et importants dans l'estimation de la probabilité de survie (Lebreton et al 1992, Sarrazin et al 1994).

Probabilités de réobservations

Les probabilités de réobservations allaient de moyennes à élevées, ce qui assurait une bonne précision des estimés de survie. Elles étaient cependant variables selon les saisons et les années, principalement en raison de pressions d'observations variables. Toutefois, une modification récente de la phénologie migratoire à l'automne (passage précoce et rapide dans les aires "traditionnelles") pourrait expliquer le déclin relatif des probabilités d'observation des deux derniers automnes, alors que l'effort était relativement similaire aux automnes précédents (principalement 1994 et 1995).

Hétérogénéité des réobservations

L'utilisation de la première réobservation l'automne ou le printemps suivant immédiatement le marquage de l'été comme période théorique de marquage a permis l'identification de deux groupes d'individus aux probabilités d'observation différentes. L'existence de ces deux groupes n'avait pu être décelé lors de l'utilisation de l'ensemble des périodes d'observation (chapitre 2). De plus, le faible effort d'observation au printemps au début de la période d'étude et l'augmentation importante de cet effort simultanément pour les deux périodes considérées ont pu masquer la mise en évidence de cette hétérogénéité, comme l'indique le test RELEASE (et notamment la partie 3.Sm) non significatif pour les données groupées. Seuls un examen détaillé du test et une bonne connaissance des conditions d'observation sur le terrain ont permis de déceler cette particularité. En définitive, nous avons conclu que les oiseaux qui ne sont pas observés lors du premier automne suivant leur marquage ont une probabilité plus faible d'être observés les automnes suivants par rapport aux oiseaux qui ont été observés lors du premier automne suivant leur marquage. Cela suggère qu'en moyenne, ce groupe est composé d'individus dont la durée de séjour dans les aires échantillonnées à l'automne est plus courte. Ces oiseaux ont une tendance constante à passer plus rapidement dans le haut-estuaire du St-Laurent, où sont effectuées la majeure partie des observations de l'automne.

L'absence de différence entre les deux groupes pour les probabilités de réobservation au printemps suggère une utilisation similaire des haltes migratoires printanières. Les départs des aires d'hivernage se font graduellement au printemps, le nombre d'oies présentes dans le secteur fleuve St-Laurent - Sud-Ouest du Québec (considéré comme les haltes migratoires printanières) augmentant progressivement. À partir de la fin avril, l'ensemble de la population de la Grande Oie des neiges se retrouve confiné à l'espace géographique discret que représente les haltes migratoires printanières (Gauvin et Reed, 1987). Leur séjour dans cet espace "restreint" se prolonge habituellement jusque la fin mai, où se produisent alors les départs massifs et simultanés vers les aires de nidifications arctiques (Gauthier et al, 1992, Joël Bêty, données de télémétrie non publiées). Ainsi, tous les individus marqués (et vivants) devraient se retrouver au printemps sur une superficie bien définie et pendant un laps de temps relativement long et ne devraient donc pas présenter de différence pour leurs probabilités de réobservation, quel que soit leur comportement automnal.

Annexe E

Carte des sites

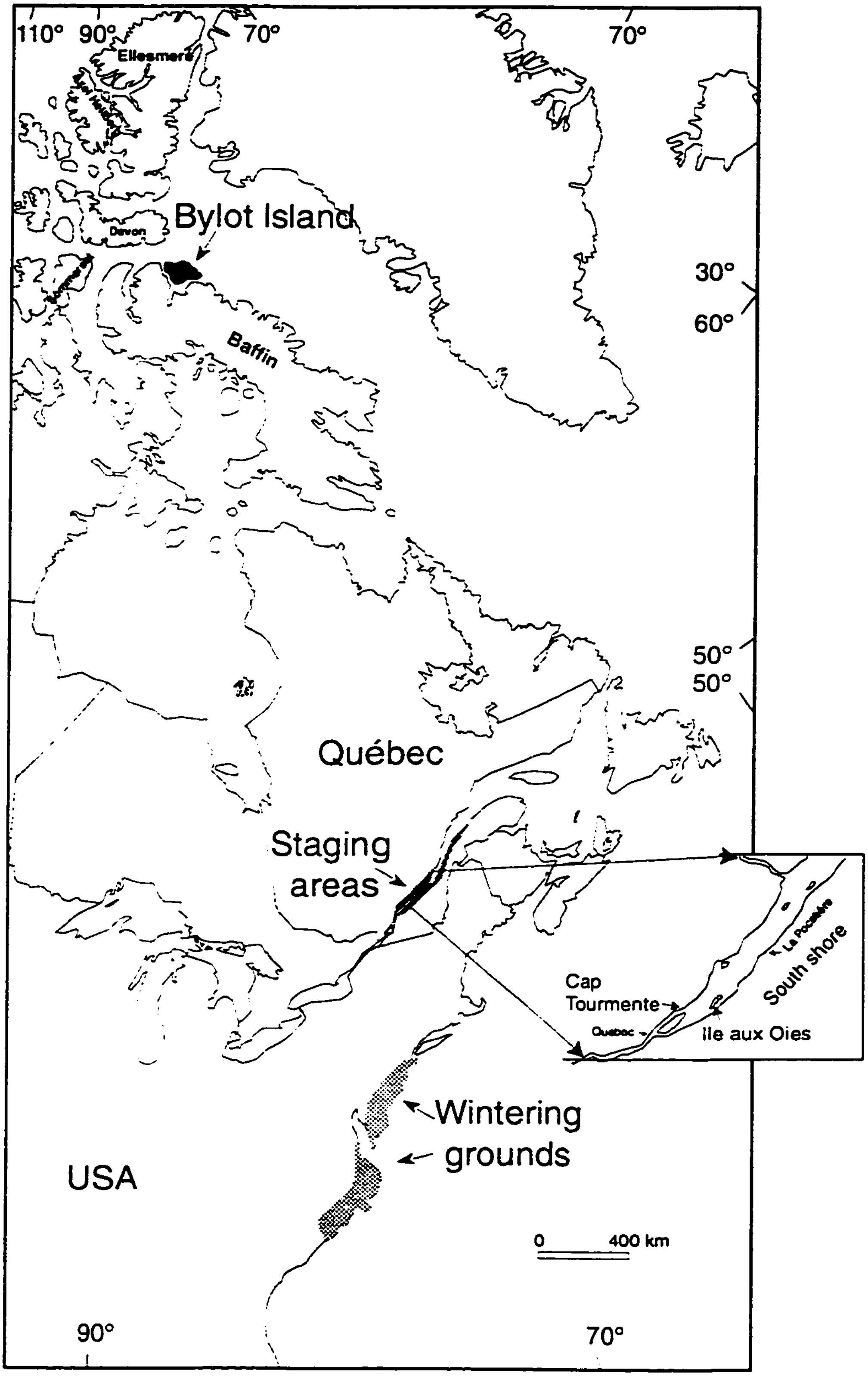
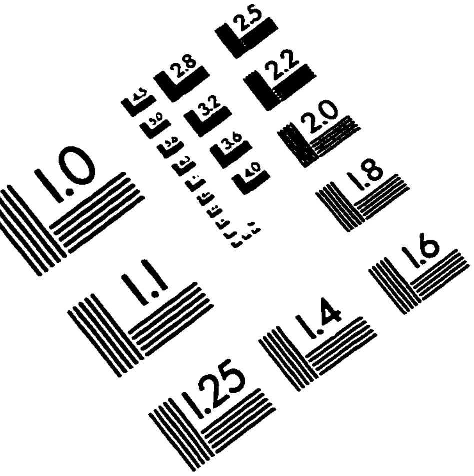
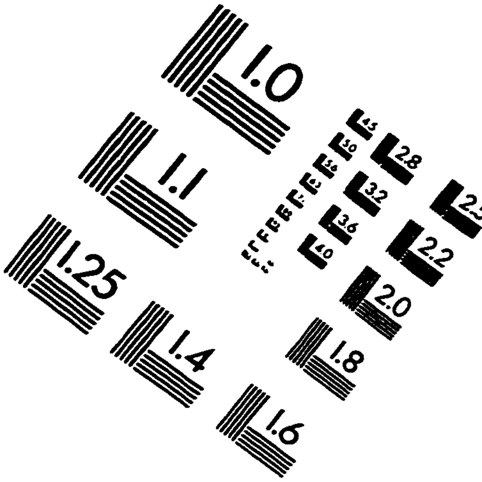
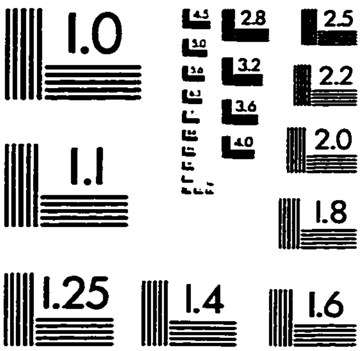
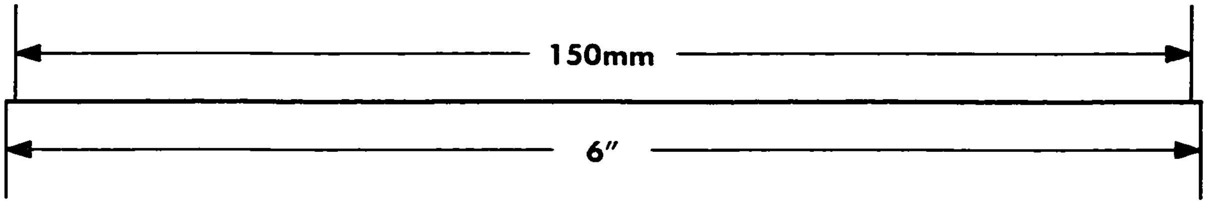


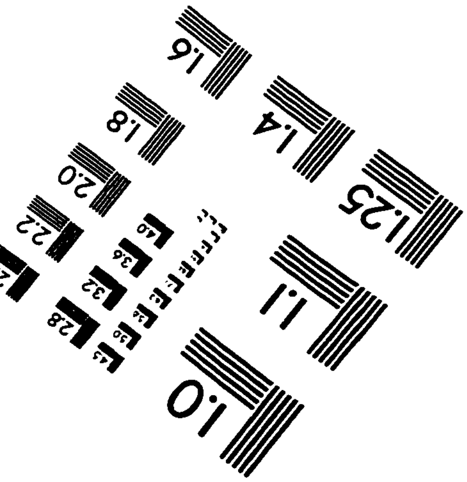
IMAGE EVALUATION TEST TARGET (QA-3)

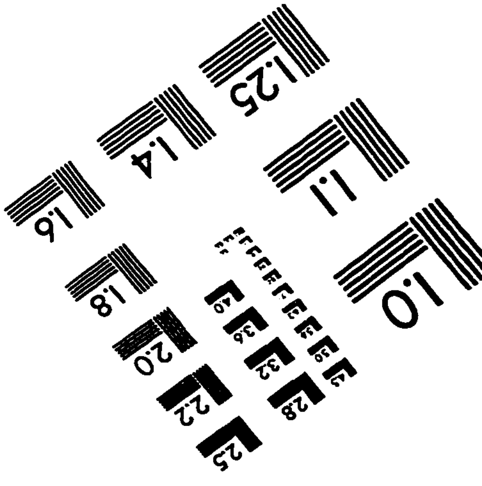












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